The Effects of Age and Sex on the Energy Intake of Captive Sea Otters (*Enhydra lutris*): Implications for Captive Management and Species Conservation

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Abstract

Sea otters (*Enhydra lutris*) are known ecosystem engineers that have significant impacts on their kelp forest and rocky intertidal communities due to their high levels of food intake. Quantifying sea otter food biomass and energy intake is a valuable way to understand potential ecological impacts of sea otter populations on ecosystems and for predicting future population trends and potential for expansion. While detailed, fine-scale, age-specific food intake is difficult to quantify in wild sea otters, there is a wealth of potential information available from otters under human care. This study used food and energy intake data from husbandry records of 10 sea otters collected over three decades at the Vancouver Aquarium. Within these husbandry records, daily food biomass intake and body mass measurements were recorded and converted to annual average food mass and gross energy intake (GEI). Age-, sex-, and mass-specific trends were also observed. Young sea otters had the highest relative ingested food mass, equivalent to ~26% of body mass, which decreased to ~20% in adult otters. Young otters similarly had the highest mass-specific GEI, where measures from near birth to year 1 were ~40% higher than at year 3, the age of sexual and physical maturity. There were also key differences in trends between sexes. Captive adult male sea otters were 25 to 42% larger than females and their GEI was 23 to 58% higher, although mass-specific GEI was almost identical for male and non-reproductive female otters at all ages, plateauing at ~650 kJ kg^{-1} d^{-1}. Despite high levels of ingested food mass, GEI was only 5 to 15% higher than for other captive marine mammals and was comparable to previous estimates for wild sea otters. These estimates of ingested food mass and energy intake requirements are valuable when modelling the ecological impact of sea otter populations and for considering the potential effects of future environmental changes.

Key Words: sea otters, *Enhydra lutris*, food intake, energetics, nutrition, growth, body mass

Introduction

Sea otters (*Enhydra lutris*) are a keystone species of rocky, coastal nearshore ecosystems along the Pacific coast of North America. As such, the amount and varieties of prey they obtain during their foraging activities have important impacts on local biodiversity. This includes protecting kelp forests from the grazing pressure of sea urchins (*Echinoidea* spp.; Estes & Palmisano, 1974; Kvitek et al., 1998), which helps enhance kelp forest biodiversity, provides essential habitat for many commercially important marine fauna species, and imparts significant positive effects on nearby coastal communities and capture fisheries (Simenstad et al., 1978; Duggins, 1980; Estes et al., 2004; Gregr et al., 2020). Age- and sex-specific estimates of food intake—both on a prey biomass and energetic basis—can be used to estimate the collective impact of sea otter populations on their immediate ecosystem and are also instrumental in modeling their ecological requirements in terms of population stability and potential range expansion (e.g., Tinker et al., 2019). While many studies have identified the type of prey consumed by wild sea otters, fewer have focused on quantifying their rates of prey and energy intake (Tinker et al., 2019; Yee et al., 2020). Despite these efforts, there is still a knowledge gap regarding long-term sea otter food and energy intake and how this varies with age and sex. Such information can give new, valuable, data-based insights into the ecology, life history, and population dynamics of sea otters.

Despite the need for understanding prey biomass and energy intake requirements of different segments of sea otter populations, these studies cannot readily be carried out on wild animals. However, valuable insights can be obtained by

examining the food intake and growth of otters managed in zoos and aquariums. In addition to informing the bioenergetics and ecology of wild sea otters, such data can also improve the husbandry of sea otters under human care. In this study, developmental changes in body mass and food and energy intake from husbandry records of a group of sea otters maintained under human care over three decades were quantified. The results provide estimates of mass-, age-, and sex-specific trends in food mass and gross energy intake that can be applied to both managed and wild otters.

Methods

This study used husbandry records of 10 sea otters (6 males and 4 females; Table 1) living under managed care at the Vancouver Aquarium (Vancouver, BC, Canada) between 1993 and 2022. The otters originated from both Alaskan and Canadian populations (northern subspecies, *Enhydra lutris kenyon*). None of the otters were born at the Vancouver Aquarium but, rather, came to the facility through rehabilitation programs or other aquariums. The otters could not breed due to either anatomical or chemical controls or physical separation.

