Energy and prey requirements of California sea lions under variable environmental conditions

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ABSTRACT: Quantifying energy demands and prey consumption of marine mammals is important to understand the population dynamics of species and their ecological role in marine ecosystems. We developed a bioenergetic model to quantify the energy and prey requirements of adult female California sea lions *Zalophus californianus*, an abundant predator that has recently experienced several years of poor reproductive success presumably associated with oceanographic changes. We also examined how changes in at-sea field metabolic rates and the proportion of time at sea — 2 mechanisms that female otariids use to compensate for changes in prey availability — affected energy requirements. Mean gross energy requirements (±SD) ranged from 12 500 ± 1900 to 21 000 ± 2200 MJ yr^{-1}, depending on reproductive status, resulting in prey consumption estimates of 1700–3000 to 2900–5000 kg prey yr^{-1}, respectively. California sea lions had energy requirements that were 3 to 4 times higher than phocid seals because of high metabolic rates and the considerable cost of lactation. Behavioral changes resulted in a 3 to 25% change in energy requirements, depending on the type and magnitude of the change, time period, and lactation status. Energy requirements may therefore increase during periods of reduced prey availability, assuming that a female does not reduce milk energy delivery to her pup. These results highlight the importance of considering behavioral responses to environmental conditions when developing and applying results from bioenergetic models to understand the relationships between energy requirements, prey availability, and reproductive success.

KEY WORDS: Bioenergetic model · Marine mammal · *Zalophus californianus* · California Current

INTRODUCTION

Marine mammals face increasing pressure from climate change and a continuing human presence in marine environments, which can have broad-reaching implications for individual fitness, population dynamics, and ecosystem health (DeMaster et al. 2001, Tyack 2008, Hoegh-Guldberg & Bruno 2010, Desforges et al. 2016). At the level of the individual, many of the negative effects of these pressures are mediated through changes in energy balance, either through decreases in energy acquisition or through increases in total energy expenditure. For example, many marine mammals alter their foraging behavior in response to oceanographic changes that affect prey abundance and distribution (Boyd et al. 1997, Weise et al. 2006, Kuhn et al. 2014), which can affect the rate of energy expenditure (Costa et al. 1989). Individuals may be able to offset these costs by increasing energy acquisition either by increasing prey consumption or by switching to energy-rich prey (Costa & Gentry 1986, Costa 2007); however, the ability to do so is driven by the availability of prey as well as the intrinsic qualities of individuals (e.g. physiological capabilities) and may come at an increased risk to the individual. Quantifying energy

demands and the influence of prey availability on energy budgets is critical for the management and conservation of marine mammal populations, especially given that food limitation has been hypothesized as a contributing factor to the poor reproductive success or population declines of several marine mammal species (Chilvers 2012, Baylis et al. 2015, McClatchie et al. 2016).

Bioenergetic models provide quantitative estimates of energy requirements by summing the costs associated with different physiological processes and animal behaviors. They have been developed for a number of marine mammal species to address both physiological and ecological questions, such as energy demands and prey requirements (Olesiuk 1993, Winship et al. 2002, Noren 2011, Rechsteiner et al. 2013, Noren et al. 2014), trophic impacts and interactions with commercial fisheries (Cornick et al. 2006, Trzcinski et al. 2006, Weise & Harvey 2008, Morissette & Brodie 2014), the risk of disease and toxin exposure (Bejarano et al. 2007), and the role of energy balance in population dynamics (New et al. 2013, 2014). Linking changes in energy budgets with reproductive success is a goal in developing bioenergetic models (Williams et al. 2006, Villegas-Amtmann et al. 2015, Costa et al. 2016) and an important component in understanding how responses to prey availability and anthropogenic disturbance ultimately affect population dynamics (Costa 2012). For capital breeders that rely solely on energy stores accumulated during foraging for reproduction, the impacts of behavioral changes on reproductive success can be estimated by simply subtracting a proportion of energy from the total energy budget during foraging, which is temporally separate from lactation (New et al. 2014, Villegas-Amtmann et al. 2015, Costa et al. 2016). This approach cannot be used for income breeders because of the temporal overlap between foraging and lactation and the reliance of females on energy gained during each foraging trip to support offspring. As a result, bioenergetic models currently have limited use for predicting the impacts of natural and anthropogenic disturbance on individual reproductive success of income-breeding species.

