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ARTICLE

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Variation in body mass and food intake of northern fur seals (*Callorhinus ursinus*)

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Abstract

Estimates of prey and energy consumption are important for effective management and conservation of marine mammals and the ecosystems they inhabit. We used routinely collected husbandry data on body mass, food intake (kilograms), and energy intake (megajoules) from northern fur seals (*Callorhinus ursinus*) in zoological institutions to examine how these variables changed throughout the year, and with age, sex, and reproduction. Fur seals exhibited seasonal changes in all three variables, but the magnitude and timing of trends varied among age and sex groups. Notably, adult males exhibited rapid increases in body mass leading up to the breeding season. Fur seals were most efficient at converting energy intake to mass gain in the spring and least efficient in the fall. Intake increased into adulthood as animals grew in body mass. Sex-specific differences in intake were detectable early in development, likely related to size dimorphism. Pregnancy was energetically inexpensive compared with lactation, with food and energy intake rapidly increasing post parturition to values that were double those during early pregnancy. This study highlights the importance of accounting for different age, sex, and life history stages when estimating prey consumption of northern fur seals.

KEYWORDS

bioenergetic model, caloric intake, energetics, fatted male phenomenon, growth, lactation, otariids

1 | INTRODUCTION

Effective management and conservation of wild populations requires a basic understanding of a species physiology, yet relevant data can be difficult to obtain for many species. This is particularly true for marine mammals because they are often widely dispersed and logistically challenging to study across some or all parts of their geographic or demographic range. Animals managed in human care (captivity) are a valuable resource to obtain basic physiological data, as they often retain similar physiological patterns despite living in physical and social environments that may be different from their natural habitats. Captive animals have been used to describe hormonal changes, food intake rates, digestive efficiency, changes in mass and body composition, and energy costs of many marine mammals (e.g., Gomez et al., 2016; Larson et al., 2003; Pagano et al., 2018; Thometz et al., 2021; Williams et al., 2007). Such data can then be applied to wild populations to understand, among other things, how individuals and populations are likely to interact with prey resources, human activities (e.g., fisheries, offshore wind farms), and the potential impact of a rapidly changing climate on population dynamics (McHuron et al., 2020; Noren et al., 2014; Pagano & Williams, 2019; Villegas-Amtmann et al., 2015).

The northern fur seal (*Callorhinus ursinus*) is a widely distributed marine mammal that spends over half the year at sea in pelagic habitats of the North Pacific Ocean (Kenyon & Wilke, 1953; Zeppelin et al., 2019). Despite their relative abundance (an estimated 620,600 individuals in 2016), the Eastern Pacific stock of northern fur seals has been listed as "depleted" under the Marine Mammal Protection Act since 1988. Stock abundance decreased ~1.8% per year from 1999 to 2019, with pup production reaching a 100-year low in 2018 (Muto et al., 2020). This stock encompasses fur seals that breed in the Bering Sea on Bogoslof Island and the Pribilof Islands (St. Paul, St. George) during the summer and fall months. The largest breeding congregation occurs on St. Paul Island where the population continues to decline at a rate of ~3.8% per year (Muto et al., 2020). While the causes have yet to be identified, food availability has been hypothesized as a contributing factor because of long maternal foraging trips, reduced maternal fat stores, and low pup growth rates on St. Paul Island (Banks et al., 2006; Kuhn, Baker, et al., 2014; Kuhn, Ream, et al., 2014), and potential competition with the largest U.S. commercial fishery (for walleye pollock) by volume. Recently, McHuron et al. (2020) quantified energy requirements and prey consumption of wild fur seals during the summer and fall to better understand the role of food availability in the current population decline. Despite this effort and the considerable physiological and ecological data available for northern fur seals, gaps remain in our understanding of energy needs and prey consumption of this species. For example, it is largely unknown how much prey adult males consume during the breeding season, or how much prey is consumed during the 6–8 months per year that fur seals spend at sea away from breeding rookeries.

The goal of this study was to use body mass and food intake data collected from northern fur seals managed in human care to better understand how these variables fluctuate across a fur seal's lifetime. We took advantage of basic husbandry data that has been routinely collected on fur seals in zoological institutions for decades, providing fine-scale observations on a considerably greater number of animals than are currently held in North American facilities. There is also a nationwide captive breeding program for this species in the United States, enabling access to data on all demographic groups, including pregnant and lactating females and their dependent pups. Specific objectives were to (1) determine seasonal and age-, and sex-related trends in body mass and food and energy intake, (2) quantify the relationship between energy intake and body mass changes and whether it differs among seasons, and (3) examine how average food intake values relate to maximum rates of intake.

2 | METHODS

2.1 | Animals

We obtained data on body mass, food intake (kilograms), and caloric intake of northern fur seals ($n = 41$) from four facilities between 1984 and 2020 (Figures S1 and S2). Data were obtained from the Seattle Aquarium (Seattle, WA), New England Aquarium (Boston, MA), Mystic Aquarium (Mystic, CT), and the University of British Columbia (UBC)/ Vancouver Aquarium (Vancouver, BC). Records occasionally included data from additional facilities (Brookfield Zoo, Brookfield, IL; New York Aquarium, Brooklyn, NY) due to transfer of fur seals among facilities for breeding or other purposes. Fur seals were of both captive ($n = 21$) and wild ($n = 20$) origin (either stranded or collected from the wild).

The age of each fur seal was either known (captive born) or estimated (wild origin) based on an average annual birth date of July 10 (Gentry, 1998) unless there was evidence to indicate a stranded animal had been born slightly later than this date. For reproductive females, implantation was assumed to occur 138 days after breeding behavior was observed or, when it was not observed, 237 days before birth (York & Scheffer, 1997). This accounts for the delay between fertilization and implantation of the blastocyte in the uterine wall. Detailed observations of the timing and occurrence of weaning was not available for all pups. In some cases, pups continued to suckle beyond the time of natural weaning for wild fur seals. When this occurred, the mother and pup were physically separated so aquarium staff could begin training the pup to eat and participate in routine care activities. When the weaning date was not available, the duration of lactation was assumed to occur from birth to several days before the start of the pup's feeding record. For pups without a feeding record during this time, we assumed that weaning occurred 122 days after birth, the average age of weaning for wild fur seals (Goebel, 2002; McHuron et al., 2020).

Fur seals at all facilities were housed together, including during the breeding season, with variable exposure to ambient environmental conditions. At the New England Aquarium, fur seals were exposed to ambient air temperatures in the main exhibit, but water temperatures were controlled between 14.4°C and 16.7°C year-round. Fur seals housed at the Seattle, Vancouver, and Mystic Aquariums were exposed to ambient air and water temperatures. The amount of food offered to animals at each feeding session varied throughout the year and was based on age, sex, season, reproductive status, and past consumption, with adjustments based on behavioral cues from each fur seal. While criteria varied among facilities, and potentially within a facility due to the considerable timespan covered by the data set, it was generally true that the amount of food (or calories) offered was increased if fur seals were motivated or expressed an interest in eating more and decreased if they exhibited a depressed appetite.

2.2 | Data collection

Body mass and food intake data were collected as part of routine husbandry at all facilities. Fur seals were trained to remain stationary on in-house platform scales (resolution of 0.01, 0.1, or 0.5 kg) using standard operant training procedures. The frequency of mass data collection varied among facilities and through time. Body masses were recorded daily for all fur seals housed at the Vancouver Aquarium ($n = 5$), whereas at the other facilities the average time between mass measurements for individual seals ranged from 6 days to 150 days (overall average = 27 days). Regularly obtaining body mass was not a routine part of husbandry practices at many facilities until the early 2000s or later; thus, measurements were less frequent for some fur seals before this time ($n = 15$; Figures S1 and S2).