Standard aquarium protocols entail sea otters being fed individually, allowing for detailed tracking of food intake. Weekly target food amounts were adjusted based upon perceived hunger levels (determined by experienced husbandry staff), which allowed for naturalistic developmental and seasonal variation. Daily (target) food intake was also curtailed if animals lost apparent interest in their food on a given day.

Table 1. Name, sex, and age range of captive sea otters (*Enhydra lutris*) used in the study at the Vancouver Aquarium

Name	Sex	Approx. age range recorded (y)
Nayak	Female	6-20
Tanu	Female	1-17
Katmai	Female	0-10*
Kunik	Female	0-7*
Tuktay	Male	10-17
Elfin	Male	0-16
Milo	Male	1-13
Mak	Male	0-7*
Rialto	Male	0-6*
Hardy	Male	0-5*

*Indicates sea otter was still alive and part of the aquarium collection at end of study

Data were extracted from both digital and handwritten records, including daily food intake of individual prey items (by mass) and semi-regular measures of body mass (animals weighed on a platform scale approximately every week). Other relevant information in the husbandry records (e.g., feeding behavior, intraspecific interactions, husbandry procedures, health issues, etc.) was also noted and used to inform interpretation of the data.

The daily food intake data for different prey items for each sea otter were amalgamated into weekly average intake. Average ingested food mass was converted into gross energy intake (GEI) in kilojoules (kJ) using the energy content extracted from various sources (Table 2). Throughout the study period, the aquarium periodically used various commercial laboratories to determine the proximate composition and energy content of representative prey samples. As the otters were typically fed partially processed commercial products (e.g., fillets, shelled), these data were supplemented by relevant published values (Oftedal et al., 2007; Pigott & Tucker, 2017) and from information available on the U.S. Department of Agriculture (USDA) seafood website (https://fdc.nal.usda.gov/index.html). All food composition and intake data were based on an "as eaten" basis.

Average ingested food mass and GEI for each week was expressed in terms of both absolute average daily intake (kg d^{-1} or kJ d^{-1}, respectively) and mass-specific daily intake (kg kg^{-1} d^{-1} or kJ kg^{-1} d^{-1}) using matched body mass data (average of measures for the same week). When no matching body mass data were available for that specific week, the average mass between the preceding and following weeks was used.

Ingested food mass and GEI of each sea otter was also averaged across developmental ages. Developmental years are expressed starting in year 0 (0 to 12 mo), followed by year 1 (13 to 24 mo), etc. The age of each otter was estimated using the Vancouver Aquarium's records based on their known date of birth or their approximate age when they arrived at the facility. For otters with reasonable estimates of birth date (specific month and year), food intake was averaged across the appropriate 12-mo period for each developmental year. For otters with no known specific birth date, food intake was averaged across corresponding calendar years.

Food intake levels were also expressed by sea otter sex. For this analysis, the average intake for each otter for each developmental year was averaged to provide a mean (± SD) intake for male and females for that age.

Table 2. Energy content (kJ kg⁻¹) of prey items consumed by sea otters residing in the Vancouver Aquarium used in this study to calculate gross energy intake. Energy density values are expressed on an "as eaten" (e.g., shelled, fillets, etc.) basis.