California sea lions *Zalophus californianus* (an abundant otariid) inhabit demersal and offshore habitats of the California Current Ecosystem (CCE). The CCE is a productive, eastern boundary upwelling system that is characterized by fine- and broad-scale oceanographic variability across multiple temporal scales (Bograd & Lynn 2003, Checkley & Barth 2009). As a result, California sea lions experience fluctuations in the availability and distribution of prey resources, particularly during El Niño events, when sea surface temperatures increase and primary productivity is reduced (Koslow et al. 2014). California sea lions typically switch their diet to compensate for these changes in prey availability (DeLong et al. 1991, Weise & Harvey 2008, Orr et al. 2011, Melin et al. 2012), but these diet fluctuations can affect energy expenditure and reproductive success (Ono et al. 1987, Costa et al. 1991, Melin et al. 2012, McClatchie et al. 2016). Despite the considerable success of the population in the last 40+ yr, there has been a decrease in pup weights in recent years and an increase in the number of stranded, emaciated young-of-the-year sea lions along the California coast (Leising et al. 2015, McClatchie et al. 2016). These trends generally coincide with reductions in the availability of energy-rich prey in southern California, indicating that food limitation may be precipitating an imbalance between energy requirements and energy acquisition of lactating females (McClatchie et al. 2016).

The overall goal of this study was to quantify the energy requirements of adult female California sea lions and determine the effect of prey availability on energy budgets and pup growth rates. We developed a bioenergetic model to quantify the annual energy and prey requirements of adult females and the specific costs associated with maintenance demands, lactation, and gestation during 3 discrete time periods (early and late lactation, post-weaning). We calculated how changes in activity costs (metabolic rates) or time–activity budgets (time spent at sea) — the 2 main behavioral responses of female otariids to changes in prey availability (Costa 2007) — affected annual energy demands and prey requirements. Because California sea lions are income breeders, we developed a separate model using the energetic and behavioral parameters from the bioenergetic model to predict how changes in prey availability affect pup growth rates. Collectively, these results contribute to a better understanding of the energy demands of income-breeding pinnipeds during an energetically expensive time period (lactation) and the role of prey availability in driving the recent decreases in reproductive success of California sea lions.

METHODS

Bioenergetic model

We estimated the energy requirements for adult female California sea lions across a single year from

the start of June to the end of May, which encompasses 1 reproductive cycle (Fig. 1). California sea lions typically give birth to a single pup in late May or June, making repeated foraging trips to and from the rookery for the entirety of the 10 to 11 mo lactation period (Harris 2016). Mating occurs 2 to 3 wk after birth (Peterson & Bartholomew 1967, Francis & Heath 1991), but active gestation does not begin until approximately November because of delayed implantation (Greig et al. 2007). Thus, during a portion of lactation, females may also be actively gestating a fetus. During the first several months of lactation (early lactation, defined here as the first 3 mo), females generally spend more time ashore and less time at sea than in late lactation (the remaining 7 to 8 mo of lactation) or the post-weaning
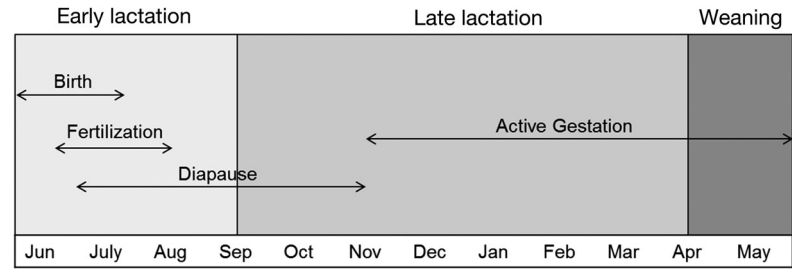

Fig. 1. Annual reproductive cycle of an adult female California sea lion showing the approximate timing of life history events used in the bioenergetic model

period. Because of these differences in costs and time–activity budgets, we estimated energy budgets separately for each of the 3 time periods (early lactation, late lactation, and post-weaning) as well as for lactating and non-lactating females. Specific values for each of the costs described in the following paragraphs are listed in Table 1.