Food intake (in kilograms) was recorded at each feeding session (2–4 per day) and summed to provide a daily total. Diets consisted of a combination of fish and squid species, with the specific composition of species often varying through time and among facilities. Fur seals housed at the Vancouver Aquarium periodically participated in research activities (Dalton et al., 2015; Rosen et al., 2012), which affected the amount of offered food independent of animal requirements. Data collected during research activities that affected food consumption were excluded from all analyses except the analysis focused on data collected during experimental trials (see below).

Caloric intake (in kilocalories) was calculated from proximate analysis of individual prey species from individual prey lots. Proximate analyses were typically conducted on each new prey lot. Daily caloric intake was calculated by multiplying the caloric content of each prey species by the total daily consumption of that prey species. We converted kilocalories to megajoules (238.8 kcal/MJ) for ease of comparison with other fur seal studies that report on energy expenditure or intake (e.g., Dalton et al., 2015; McHuron et al., 2020). Caloric intake was not included for fur seals at the Seattle Aquarium because proximate analyses of prey were infrequent.

Two sets of experimental trials were conducted with the five fur seals at the Vancouver Aquarium, where animals were continuously offered unlimited access to one prey type (either herring or squid) over an 8 hr period, for several days. A total of 4–6 daily trials were conducted per seal in the summer, fall, or winter. Trials were conducted when fur seals were between 10–18 months old (not included here) and again when they were 6–7 years of age. A complete description of methodology and a detailed analysis of results from early trials (10–18 months) can be found in Rosen et al. (2012). These trials were conducted in an unrelated study to estimate maximum consumption rates but are included here because they are relevant for bioenergetic modeling efforts, and also provide context for how food intake from animals managed in human care compare with physical limitations of food intake.

2.3 | Statistical analyses

Fur seals were categorized into seven demographic groups, with separate analyses conducted for each group unless otherwise stated. This was done because of a priori expectations that patterns would differ among these groups. Demographic groups were as follows: dependent (suckling) pups, weaned pups (nonsuckling pups <1 year old), juveniles (ages 1–3), subadult males (ages 4–7), adult males (ages ≥8), nonreproductive adult females (ages ≥4), and reproductive adult females (ages ≥ 4 and pregnant or lactating; Table 1). Because we had longitudinal records across multiple years, individual fur seals occurred in more than one group.

2.3.1 | Body mass and intake

Because initial plots revealed nonlinearity in the data, we used generalized additive mixed models (GAMMs) to assess how body mass, food intake, and energy intake varied throughout the year, with age, and by sex (when appropriate).

TABLE 1 Summary of data from northern fur seals by group, including the age and body mass range, and the number of individuals that contributed to each data set (*n*).

Group	Age (years)	Body mass (kg)	*n* Body mass	*n* Food (kg)	*n* Energy (MJ)
Dependent pup					
Female	Birth–0.45	4.3–17.5	7	NA	NA
Male	Birth–0.46	4.7–22.0	8	NA	NA
Weaned pup					
Female	0.30–0.99	7.1–17.5	13	10	10
Male	0.24–0.99	9.3–23.1	10	7	6
Juvenile					
Female	3.99	7.7–34.0	16	12	12
Male	1.0–3.99	13.5–69.6	12	9	7
Subadult male	4.0–7.99	31.5–264.50	13	11	7
Adult male	8.0–20.4	85.0–304.5	10	10	7
Adult female					
Nonreproductive	4.0–25.3	18.9–69.0	19	20	18
Pregnant	7.4–15.1	28.1–52.6	2	5	3
Lactating	8.1–15.4	29.0–47.2	2	5	3

Separate models were run for each variable and demographic group. We used weekly average values for food and energy intake to reduce computational time, which were calculated by averaging daily values for a given fur seal in each week within each year. For juveniles, subadults, nonreproductive adult females, and adult males, explanatory variables included the week within the year, age (rounded down to year), and sex (juveniles only). For weaned pups, explanatory variables were sex and the number of days since May 1 in the birth year. The number of days since May 1, which was an arbitrary date selected because the earliest birth occurred in May, did a better job of representing time within the year than age (in days) because some captive-bred animals were born considerably earlier (May and June) than the average birth time (July) of wild pups (Gentry, 1998). For reproductive females, explanatory variables were the time from parturition and age (rounded down to year) at the start of pregnancy. The analysis for dependent pups was limited to body mass with the explanatory variables of sex and age (days from birth). Explanatory variables modeled as smoothed effects included week, age (but see below), number of days since May 1, and time from parturition, using either cyclic cubic (week) or thin plate regression (all others) splines. Sex was modeled as a fixed parametric effect, as was age when there was a limited range of ages (juveniles, subadult males) since initial inclusion as a smooth effect indicated age for these groups was essentially linear (effective degrees of freedom near 1).

For all groups except reproductive females, the random effects were fur seal identity (to account for repeated measures) and facility (random intercept). When there were fewer than five facilities, facility was included as a fixed parametric effect (Bolker et al., 2009). For reproductive females, the only random effect was a unique value for each fur seal per reproductive event due to a limited number of fur seals in each analysis.

GAMMs were conducted using the *gam* or *bam* functions in the R package *mgcv* (Wood, 2017). The default link function ("identity") was used for all models except those for food and energy intake of weaned pups. In these two analyses, a log-link function was used to ensure positive fitted values. Model assumptions were checked using residual and autocorrelation plots and autocorrelation structures were included as necessary. The smoothing basis dimension (*k*) was left as the default, unless the default value exceeded that allowed by the data or diagnostics indicated it needed to be adjusted upwards (residual plots and/or $p \leq .05$ from *gam.check* function). In the few cases where one or more assumptions did not appear to be met, the response variable was log-transformed and residuals rechecked. To identify the best fitting model, we compared models with different combinations of explanatory variables; fur seal identity was included in all models to account for repeated measures. We also explored which random structure for fur seal identity—intercept, slope, and intercept, or smooth (as a function of week or day)—produced the best fit. Model comparisons were made using the *compareML* function from the R package *itsadug* (van Rij et al., 2020).

2.3.2 | Growth efficiency

General linear or linear mixed effects models were used to explore how efficient fur seals were at converting energy intake into body mass (i.e., relationship between energy intake and body mass changes), with separate models run for nonreproductive adult females, adult and subadult males, and juveniles. Mass changes were calculated between successive measurements and divided by the time interval between measurements, resulting in a daily mass change estimate. We only retained data where the time between successive measurements was 7–30 days; the lower limit of 7 days was imposed to better capture meaningful growth, whereas the upper limit was to ensure that fluctuations in mass were not missed between the two measurements. For UBC animals that were weighed daily, we selected measurements at 7-day intervals. Daily energy intake was calculated by averaging the energy intake data that occurred between the two mass measurements. Additional variables considered in each model were season (spring: March–May, summer: June–August, fall: September–November, and winter: December–February), age (rounded down to year), and sex (only juveniles). Fur seal identity was also included, either as a random intercept or a fixed effect if there were less than five fur seals in the data set.