Prey item	Energy content (kJ kg⁻¹)	Source(s)
Surf clam	3,520	Commercial analysis
Butter clam	2,610	Oftedal et al., 2007
Propeller clam	3,030	U.S. Department of Agriculture (USDA)*
Razor clam	3,190	Commercial analysis
Horse clam	3,030	USDA
Bay clam	3,030	USDA
IQF clam	3,030	USDA
Unspecified clam	3,110	Estimated from other types of clams
Mussel	1,800	Oftedal et al., 2007
Oyster	3,290	Pigott & Tucker, 2017
Scallop	3,710	USDA
Geoduck	3,820	USDA
Abalone	4,120	Oftedal et al., 2007; commercial analysis
Sea urchin	1,610	Oftedal et al., 2007
Sea cucumber	470	Oftedal et al., 2007
Squid	3,200	Oftedal et al., 2007; commercial analysis
Prawn	2,850	USDA
Shrimp	2,360	Commercial analysis
Crab	3,320	Oftedal et al., 2007
IQF cod	2,890	USDA
Cod	3,260	Pigott & Tucker, 2017
Pollock	4,260	Commercial analysis
Rockfish	4,320	Commercial analysis
Arrowtooth	4,450	USDA
Capelin	3,430	Commercial analysis
Sole	3,810	USDA
Sand dab	2,090	USDA
Salmon	7,250	Pigott & Tucker, 2017; commercial analysis
Turbot	4,080	USDA
Octopus	4,080	Oftedal et al., 2007

*The U.S. Department of Agriculture's *FoodData Central* (https://fdc.nal.usda.gov/index.html) is a data system that contains nutritional profiles of a variety of raw and processed foodstuffs.

Results

At age 0, the average body mass of female (14.9 ± 1.8 kg) and male (14.5 ± 1.0 kg) sea otter pups was essentially identical (Figure 1). The body mass of female otters largely plateaued by year 2 at 25.5 ± 0.6 kg, with only marginal increases in mass after that age. By year 2, male otters were significantly heavier than females at 30.6 ± 0.6 kg, and their mass slowly but steadily increased in subsequent years, reaching a plateau at ~10 y.

As expected, ingested food mass relative to body mass was highest in younger sea otters. In year 0, male otters consumed the equivalent of 24.5 ± 3.5 kg food per kg body mass per day (i.e., 24.5%), while females consumed 27.0 ± 2.0 kg kg⁻¹ d⁻¹ (27.0%) (Figure 2). By year 3, this had decreased to 18.3 to 19.1% for both sexes, and food mass intake levels subsequently fluctuated between 17.2 and 21.1% for both male and female otters.