Table 1. Description and values of parameters used to estimate the net and gross energy requirements of adult female California sea lions. Values are shown as mean ± SD where available. The minimum and maximum values used to truncate the distribution of each parameter in the bioenergetic model are also shown where applicable. FMR: field metabolic rate; FMR_{sea}: field metabolic rate at sea; FMR_{land}: field metabolic rate ashore; NA: not applicable

Variable	Value	Min.–max.	Data source
FMR			
Daily FMR_{sea} (MJ d^{-1} $M^{-0.75}$)	1.35 ± 0.24	0.86–1.6	McHuron (2016)
Daily FMR_{land} (MJ d^{-1} $M^{-0.75}$)	0.60 ± 0.01	0.58–0.62[a]	Williams et al. (2007)
Female mass (M) (kg)	80 ± 10	60–110	Laake et al. (2016)
Proportion of time at sea (P_{sea})			Unpubl. data[b]
Early lactation	0.53 ± 0.08	0.42–0.64	
Late lactation	0.75 ± 0.05	0.62–0.84	
Post-weaning	0.71 ± 0.03	0.67–0.77	
Duration (D) (d)			Melin et al. (2000), Harris (2016)
Early lactation	92	NA	
Late lactation	228 ± 4	208–273	
Post-weaning	273 – D of late lactation	NA	
Lactation			
Daily milk intake (MI) (MJ d^{-1} $M^{-0.83}$)			Oftedal et al. (1987a,b)
Early lactation	1.38 ± 0.16	1.06–1.70[a]	
Late lactation	1.81 ± 0.20	1.41–2.21[a]	
Mass at birth (M_{birth}) (kg)	8.0 ± 0.9	07–10	Ono et al. (1987)
Mass at end (M_{end}) (kg)	M_{birth} + (0.085D)	NA	Oftedal et al. (1987b)
Duration	Same as above	NA	
Gestation			
Fetus composition (%)			Oftedal et al. (1987b)
Fat	4.80	NA	
Protein	19.30	NA	
Energy content (MJ kg^{-1})			Costa et al. (1987b)
Fat	39.33	NA	
Protein	23.4	NA	
Other			
Proportion metabolizable energy ($P_{metabolized}$)	0.87 ± 0.06	0.76–0.95	Costa (1986)

[a]Values estimated from mean and SD; [b]From S. Melin (early lactation and post-weaning) and E. McHuron (late lactation)

The net energy (E_{net}) required per year by an adult female can be viewed as the sum of 3 main energy (E) costs: (1) field metabolic rate (E_{FMR}), which includes energy expended for digestion, maintenance, thermoregulation, and locomotion; (2) lactation ($E_{lactation}$); and (3) gestation (E_{fetus}) such that:

$$E_{net} = E_{FMR} + E_{lactation} + E_{fetus} \qquad (1)$$

The gross energy needed to meet these costs is greater because not all of the ingested energy is digestible, and some of the energy is lost as urine and feces. If $P_{metabolized}$ represents the proportion of energy available for metabolism, the gross energy (E_{gross}) needs are:

$$E_{gross} = \frac{E_{net}}{P_{metabolized}} \qquad (2)$$

Because California sea lions display asymptotic growth in both mass and length (Laake et al. 2016), we assumed that the energy associated with yearly growth was negligible.

The costs associated with E_{FMR} can be broken down into energy expenditure while at sea and ashore, such that for each time period of length D (d):

$$E_{FMR} = (FMR_{sea} M^{0.75})(P_{sea}D) \\ + (FMR_{land} M^{0.75})((1-P_{sea})D) \qquad (3)$$

where FMR_{sea} and FMR_{land} are the daily mass-specific metabolic rates (MJ d^{-1} $M^{-0.75}$) while at sea and ashore, respectively; M is the mass of the female; and P_{sea} is the proportion of time spent at sea during that time period. The annual energy needs associated with FMR for lactating and non-lactating females were calculated by summing estimates of E_{FMR} across the 3 time periods. Estimates of FMR_{sea} were obtained from measurements of carbon dioxide production from free-ranging adult female California sea lions (McHuron 2016). Estimates of FMR_{land} were obtained from oxygen consumption measurements of the standard metabolic rate (SMR) from reproductive and non-reproductive adult female California sea lions held in captivity (Williams et al. 2007). We used the same FMR_{land} for both lactating and non-lactating females because Williams et al. (2007) found no significant differences in SMRs between reproductive and non-reproductive animals. We assumed that the rate of energy expenditure at sea did not change throughout the year or between reproductive stages. Data on the proportion of time spent at sea and ashore for each time period were obtained from tracking data from adult females between 2005 and 2013 (Table 1). We assumed that females without a pup would behave in similar ways to females during the post-weaning period regarding the amount of time spent at sea and ashore.