All model combinations (without interactions) were run using the *dredge* function from the *MuMIn* package (Barton, 2018). Model comparisons were made using AIC and we selected the top model and all models within 2 ΔAIC.

Model assumptions were checked using residual plots. Residual plots indicated that residuals from the adult female and juvenile analyses were leptokurtic, however, linear mixed models appear to be robust to violations of distribution assumptions (Knief & Forstmeier, 2021; Schielzeth et al., 2020) so we present the results from these analyses. Multiple comparisons were made using Tukey's test and the *glht* function from R package *multcomp* (Hothorn et al., 2008).

2.3.3 | Maximum food intake rates

We calculated the average daily food intake of each fur seal during the months that experimental feeding trials were conducted. This average was meant to represent the typical intake of each fur seal and did not include food intake during feeding trials. We compared these average intake values to intake during the feeding trials. We focused on data collected when the animals were adults, as the juvenile data have already been presented elsewhere (Rosen et al., 2012). We did not conduct any statistical tests on the feeding trial data, as our primary interest here was simply in quantifying the maximum daily food intake of adult female fur seals.

3 | RESULTS

The age of fur seals in the study ranged from birth to 25.4 years, with body masses that spanned 4.3 kg to 304.5 kg (Table 1). Birth dates of captive-born pups ranged from May 28 to August 23. There were multiyear records for 39 of the 41 fur seals in the study, with an average contribution by each fur seal of 9.7 years and a range of 0.7–25.2 years (Figures S1 and S2). For each demographic group, the average amount of time we had data for each fur seal was 6.5 years (adult males), 8.5 years (adult females), 2.4–3.2 years (pregnant and lactating females), 2.9 years (subadult males), 2.4–2.6 years (male and female juveniles), 0.5 years (weaned pups), and 0.2–0.3 years (male and female dependent pups).

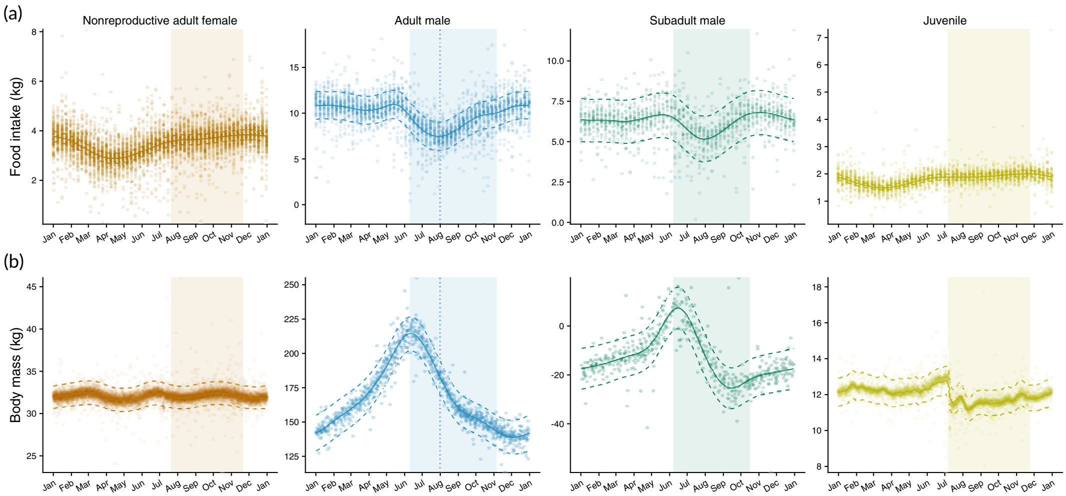

FIGURE 1 Partial effects plots from generalized additive mixed models showing how food intake (a) and body mass (b) of adult, subadult, and juvenile northern fur seals managed in human care changes within the year. Dashed lines are 95% confidence intervals and points are partial residuals after accounting for autocorrelation. The intercept from each model was added to the estimates. The shaded box in each subplot corresponds to the average time wild fur seals of each demographic group use the breeding rookeries, as estimated from Bigg (1986), Kenyon and Wilke (1953), and satellite-tracking data (McHuron et al., 2020). The dotted line in the adult male subplot is the approximate time that wild males abandon territories (Bartholomew & Hoel, 1953). Estimates were back transformed from a log scale where appropriate.

TABLE 2 Model output from generalized additive mixed models for food intake (kg) of northern fur seals managed in human care, including the number of data points (*n*), the percentage of deviance explained by the model, estimates with 95% confidence intervals (linear effects), and effective degrees of freedom (nonlinear effects). Effects associated with facility and fur seal are not shown.

			Linear effects			Non-linear effects		
Parameter	***n***	**Deviance**	**Estimate**	***t***	***p***	***edf***	***F***	***p***
Weaned pup	472	0.93						
Days since May 1						14.20	9.48	<.001
Juvenile[a]	2,920	0.84						
Age			0.18 (0.16–0.20)	16.10	<0.001			
Sex (male)			0.34 (0.17–0.51)	3.89	<0.001			
Week						5.86	7.79	<.001
Subadult male	1,473	0.72						
Age			0.19 (0.02–0.36)	2.13	0.03			
Week						4.98	1.73	<.001
Adult male	3,405	0.40						
Age						3.39	2.80	.02
Week						8.46	3.00	<.001
Adult female	7,289	0.48						
Age						6.44	9.48	<.001
Week						5.95	6.00	<.001
Reproductive female	399	0.91						
Weeks from birth						21.22	5.70	<.001

[a] Parameter estimates from a model with log-transformed response variable.

Average daily food and energy intake values were highest for adult males (10.0 kg, 44.2 MJ), followed by subadult males (6.9 kg, 31.2 MJ), lactating females (6.2 kg, 26.1 MJ), nonreproductive adult females (3.5 kg, 15.2 MJ), pregnant females (3.5 kg, 14.5 MJ), juveniles (3.1 kg, 13.2 MJ), and weaned pups (1.5 kg, 7.1 MJ). There was considerable deviation from these values within each group, with a maximum daily average prey intake of 22.5 kg (adult males), 14.3 kg (subadult males), 10.8 kg (lactating females), 8.3 kg (nonreproductive adult female), 6.8 kg (pregnant females), 9.0 kg (juveniles), and 5.2 kg (weaned pups). As a proportion of body mass, fur seals consumed a daily average of 5.7% (adult males), 8.7% (subadult males), 9.0% (weaned pups), 10.2% (nonreproductive adult females), 10.4% (pregnant females), 11.9% (juveniles), and 18.1% (lactating females), with maximum estimates that ranged from 15.5% in adult males to 26.8% in weaned pups. On average, body mass fluctuated by 3.3 kg (weaned pups) to 63.3 kg (adult male) within the calendar year. The largest fluctuation was for an adult male that lost 167.5 kg between June and December.

The following analyses are primarily focused on descriptions of trends instead of predictions of absolute intake and body mass. As such, we present the partial effects plots for all GAMM outputs, which show just the effects of the variable of interest, such as season or age. To make interpretations of plots more intuitive, the intercept for each model was added to the partial effects. For completeness, all predictions can be found in Table S1 and Figures S3–S6.

3.1 | Seasonal trends

Seasonal variation in food intake, energy intake, and body mass was present for all demographic groups, but the magnitude and timing of trends varied among groups (Figures 1 and S7, Tables 2–4). Adult males exhibited the most

TABLE 3 Model output from generalized additive mixed models for energy intake (MJ) of northern fur seals managed in human care, including the number of data points (*n*), the percentage of deviance explained by the model, estimates with 95% confidence intervals (linear effects), and effective degrees of freedom (nonlinear effects). Effects associated with facility and fur seal are not shown.