These same age- and sex-related trends were observed when ingested food intake was converted
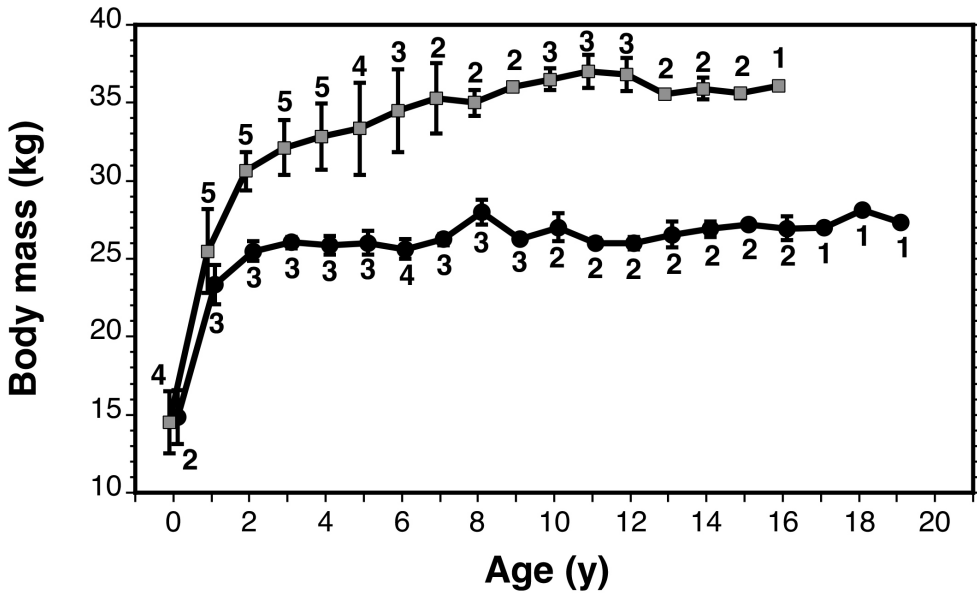
Figure 1. Average (± SD) body mass (kg) during each developmental year for male (grey squares) and female (black circles) sea otters (*Enhydra lutris*). Age refers to the start of the interval (e.g., age 0 = 0 to 12 mo), and data points are offset for clarity. Numbers above/below data points indicate how many individual otters contributed to the mean (and can be applied for all following figures). A single annual average intake value for each otter contributed to the grand mean; points with no error bars designate data from only one otter.
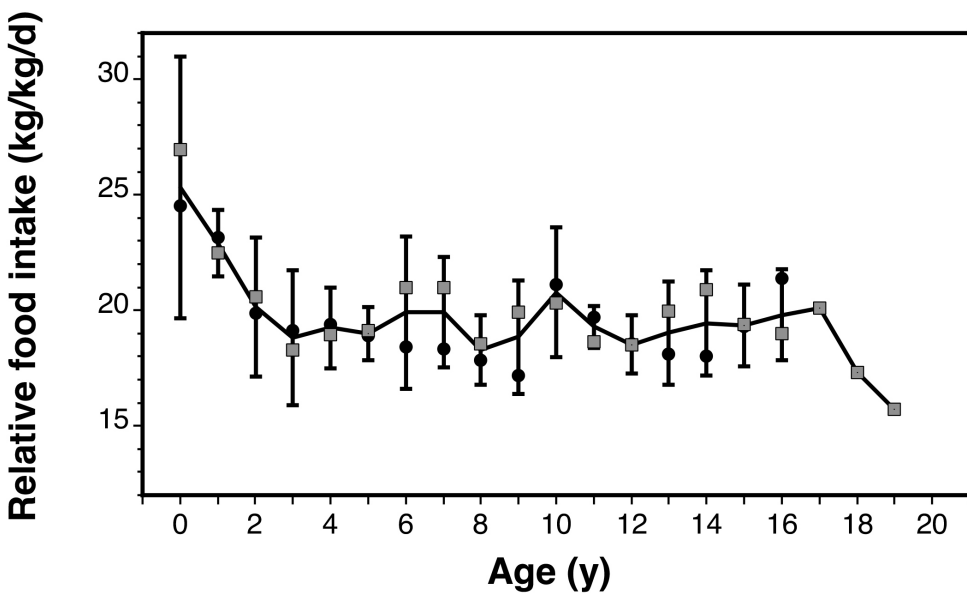

Figure 2. Ingested food mass intake in relation to body mass with sea otter age. The solid line and error bars designate the overall average (± SD; all otters combined) ingested food mass expressed relative to body mass ((kg food per kg body mass per day) during each developmental year. Separate mean values for male (grey squares) and female (black circles) otters are overlaid.
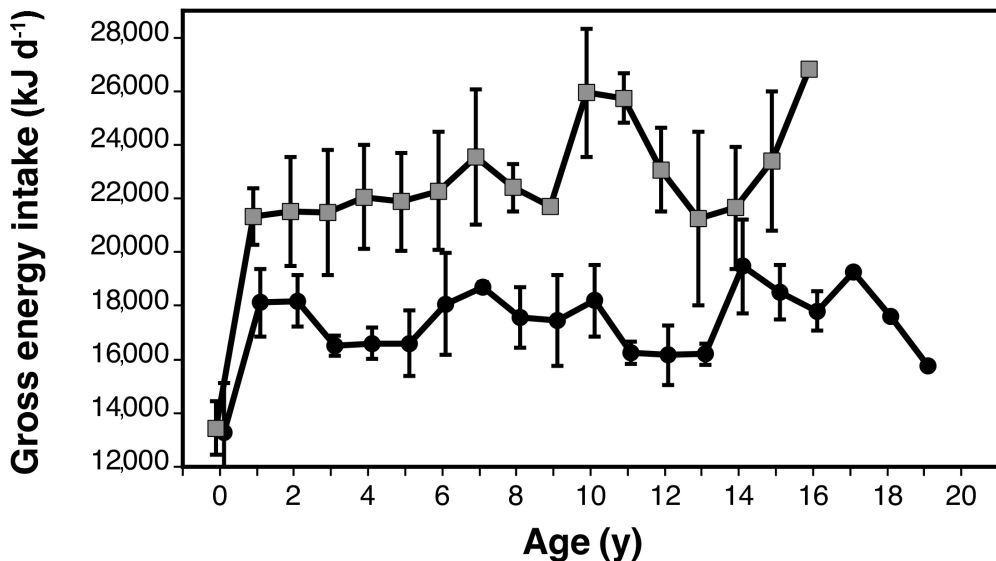
Figure 3. Average (± SD) gross energy intake (GEI) (kJ d^{-1}) during each developmental year for male (grey squares) and female (black circles) otters