The cost of lactation (L) was calculated by estimating the total milk intake by a pup for each time period lasting D days by:

$$L = \left[MI\left(\frac{M_{begin} + M_{end}}{2}\right)^{0.83} \right] D \qquad (4)$$

where MI is the daily mass-specific milk intake rate (MJ day^{-1} $M^{-0.83}$), and M_{begin} and M_{end} are the mass of the pup at the beginning and end, respectively, of either early or late lactation. We used the value from Oftedal et al. (1987b) for milk intake rates (g milk d^{-1}) during early lactation for both time periods because of a lack of data on milk intake rates during late lactation for this species. In support of this assumption, Donohue et al. (2002) found that mass-specific milk intake rates (ml kg^{-1} d^{-1}) of northern fur seal pups *Callorhinus ursinus* did not change throughout lactation. The mean milk intake rate was converted to mass-specific energy estimates based on the energy content of milk during early (3.46 kcal g^{-1}) and late lactation (4.54 kcal g^{-1}; Oftedal et al. 1987a). The mass of the pup at the end of early and late lactation was calculated assuming an initial average birth mass of 8.0 ± 0.9 kg and an average growth rate of 0.085 kg d^{-1} (Oftedal et al. 1987b, Ono et al. 1987).

The cost of a fetus (E_{fetus}) was calculated by summing the costs associated with the heat increment of gestation (HIG), the energy content of a newborn pup, and the growth of the placenta and uterus. We calculated the HIG as:

$$HIG = 4400 M_{birth}^{1.2} \qquad (5)$$

and converted this value from kilocalories to megajoules (Brody 1945). The energy content of a newborn pup was calculated based on the chemical composition of the fetus (Oftedal et al. 1987b) and the energy content of fat and protein (Costa 1987). As in Winship et al. (2002), we assumed that fetal tissue represented 80% of the energy costs associated with the gravid uterus, with the remaining 20% associated with uterine and placental tissue. Because implantation does not occur until November (Greig et al. 2007), the cost of a fetus was only assessed for late lactation and the post-weaning period. Fetal growth in marine mammals is not linear across active gestation (Trites 1991, Yunker et al. 2005); however, the costs of gestation are roughly equal between late lactation and the post-weaning period because of differences in the length of each time period. As a result, the fetus gains approximately the same amount of mass during the 7 to 8 mo of late lactation

as during the 1 to 2 mo of the post-weaning period (Trites 1991). We thus split the cost of the fetus equally between the 2 time periods. The HIG was included as a separate cost because although FMR data were collected from presumably pregnant females, these measurements occurred very early on in active gestation.

To incorporate variability into our estimates and allow some input parameters to be dynamic, we simulated a population of 40000 adult females that varied in mass, pup mass at birth, length of late lactation and the post-weaning period, metabolic rates, energy delivery to the pup, proportion of time at sea, and the proportion of ingested energy available for metabolism. We assigned values to each female by randomly sampling from a truncated normal distribution with a mean and standard deviation for each of these variables, except the duration of the post-weaning period. Parameter values were truncated based on the minimum and maximum values in Table 1. The duration of early lactation was fixed at 92 d, and the duration of the post-weaning period was the number of days between the end of lactation and May 31. We examined how changes in energy requirements were affected by incremental changes in at-sea FMR and the proportion of time spent at sea by re-running the model assuming each parameter was ±10 to 30% of the original value used in the model. Each parameter was varied while holding all other parameter values constant at their mean. Although sensitivity analyses are typically conducted because of uncertainty in parameter estimates, the values we used for at-sea FMR and the proportion of time at sea were derived from data collected from free-ranging adult female California sea lions. Thus, we discuss the result of these analyses in the context of changes in prey availability and not model uncertainty.