			Linear effects			Nonlinear effects		
Parameter	*n*	Deviance	Estimate	*t*	*p*	*edf*	*F*	*p*
Weaned pup[a]	445	0.91						
Sex			0.15 (−0.19–0.48)	0.85	.39			
Days since May 1						19.04	8.16	<.001
Juvenile[b]	2,689	0.71						
Age			0.20 (0.18–0.22)	17.16	<.001			
Sex (male)			0.38 (0.23–0.53)	5.00	<.001			
Week						5.71	8.78	<.001
Subadult male	625	0.59						
Age			3.87 (2.46–5.28)	5.38	<.001			
Week						5.52	2.92	<.001
Adult male	2,513	0.36						
Age						1.23	1.20	.41
Week						11.84	1.86	<.001
Adult female	5,886	0.39						
Age						9.97	6.17	<.001
Week						11.22	8.13	<.001
Reproductive female	343	0.91						
Weeks from birth						24.72	4.24	<.001

[a] Parameter estimates from a model with a log-link function.
[b] Parameter estimates from a model with log-transformed response variable.

pronounced seasonal variation in all three variables, with the greatest food and energy intake in the winter and spring, which declined in June and reached its lowest point in the beginning of August. Body mass increased from January to mid-June, particularly from April onwards, with males estimated to gain over 70 kg of mass during this time. Subadult male trends in food intake and body mass largely mirrored those of adult males, but the magnitude of seasonal changes was considerably less. Nonreproductive adult females and juveniles exhibited similar patterns to each other in food and energy intake, with intake declining from January to April and then increasing to a plateau in July (juveniles) or August (adult females). While models containing day of the year were better fits than those without, variation in body mass associated with time of year was minimal (~1–2 kg) for nonreproductive adult females and juveniles. There were declines in juvenile body mass in July and then again in August, which corresponded with the birth dates of many of the fur seals in our study (i.e., a fur seal was heavier in June than in July because it was almost an entire year older).

3.2 | Age- and sex-related trends

All demographic groups exhibited changes in food intake, energy intake, and body mass with age (Figures 2 and S8). For adults, food and energy intake increased slightly during the first 2 (adult males) to 4 years (nonreproductive adult females) before plateauing or even declining late in life. Despite relatively small changes in intake, body mass

TABLE 4 Model output from generalized additive mixed models for body mass (kg) of northern fur seals managed in human care, including the number of data points (*n*), the percentage of deviance explained by the model, estimates with 95% confidence intervals (linear effects), and effective degrees of freedom (nonlinear effects). Effects associated with facility and fur seal are not shown.

			Linear effects			Nonlinear effects		
Parameter	*n*	Deviance	Estimate (95% CI)	*t*	*p*	*edf*	*F*	*p*
Dependent pup	128	0.99						
Age						8.2024.48		<.001
Weaned pup	1,335	0.99						
Sex (male)			3.54 (1.51–5.58)	3.42	<.001			
Days since May 1						26.56	15.89	<.001
Juvenile[a]	6,382	0.94						
Age			0.22 (0.21–0.22)	97.40	<.001			
Sex (male)			0.51 (0.40–0.62)	9.10	<.001			
Day						58.28	3.54	<.001
Subadult male	559	0.92						
Age			16.01 (14.70–17.30)	24.05	<.001			
Day						6.97	8.27	<.001
Adult male	1,286	0.84						
Age						9.64	32.51	<.001
Day						7.31	12.59	<.001
Adult female[a]	14,763	0.95						
Age						10.10	468.95	<.001
Day						9.62	2.22	<.001
Reproductive female	285	0.97						
Age						2.03	9.71	<.001
Days from birth						29.59	12.62	<.001

[a] Parameter estimates from a model with log-transformed response variable.

increased steadily up until approximately 15 years of age for both sexes, with body mass of adults exhibiting a slight decline above 15 (males) or 20 (females) years of age. Body mass of juveniles and subadult males increased linearly, with subadult males exhibiting a steeper increase compared with juveniles despite relatively small increases in food and energy intake (Figures 2 and S8). By the time individuals reached the juvenile stage, sex-specific differences were present for all three variables (Tables 2–4).

3.3 | Reproductive females and pups in first year of life

Food and energy intake of pregnant females remained largely unchanged until just under 2 months before birth, when intake increased and then subsequently decreased for the last month of pregnancy (Figures 3a and S9). Body mass increased slowly during much of pregnancy, with rapid increases beginning at just over three months from birth (Figure 3b). Overall, females gained roughly three times the mass of a newborn pup during pregnancy; total mass gains of individual females ranged from 11.8 to 17.5 kg. There was a sharp decline in body mass at the end of pregnancy; this was mostly driven by the birth of the pup, although there was a small decline in body mass in the final week of pregnancy (Figure 3b). About half of the pregnant females consumed little to no food on the day of parturition.

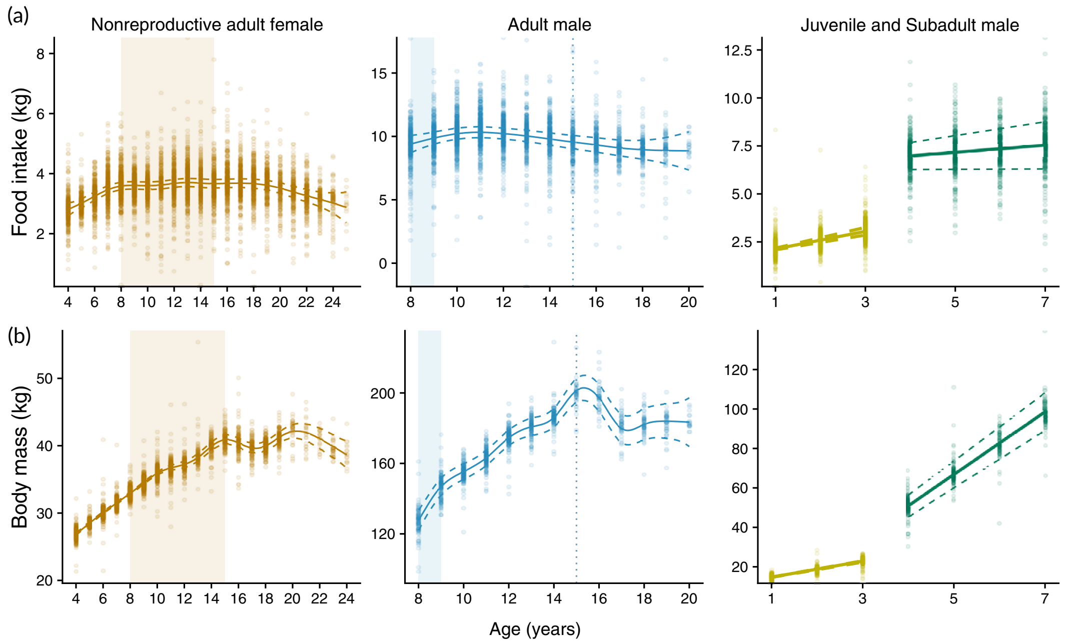

FIGURE 2 Partial effects plots from generalized additive mixed models showing how food intake (a) and body mass (b) of adult, subadult, and juvenile northern fur seals managed in human care change with age. Dashed lines are 95% confidence intervals and points are partial residuals after accounting for autocorrelation. The intercept from each model was added to the estimates. The shaded box in each adult subplot represents the ages when wild fur seals exhibit the greatest pregnancy rates (>80%) and territory-holding behavior (Kiyota, 2005; Lander, 1981; Vladimirov, 1987). The dotted line in the adult male plot represents the maximum observed age in the wild. Estimates were back transformed from a log scale where appropriate.