to energy intake. GEI was lowest for the year 0 sea otters, with essentially identical mean levels of intake between male (13,440 ± 990 kJ d^{-1}) and female (13,270 ± 1,870 kJ d^{-1}) otters (Figure 3). This level of intake only reflects the latter part of the first developmental year after integration of the animals into the regular aquarium holding facility (from either rehabilitation or other facilities). In the wild, otter pups only become nutritionally independent at ~6 to 8 mo. After the first year, the GEI for our male otters was significantly higher than that for females of the same age. For female otters, the GEI increased in year 1 and then initially peaked in year 2 (18,180 ± 960 kJ d^{-1}), with a distinct decrease to about 16,500 kJ d^{-1} in years 3 to 5; this drop was not attributable to a change in study animals or calendar year. In subsequent years, average GEI for non-reproductive female otters varied between 16,100 and 19,500 kJ d^{-1}. For male otters, there was a dramatic increase in the GEI from year 0 to year 1 (13,440 ± 990 to 21,330 ± 1,050 kJ d^{-1}), with a slower but continual increase as the otters matured. As with females, there was variation in subsequent annual averages ranging from ~21,500 to ~26,000 kJ d^{-1} in older individuals.

When taking differences in body size into account, mass-specific GEI was almost identical for male and female sea otters at all ages (Figure 4). As expected, mass-specific GEI for male and female otters was highest in year 0 (926 ± 25 and

903 ± 40 kJ kg^{-1} d^{-1}, respectively). There was a steep decline over years 1 through 3 when relative intake reached 665 ± 61 and 634 ± 10 kJ kg^{-1} d^{-1}, respectively. Relative intake in subsequent years varied between 598 and 723 kJ kg^{-1} d^{-1}, with no overall difference between male and female otters.

Discussion

Overall, patterns of changes in food biomass and energy intake with age fit the general mammalian model for which absolute intake increases during development and then levels off as animals reach physical maturity. This trend is primarily due to the allometric relationship between body mass and resting metabolic rates—that is, larger bodies have higher absolute energy requirements—tempered by the increased costs associated with early, rapid physical growth. The results of the current study provide specific quantitative estimates of developmental changes in ingested food mass and GEI in sea otters, and examine how they relate to body mass and each other.

In this study, the sea otters' GEI rapidly increased over the first few years of development. There was a plateau in GEI at age 3 in female otters, coinciding with a similar pattern in body mass. While annual increases in GEI for male otters were also smaller after age 3, there was more of a sustained annual increase after this age for male otters than for female otters. This
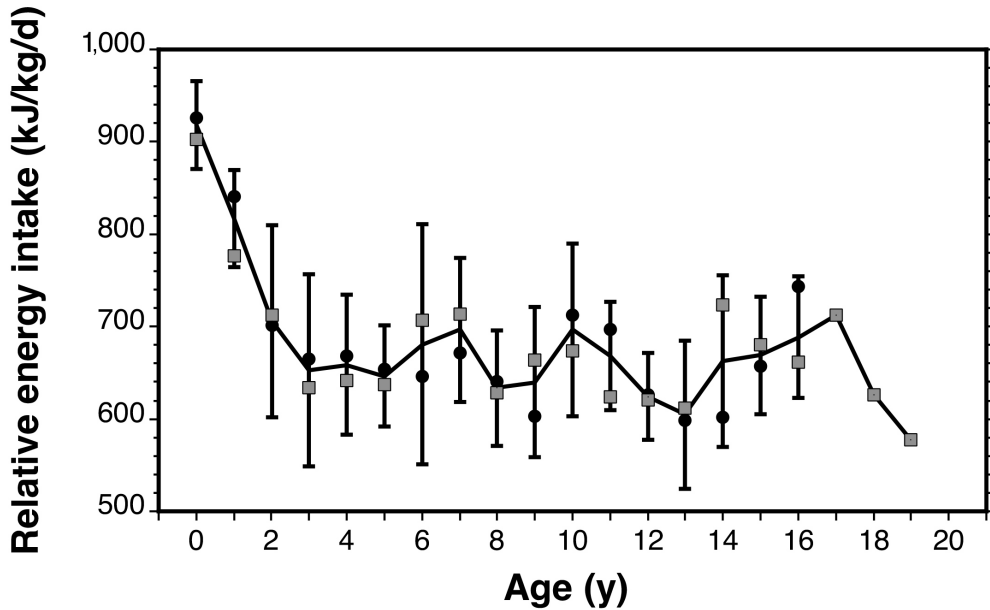
Figure 4. Mass-specific GEI of sea otters with age. The solid line and error bars designate the overall average (± SD; all otters combined) mass-specific GEI (kJ per kg body mass per day) during each developmental year. Separate mean values for male (grey square) and female (black circle) otters are overlaid.