Prey requirements

We combined gross energy requirements from the bioenergetic model with data on the average energy content of prey to estimate the amount of prey consumed on a daily and annual basis. Adult female California sea lions consume a diverse array of species that fluctuates seasonally and annually (Orr et al. 2011), but their diet is dominated by northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific whiting or hake *Merluccius productus*, market squid *Doryteuthis opalescens*, and rockfish *Sebastes* spp. Available diet data for adult female California sea lions are limited to frequency of occurrence from scat analysis, which can result in an unre-

liable estimate of the biomass of each prey species in an individual's diet (Sweeney & Harvey 2011). We therefore calculated prey consumption based on the energy content of rockfish (4.2 kJ g^{-1}) and Pacific sardine (7.3 kJ g^{-1}; Glaser 2010), which are, respectively, the lowest- and highest-energy prey items frequently consumed by sea lions. Resulting consumption estimates therefore represent a minimum and maximum estimate of the amount of prey consumed, with the understanding that actual prey consumption likely falls between those 2 values.

Effects of prey availability on pup growth

We assumed that pup growth rates could be predicted based on the length of the maternal cycle, which consists of a foraging trip to sea and energy delivery to the pup ashore. Because California sea lions do not appear to alter the amount of time spent ashore in response to trip duration (McHuron et al. 2016), changes in the length of the maternal cycle are primarily driven by trip duration. We assumed that a female did not terminate a foraging trip until she acquired enough energy to meet a predetermined energetic target that was based on her own energy needs and those of her pup for the length of the maternal cycle. Thus, the average trip consists of a number of unsuccessful days ($\bar{k}$) and a number of successful days ($\bar{s}$) of foraging. The length of the maternal cycle is then calculated by adding the total trip duration (number of foraging days + average travel time ($2\bar{\tau}$) to the average time ashore, which was held constant regardless of trip duration. We estimated $\bar{k}$, $\bar{s}$, and $\bar{\tau}$ using existing tracking and diving data.

We used a negative binomial (NB) distribution (Mangel 2006) to calculate the probability that a female would need *x* foraging days to reach her energetic target. The average probability of finding food $\bar{\lambda}$ was calculated using $\bar{k}$ and $\bar{s}$ (see Supplement at www.int-res.com/articles/suppl/m567p235_supp.pdf). This allowed us to predict the distribution of the duration of foraging trips under different scenarios of prey availability by altering the probability of finding food and calculating the resulting average pup growth rate based on the length of the maternal cycle. The average energetic target was calculated based on the energy requirements of an 80 kg adult female and her 15 kg pup maintained at the average growth rate (0.085 kg d^{-1}) for the average length of the maternal cycle (female and pup mass values were arbitrarily chosen for illustrative purposes). We
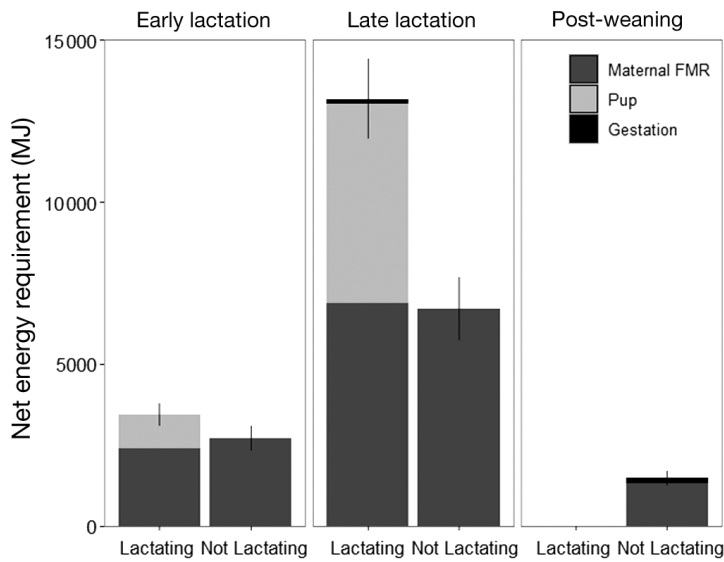
Fig. 2. Mean net energy requirements (MJ) ± SD for an adult female California sea lion at different reproductive stages (early lactation, late lactation, and post-weaning). Values are separated by the type of cost and presented separately for lactating and non-lactating females where appropriate. For simplicity, we present the cost of gestation during late lactation for lactating females only, but it is possible to be non-lactating and pregnant during this time period. FMR: field metabolic rate