Once lactating, females exhibited rapid increases in food and energy intake that plateaued 5–6 weeks after parturition. At peak values, food and energy intake during lactation were estimated to roughly double from intake during early pregnancy (Figure 3a). Similarly, food intake of a lactating female 8 weeks post parturition was 1.9 times that of a nonreproductive female at the beginning of September. On average, individual females exhibited a maximum food intake during lactation that was 2.6 times the average intake during the first 6.5 months of pregnancy. Food and energy intake declined after approximately 3.5 months post parturition until the end of lactation (weaning). Body mass remained largely unchanged throughout lactation except for a slight increase that began around 2.5 months after parturition and continued until weaning. The lactation duration of females with known wean dates was 4.4 ± 0.9 months, with half the females having lactation durations that exceeded the maximum duration of wild fur seals by as much as 32 days.

Dependent pups exhibited steady body mass gains throughout most of the time they suckled (Figure 3c). Body mass plateaued for roughly 25 days between the second and third month of age before increasing to a peak around 4.4 months of age. Data from three mother-pup pairs confirmed that pups continued to grow during periods when their mothers did not increase their food or energy intake (Figure 3d). While male pups were slightly heavier than females, the inclusion of sex did not considerably improve model fit.

Following weaning in late October and November, pups increased food and energy intake until January; intake plateaued through much of the winter and then increased from April onwards to their first birthday (Figures 4 and S10). Body mass of weaned pups declined sharply during the initial increase in intake, followed by an increase from December to January, a shallow decline until March, a steeper decline from March to May, and then an increase from May onwards (Figure 4). Male pups were heavier than female pups and consumed more energy than females, although not statistically

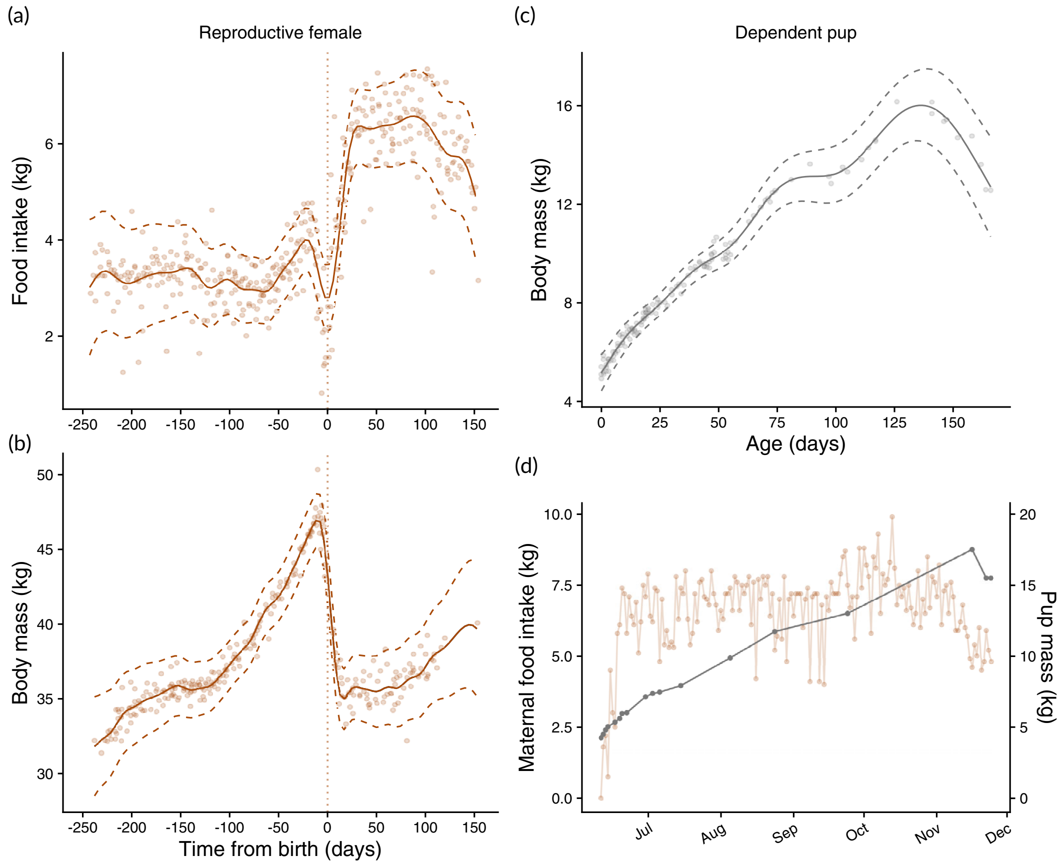

FIGURE 3 Partial effects plots from generalized additive mixed models showing how food intake (a) and body mass (b) of pregnant or lactating female northern fur seals managed in human care change with time from birth, and how body mass of dependent pups changes with age (c). Data are from five reproductive events from two females (a) or eight reproductive events from five females (b). In d, an example of changes in maternal average daily prey intake (colored) and pup mass (gray) during lactation is shown for a single mom-pup pair. Dashed lines (in a–c) are 95% confidence intervals and points are partial residuals after accounting for autocorrelation. The vertical dotted line (in a and b) denotes the day of birth. The intercept from each model was added to the estimates.

more food. Differences in the importance of sex in the energy vs. food intake model was likely a result of dietary differences.

3.4 | Growth efficiency

There was only one model that best described the variation in daily body mass changes for each demographic group. The next best models had ΔAIC values that ranged from 2.2 (adult males) to 33.7 (adult females). Body mass changes were significantly related to daily energy intake and age for all groups; fur seals experienced mass gains with greater energy intake and patterns for older animals reflected their greater total energy costs. Seasonal differences in growth efficiency were detected for all demographic groups except subadult males (Table 5, Figure 5). Fur seals had the highest growth efficiencies in the spring and lowest in the fall, and while season was not in the best fit model for subadult males, the data also followed this trend. The magnitude of seasonal effects was greatest for adult males,

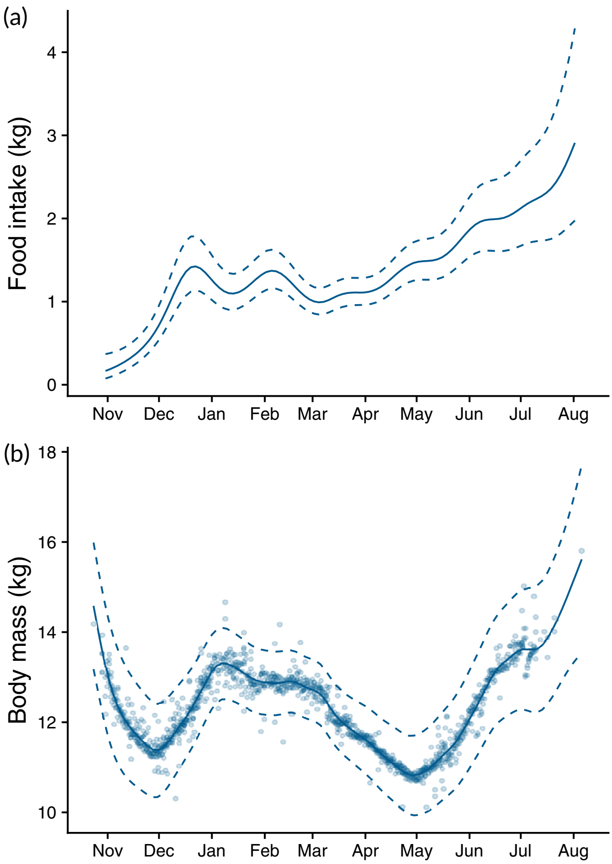

FIGURE 4 Partial effects plots from generalized additive mixed models showing how food intake (a) and body mass (b) of northern fur seals managed in human care change during their first year of life, once they were independent from their mother to age one. Dashed lines are 95% confidence intervals and points (in b) are partial residuals after accounting for autocorrelation. In (a), partial residuals are not shown because a log-link function was used for the analysis, but the plot shows the fit on the response scale. The intercept from each model was added to the estimates.