coincided with the longer growth period of male otters over their lifetime compared to females.

The differences in body mass also partly explains the disparities in GEI between mature males and females. After age 3, male sea otters were 25 to 42% larger than females, and the GEI of male otters was 23 to 58% greater than that of females for any given developmental year. These differences in the captive otters mirrored the sexual dimorphism seen among wild individuals. For example, adult male Aleutian sea otters are generally more muscular and heavier than adult females, with adult males weighing around 32.3 kg and females around 24.4 kg on average (Laidre et al., 2006).

However, body mass alone does not explain either sex-related or developmental changes in GEI. Trends in mass-specific energy intake reflect changes in underlying energetic requirements independent of these mass changes. In most mammals, younger animals have a higher intake relative to their body mass. As expected, the youngest sea otters in our study had the highest mass-specific GEI; the relative intake of otters in year 0 was ~40% greater than in year 3. This developmental pattern of decreases in relative energy intake followed by a plateau around the time of physical maturity is consistent with those of other marine mammal species held in aquariums, including

dolphins, killer whales (*Orcinus orca*), and seals (Innes et al., 1987; Perez et al., 1990; Reddy et al., 1994; Williams et al., 2011).

The higher mass-specific intake of young animals is partly attributable to their higher costs of growth. During this initial developmental period, the rapid increase in body size of pups demands a substantial amount of energy, and an inability to meet these energetic needs can negatively impact sea otters' long-term growth and development as they transition into the juvenile age class (McCue, 2010; Hector & Nakagawa, 2012).

It has also been hypothesized that the high food intake requirements of young sea otters are attributable to compromised thermoregulation due to their higher surface area to volume ratio. As a result, pups will have to compensate by increasing internal heat production, thereby elevating their metabolic demand (Costa & Kooyman, 1982). However, this cost is at least partly offset by thermal substitution of the heat increment of feeding towards thermoregulation (Costa & Kooyman, 1984).

Increased activity also likely contributes to greater relative energy intake in sea otter pups. Energy budget studies have quantified the cost of the behavioural observation that older pups and younger juveniles spend more time engaging in energetically costly behaviours than adults do, including playful social interactions and swimming

(Estes et al., 1986; Ralls & Siniff, 1990; Thometz et al., 2014). Young otters are also less adept at obtaining and handling prey such that they may also spend more time foraging and feeding throughout the day, even in an aquarium setting.

Differences in activity patterns among mature sea otters can also result in sex-related differences in energy requirements. Daily activity budgets differ between sexes in wild sea otters, whereby adult males spend more time on activities that require higher levels of energy expenditure. Adult males in the wild spend more of their time than females transiting, self-grooming, and foraging (Finerty et al., 2009; Cortez et al., 2016). These behavioural differences would result in higher levels of mass-specific energy intake in males. However, these differences were not apparent in the mass-specific intake of the adult captive otters, likely as there was no opportunity for greater transiting or foraging activities.