both on an absolute and relative (to body mass) scale. For a given energy intake, body mass changes in fall vs. spring differed by 0.84 kg/day (adult male), 0.06 kg/day (nonreproductive adult females), and 0.03 kg/day (juveniles). Differences between other seasons were more variable among groups; all seasons were significantly different from each other for nonreproductive adult females, whereas summer-winter was not different for adult males ($p = .96$), and fall–winter ($p = .79$) and summer–spring ($p = .93$) were not different for juveniles. For juveniles, males lost more mass than females for a given level of energy intake.

3.5 | Maximum food intake rates

Adult female fur seals from the Vancouver Aquarium, which ranged in weight from 21.3 to 37.2 kg, consumed between 0.6 and 9.4 kg of food during experimental feeding trials. As a proportion of body mass, fur seals consumed an average of 14.5% (October) to 26.4% (July) of food in 8 hr, with maximum values up to 34.0%. In general, fur seals appeared to consume greater amounts of prey during squid feeding trials compared with herring feeding trials, but as trials were not conducted in the same months, this could have been due to interannual variation in motivation. On

TABLE 5 Model output from linear or linear mixed effects models on factors affecting bod mass changes of northern fur seals managed in human care, showing the number of data points (*n*), r^2 values (either adjusted or marginal), associated *F* and *p* statistics, and parameter estimates with 95% confidence intervals. Estimates are shown relative to winter (season) or female (sex) values. Fur seal was included in all models, either as a fixed or random effect (see text) but results are not shown here.

Parameter	*n*	r^2	*F*	*p*	Estimate [95% CI]
Juvenile	1,396	0.24			
Energy intake			272.18	<.001	0.014 [0.012, 0.016]
Season			17.74	<.001	Sp: 0.027 [0.016, 0.037] Su: 0.023 [0.013, 0.034] F: −0.005 [−0.015, 0.006]
Age			125.18	<.001	−0.035 [−0.041, −0.029]
Sex			17.93	<.001	M: −0.062 [−0.090, −0.034]
Subadult male	114	0.25			
Energy intake			20.16	<.001	0.015 [0.009, 0.021]
Age			8.79	<.01	−0.110 [−0.182, −0.038]
Adult male	479	0.42			
Energy intake			161.77	<.001	0.023 [0.020, 0.027]
Season			63.31	<.001	Sp: 0.610 [0.470, 0.751] Su: −0.036 [−0.179, 0.108] F: −0.235 [−0.369, −0.101]
Age			4.26	.04	−0.016 [−0.031, −0.001]
Adult female	2,245	0.23			
Energy intake			554.58	<.001	0.015 [0.013, 0.016]
Season			30.99	<.001	Sp: 0.018 [0.007, 0.030] Su: −0.016 [−0.028, −0.005] F: −0.038 [−0.049, −0.027]
Age			34.92	<.001	−0.005 [−0.007, −0.003]

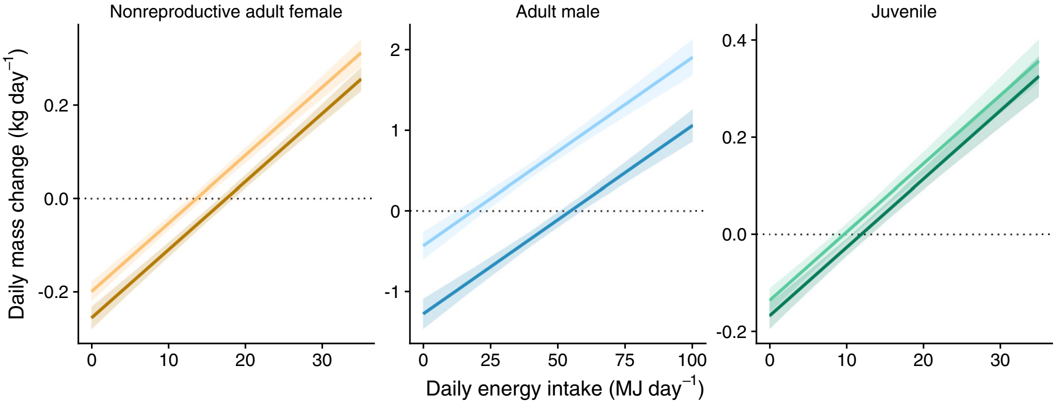

FIGURE 5 Marginal effects of the relationship between daily changes in body mass (kg) and average daily energy intake of nonreproductive adult female, adult male, and juvenile northern fur seals. Separate regression lines with 95% CI are shown for spring (lighter) and fall (darker), the two seasons with the largest differences.

average, fur seals consumed twice as much prey during feeding trials compared with average consumption during the same month trials were conducted in.

4 | DISCUSSION

4.1 | Seasonal, age, and sex-related patterns

Seasonal fluctuations in food (and energy) intake and body mass were most notable for adult males, who exhibited rapid mass gains in the spring leading up to the time when their wild counterparts begin arriving on breeding rookeries in May and June (Bigg, 1986). This rapid gain, often known as the "fatted" male phenomenon (Du Mond & Hutchinson, 1967; Schusterman & Gentry, 1971), presumably occurs because adult males need to build up energy reserves to sustain themselves while they attempt to hold and defend territories on breeding rookeries. Seasonal fattening has been noted previously for two wild-caught males held in captivity (Spotte & Adams, 1979), and in other captive and wild otariids that have similar breeding systems (Arnould & Warneke, 2002; Kastelein et al., 2000; Winship et al., 2001). During the breeding season, adult males were generally housed with other fur seals and displayed territorial behavior, even when females were not present. They did not, however, experience the same degree of mass loss as wild adult males (Gentry, 1998) since feeding and defending territory are not mutually exclusive behaviors in captivity. Territorial adult males lost an average of 32% of their body mass across an average of 46 days of fasting (Gentry, 1998), whereas captive males only lost ~21% of their body mass from June to August. Food intake began to increase in the beginning of August, which coincides with the time that adult males in the wild abandon their territories (Peterson, 1965), although body mass continued to decline until December. Given the disparity in mass loss patterns between captive and wild fur seals during the breeding season, it is unclear whether body mass and intake patterns of wild adult male fur seals would mirror those of captive ones.