In general, sea otters are known to have high levels of food intake and a disproportionate impact on shaping their local ecosystem (Estes, 2015). Both male and female adult otters in this study consumed the equivalent prey mass of ~20% of their body mass every day. This is certainly much higher than the relative food mass intake levels of 1 to 3% of body mass reported for other marine mammals under human care (e.g., Kastelein et al., 1994, 2000, 2003a, 2003b; Rosen & Worthy, 2018, Figure 29.6), and even higher than the 12% reported for young, growing pinnipeds (Innes et al., 1987). Other marine mammals have been shown to possess a finite physiological capacity to increase food consumption in response to changing prey conditions (e.g., Rosen & Trites, 2004; Rosen et al., 2012). It would be interesting to investigate whether sea otters, with their higher rates of ingested food mass relative to body mass, have the same capacity to increase food intake levels.

Since required ingested food mass is directly related to the energy density of the prey, GEI levels provide a more direct comparison for the energetic requirements of sea otters to those of other marine mammals. Perez et al. (1990) produced an allometric equation predicting GEI based upon data from 115 pinnipeds and other marine mammals in aquariums and zoos. This equation (where GEI = $1{,}556\ M^{0.73}$) predicts that a 26 kg female otter would consume 16,800 kJ d^{-1} and a 32 kg male would consume 19,500 kJ d^{-1}. The otters in our study consumed only slightly more (5 to 15%) than these estimates. This disparity between high levels of ingested food mass and average levels of GEI demonstrates how the differences in food mass intake of otters compared to other marine mammals is largely due to a lower average energy prey density (Tinker et al., 2019).

This raises the question of how the intake of captive sea otters compares to wild sea otters. While previous studies have demonstrated that marine mammals under human care show similar developmental and seasonal patterns in growth, physiology, and food intake as their wild counterparts, the actual levels of energy intake may differ. If nothing else, foraging expenditures are severely decreased in aquariums, although this may conversely allow additional time for other high-energy social activities. Additionally, even though the otters in this study experienced natural environmental water and air temperatures, they were situated within the southern portion of their range. Even among managed marine mammals, environmental temperatures are known to be related to energy intake levels (e.g., Kastelein et al., 2018; Rosen et al., 2021). Wild otters inhabiting more northern habitats may have higher energy requirements than those estimated in the present study due to additional thermoregulatory costs.

While there are no direct GEI measures of wild sea otters, activity-based bioenergetic models predict that adult male otters expend 16 to 19 MJ d^{-1} (Yeates et al., 2007; Finerty et al., 2009), and adult females (without pups) expend 10.4 MJ d^{-1} (Thometz et al., 2014). Assuming a ~40% loss through digestion (Costa & Kooyman, 1984), this would result in an approximate GEI of 29 and 17 MJ d^{-1} for male and female otters, respectively. In comparison, the GEI of our male and female captive otters averaged 23.5 and 18 MJ d^{-1}, respectively, which is surprisingly similar to these rough estimates for their wild counterparts. The largest difference was between wild and managed adult males. Most of the study males were subject to procedures to limit aggression and procreation (e.g., orchiectomy or contraception); these behaviours are energetically demanding (Finerty et al., 2009), and the procedures can cause a suite of hormonal changes that might affect appetite. It is also interesting to note that the drop in GEI for the captive females during years 3 to 5 coincided with the period when females would normally be reproductively active (our study animals were not).

Overall, the present study demonstrated that sea otters under human care require high levels of ingested food mass to fulfill their energetic requirements. However, average daily energy requirements are not dramatically higher than those of other marine mammals held in aquariums. Further, this level of energy intake among managed otters is not dissimilar to that estimated for wild individuals. The high levels of food mass are largely the result of the energy density of the typical sea otter diet, whether in an aquarium or in the wild. This difference between ingested food mass and energy intake requirements is an important factor when designing

the diets of otters under human care. It is also an important characteristic to consider when determining the potential effect of environmental changes on individual otter energy balance and population health (Davis et al., 2019; Tinker et al., 2021).

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