Subadult males exhibited similar temporal patterns as adult males but of considerably lesser magnitude. We did not investigate whether there was age-specific timing in the onset of this pattern or the magnitude due to limited sample size. For other species, such seasonal patterns have been noted to emerge around the time males reach sexual maturity (Kastelein et al., 2000; Schusterman & Gentry, 1971) and increase in magnitude with age (Schusterman & Gentry, 1971). There was a much shorter temporal gap between when food intake began to increase (August) and body mass recoverered (September) for subadult males compared with adult males.

Nonreproductive adult females and juveniles exhibited seasonal fluctuations in intake and body mass of varying and sometimes small magnitude. Both groups exhibited increases in food intake during the spring, which corresponded with slight but relatively minor increases in body mass leading up to the time when their wild counterparts arrive on breeding rookeries in July onwards. Food and energy intake remained elevated through the fall. While this resulted in a slow increase in body mass among juveniles, there was a decrease in adult female body mass from July–September, despite the high levels of food intake. Seasonal patterns in body mass changes for juveniles and adult females were similar to those documented by Trites and Bigg (1996) from fur seals that were shot at sea, suggesting that patterns in food and energy intake may also be similar despite a lack of empirical data for comparison.

Increased mass gain in the spring was facilitated not only by higher energy intake but also because of an increase in growth efficiency during this time, particularly for adult males. Subadult males were the only group for which we did not detect an increase in growth efficiency, which may have been due to limited sample size or because of an interaction associated with the transition to sexual maturity. Seasonal differences in growth efficiency could be achieved through a variety of mechanisms, including differences in tissue investment (i.e., fat vs. lean mass), changes in activity or thermoregulatory costs, changes in resting metabolic rates, or increases in digestive efficiency. While it is likely that fur seals prioritize different types of tissue growth during their lives, this is unlikely to contribute to the patterns observed here since the body mass gained by adult males during the spring is believed to be predominantly fat (Boyd & Duck, 1991; Scheffer & Wilke, 1953), which is more energy dense than lean tissue. Behavioral or thermoregulatory changes are also an unlikely explanation; captive and wild fur seals have very different activity budgets and environments yet exhibit similar fluctuations in body mass, and they appear to develop broad thermal limits relatively early in life (Dalton et al., 2014). It is also difficult to envision how wild fur seals would keep activity costs low while maintaining high foraging rates to maximize intake in the spring. There is some support for the other two explanations. For example, resting metabolic rates of many pinnipeds are elevated during their annual molt (Ladds et al., 2017; Thometz et al., 2021; Williams et al., 2007), and elevated resting and field metabolic rates have been detected in northern fur seals during the fall (Dalton et al., 2015; McHuron et al., 2019) when much of the molt occurs (Scheffer & Johnson, 1963). There also is some evidence to suggest that digestive efficiencies may change with meal size or energy ingested (Lawson et al., 1997), although digestive efficiency in northern fur seals was negatively related to meal size (Gomez et al., 2016). Regardless of the specific pathway, hormones likely play an important role in modulating seasonal changes in body mass, food intake, and metabolism (Bubenik et al., 1998; Dardente et al., 2014; Ryg & Langvatn, 1982).

Northern fur seals gained mass and increased food and energy intake into adulthood, which was not surprising given the growth curves that have been previously documented for this species (Lander, 1981; Scheffer & Wilke, 1953; Trites & Bigg, 1996). We observed an increase in growth for male fur seals starting at 4 years of age, which coincides with sexual maturity (Scheffer & Wilke, 1953). This trend has previously been documented for northern fur seals and other otariids (Arnould & Warneke, 2002; McKenzie et al., 2007; Trites & Bigg, 1996; Winship et al., 2001). Once they reached adulthood, fur seals continued to increase in body mass for another 6–7 years without corresponding increases in food or energy intake. It is unclear exactly how this was achieved. Body mass senescence is rarely detected in wild pinnipeds (Arnould & Warneke, 2002; Bowen et al., 2006; McKenzie et al., 2007; Trites & Bigg, 1996; Winship et al., 2001) but see Proffitt et al. (2007), yet we detected body mass declines beginning around 15 (males) and 20 (females) years of age. This may be because wild fur seals, particularly males, do not live long enough to experience senescence or because of condition-dependent mortality in wild populations (Hämäläinen et al., 2014).

Northern fur seals exhibit strong sexual size dimorphism, which was readily detectable in our study for all three variables by the time fur seals reached the age of 1. Increased food and energy intake was likely the result of greater absolute energy needs due to a larger body size. Sexually dimorphic mammals also exhibit sex-specific growth strategies (Arnould & Hindell, 2002; Schulte-Hostedde et al., 2001), which also could have contributed to sex-specific differences in food and energy intake.

4.2 | Reproductive females and pups in their first year of life

Reproduction is energetically costly for mammals (Gittleman & Thompson, 1988; Oftedal, 2000). Lactation costs generally exceed those of gestation (e.g., Gallagher et al., 2018; Kurta et al., 1989; Speakman, 2008; Villegas-Amtmann et al., 2015), and our findings are consistent with this pattern. Food and energy intake of pregnant fur seals remained relatively unchanged until late gestation when there was a slight increase, whereas peak food and energy intake during lactation was approximately double what was consumed during early gestation. The consistency of food and energy intake throughout much of gestation is unlikely to be a side effect of captivity, as evidence from humans indicate that large increases in body mass occur despite little to no increase in energy intake (Jebeile et al., 2016). Metabolic depression has been detected in mammals during pregnancy (Becker et al., 2013; Hedd et al., 1997; Sparling et al., 2006), which may largely offset energy costs and be an adaptation for sustaining pregnancy under marginal environmental conditions (Prentice & Goldberg, 2000). In humans, the total cost of pregnancy increases with preconception body condition, suggesting that body mass and intake of wild fur seals may deviate from the patterns observed here when experiencing food-limited conditions. Reduced intake late in gestation may seem counterintuitive since gestation costs would seemingly be at their highest based on fetal mass and growth patterns (Trites, 1991), and continued increases in maternal body mass until parturition. Despite this, reduced intake in the final days or weeks of pregnancy is commonly exhibited by mammals in human care (Kastelein et al., 1990, 2000; Künkele, 2000; Robeck et al., 2005; Speakman, 2008; Williams et al., 2007). One hypothesis for this decrease is that the growing fetus competes for space with the alimentary tract, thereby limiting a female's ability to physically ingest and process prey (Speakman, 2008). The migratory return of pregnant fur seals to breeding rookeries is quite rapid (Trites & Bigg, 1996), with satellite-tracked females exhibiting high transit rates and little foraging in the first or second week of June (J.T.S., unpublished data), providing some indication that intake of wild fur seals may also be reduced just prior to parturition. The increase in body mass up until parturition includes fetal growth, variable amounts of fat deposition, and fluid accumulation (Most et al., 2018), which may explain why body mass increased until the final week of pregnancy despite reductions in food and energy intake.

Body mass following parturition quickly returned to levels observed during mid gestation and thereafter remained unchanged throughout much of lactation. In contrast, food and energy intake rapidly increased following parturition, peaking at ~1.1 months post parturition before decreasing from ~3 months until the end of lactation. The doubling of food intake during lactation was similar to what was observed in the experimental feeding trials, suggesting that females likely need to consume close to their physical limit to support their growing pup, particularly as foraging trips are interspersed with onshore nursing visits in wild fur seals. In support of this, estimates of food intake derived from doubly labeled water indicate that lactating northern fur seals consumed an average of 9.5–10.0 kg of prey per day at sea (depending on assumed prey water content; McHuron et al., 2019). There has only been one empirical estimate of the relative costs of lactation in free-ranging northern fur seals, which found that lactating females consumed 1.6 times more food than nonlactating ones (Perez & Mooney, 1986). A more recent bioenergetic modeling effort based on empirically derived estimates of female metabolic rates and pup milk intake predicted that energy needs were 1.7 times greater during lactation than nonlactation at the same time of the year (McHuron et al., 2020). It is unclear why our estimates are slightly higher, but it could have been because of limited sample size (five reproductive events from two females), that captive females have more flexibility (lower nonreproductive intake) in how much they can increase food intake because they are fed daily or have lower energy costs, or a result of ready access to food by captive females.

It was unexpected that food and energy intake of nursing females remained constant throughout much of lactation because Donohue et al. (2002) found that milk energy intake of northern fur seal pups up to 3.3 months of age increased as they grew. It is possible that females initially consumed an excess of energy that was stored and later mobilized, however, the lack of large fluctuations in body mass during early lactation does not support this hypothesis. It is therefore unclear whether this finding of constant food intake during much of lactation is applicable to wild lactating fur seals. The decrease in food and energy intake towards the end of lactation may represent the start of the weaning process, which in some otariids appears to be characterized by changes in milk composition and reductions in mass-specific milk energy intake rates (Arnould & Hindell, 2002; Georges et al., 2001).

Dependent pups exhibited continuous but nonlinear growth for the first 4.4 months of life followed by a decline in mass that persisted until weaning. This pattern contrasts with that of wild northern fur seal (and other otariid) pups that exhibit cyclical oscillations in body mass between maternal visits (Chambellant et al., 2003; Gentry, 1998), but the overall growth trajectories appear to be quite similar between captive and wild northern fur seals. Boltnev et al. (1998) and Donohue (1998) both found relative growth rates (as a percentage of body mass) that were highest early in lactation and lowest during the most intensive part of the postnatal molt period, which was assumed to occur at 1.4–2.6 months or 2–3 months of age, respectively. We detected a similar pattern, with relative growth rates of 1.5%/day early in lactation that slowed to 0.1%/day from 2.5 to 3.2 months of age. Slower growth during peak molt has been attributed to increased maintenance costs associated with thermoregulation and growth of new fur (Donohue et al., 2002), and while the timing was slightly later than what has been observed for wild pups, this is the most likely explanation for the reduction in growth rates of captive fur seals. Metabolic demands of wild pups decrease following molt (Donohue et al., 2002), which may have contributed to the ability of captive pups to rapidly gain mass late in lactation despite a lack of increase in maternal food or energy intake. Average lactation durations were longer than what has been observed in the wild, likely because animals managed in human care cannot exhibit the behaviors that terminate lactation (i.e., dispersal, migration).

Once weaned, the food and energy intake of pups increased rapidly from the time of weaning until mid-December. Intake during much of this time was not, however, enough to cover energy demands since pups lost mass until the beginning of December, presumably through metabolism of fat stores. Immediately follow weaning when food intake was near zero, pups were predicted to lose 0.87%–1.15% of their body mass per day. In the wild, pups begin diving almost immediately upon departure from natal rookeries (Baker, 2007; Lea et al., 2010), presumably in search of food; however, patterns in food and energy intake may not necessarily follow those documented in this study because wild pups may not immediately encounter prey or be able to catch it when they do. Based on the above relative mass loss rates, a wild pup could lose upwards of 1.6–2.0 kg of mass per week if unable to find prey. This does not account for any additional thermoregulatory or activity costs that wild pups may experience. Intake plateaued between December and January, yet captive fur seal pups experienced mass gains from December into February, suggesting that metabolic needs may be reduced during this time. These findings are generally consistent with those of Rosen et al. (2014), who found that young northern fur seals lost less mass during 48 hr fasting periods and had lower resting metabolic rates in winter compared with summer. The animals in their study were included in this one, although we had data from an additional 19 animals that supported this trend. Since wild fur seal pups may encounter water <6°C postdispersal (Baker, 2007; Lea et al., 2009; Zeppelin et al., 2019), it is possible they may experience additional thermoregulatory costs that could impact body mass or prey intake during this time; however, there is conflicting evidence as to whether such temperatures would be within (Donohue et al., 2000) or outside (Rosen & Trites, 2014) their thermoneutral zone.

4.3 | Insights gained and application to wild fur seals

Our study provides a better understanding of the relative prey and energy needs of northern fur seals throughout their lives, and the interplay between energy intake and body mass changes. Such insight is important in assessing when fur seals might be most vulnerable to reductions in prey availability and for quantifying their role in marine food webs. Our findings clearly illustrate the drastic fluctuations in food intake that can occur throughout the year for some demographic groups. Similar fluctuations have been detected in other pinnipeds (Kastelein et al., 1990, 1995, 2000; Noren et al., 2014; Rosen et al., 2021), supporting the hypothesis that seasonal variation is driven by hormonal changes associated with key life history events. In migratory species like northern fur seals, this means they can have differing impacts on the ecosystems they inhabit depending on how their use of a given ecosystem overlaps with seasonal patterns in prey intake. The estimates of maximum prey intake rates presented here provide context for whether estimates of prey intake from bioenergetic models are realistically achievable and can be useful in parameterizing behavioral models to avoid unrealistic mass gains when simulated individuals encounter abundant prey resources (e.g., McHuron et al., 2021).

The mismatches we detected between energy intake and energy expenditure indicate there is a need to better understand the mechanisms that drive food intake and the interplay between food intake, season, and body condition. Knowledge of these mechanisms would help better parameterize individual-based behavioral models that often assume that animals will maximize food intake if it is available, and that when disturbed, will attempt to "make up" for lost foraging opportunities. These mismatches also illustrate the pitfalls of simply using estimates of energy expenditure to estimate prey consumption (or vice versa).

A key application of food and energy intake data derived from captive animals is to estimate prey intake of wild populations, either in species-specific efforts (e.g., Noren et al., 2014) or large end-to-end ecosystem models (e.g., Gaichas et al., 2015). Careful consideration should be used in extrapolation because fur seals (and other species) in zoological institutions often do not experience similar social, environmental, or foraging conditions as their wild counterparts, all of which are likely to influence the amount of food they consume. In addition to the potential for mismatches in relative trends, captive fur seals do not have to expend the same level of effort to find or capture prey and are fed daily. While food and energy intake of captive fur seals likely underestimates prey consumption in wild fur seals, such estimates provide at minimum a lower bound on consumption that can be used to inform ecosystem models and other bioenergetic modeling efforts. The vast differences in body mass and intake among the different age, sex, and reproductive groups highlights the importance of modeling prey intake separately for northern fur seals and likely other species that share similar life history characteristics. These revelations are not new but are worth reiterating given the continued and often direct application of captive-derived food intake data to wild populations.

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AUTHOR CONTRIBUTIONS

Elizabeth McHuron: Conceptualization; formal analysis; methodology; project administration; visualization; writing – original draft; writing – review and editing. **David Rosen:** Conceptualization; data curation; investigation; resources; writing – review and editing. **Julie Carpenter:** Data curation; investigation; resources; writing – review and editing. **Patricia Leonard:** Data curation; investigation; resources; writing – review and editing. **Gayle Sirpenski:** Data curation; investigation; resources; writing – review and editing. **Jeremy Sterling:** Conceptualization; methodology; supervision; writing – review and editing.

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