reduced $\bar{\lambda}$ by 10, 20, or 30% to simulate changes in prey availability relative to average conditions. We assumed that female sea lions either had no behavioral ability to compensate for these reductions, resulting in an increase in trip duration, or could increase their effort (at-sea FMR) by up to 50% in an effort not to alter trip durations. We calculated the resulting probability distributions of trip duration and pup growth rates for each combination of reduced prey availability and compensation scenario. See the Supplement for a complete description of the model and its assumptions and for all values used for average conditions.

RESULTS

Net energy requirements (mean ± SD) for adult female California sea lions ranged from 10 700 ± 1600 to 18 100 ± 1700 MJ yr^{-1}, depending on reproductive status. The differences in energy budgets with reproductive status were mainly due to the costs associated with lactation, which comprised 30 and 47% of a female's energy costs during early and late lactation, respectively (Fig. 2). Gestation was relatively inexpensive, comprising ≤10% of the total energy budget for both late lactation and the post-weaning

period (Fig. 2). Gross energy requirements (mean ± SD) ranged from 12 500 ± 1900 MJ yr^{-1} for a non-pregnant female with no pup to 21 000 ± 2200 MJ yr^{-1} for a pregnant, lactating female. Based on these estimates, a non-pregnant female with no pup is predicted to consume 1700 to 3000 kg prey yr^{-1} compared with 2900 to 5000 kg yr^{-1} for a pregnant, lactating female. Assuming a non-reproductively active female spent 71% of her time at sea, she would need to consume an average of 48 ± 7 MJ d^{-1} or 6.6 to 11.4 kg prey d^{-1} while at sea. In contrast, a reproductively active female that spent 69% of her time at sea would need to consume an average of 83 ± 9 MJ d^{-1} or 11.4 to 19.8 kg prey d^{-1} while at sea. Because of differences in the cost and the proportion of time spent at sea among time periods, these daily estimates for a pregnant, lactating female were slightly lower during early lactation (83 ± 10 MJ d^{-1}), slightly higher during late lactation (90 ± 10 MJ d^{-1}), and markedly lower during the post-weaning period (54 ± 9 MJ d^{-1}).

Behavioral changes resulted in a 3 to 25% change in energy requirements depending on the type of behavior, magnitude of change, time period, and lactation status (Table 2). Changes in at-sea FMR had a greater impact on energy requirements than changes in the proportion of time spent at sea, altering annual energy budgets by almost twice as much. The effect of changes in either parameter had a greater relative impact on the energy requirements of non-lactating compared with lactating females. For example, a 10% increase in at-sea FMR resulted in a 9% increase in gross annual energy requirements for a non-lactating female, whereas a lactating female only experienced a 5% increase in costs. The timing of changes (i.e. early or late lactation) in either parameter had a slight effect on the magnitude of the percentage change, but this was only apparent for lactating females.

Based on the output from the NB model, there was a rapid decrease in mean pup growth rate when female sea lions could only increase trip duration to account for reductions in prey availability, with the mean pup growth rate falling below zero when relative prey availability was <70% (Fig. 3). Under the alternate scenario of increased effort, female sea lions could increase at-sea FMR and maintain constant milk delivery to the pup until prey availability was <70% of average conditions (Fig. 3). This assumes that they were able to offset or absorb the

Table 2. Effect of changes in the mean value of at-sea field metabolic rate (FMR_{sea}) and percentage of time spent at sea (% sea) on net (MJ period^{-1}) and total gross (MJ yr^{-1}) energy requirements of adult female California sea lions. Changes were calculated by varying the mean of each parameter while holding all other parameter means constant. Values are separated by time period (early lactation [Early], late lactation [Late], and post-weaning [Post]) and lactation status (not lactating/lactating) within each time period. NA: not applicable

	Percentage change from model parameters (%)						
	−30	−20	−10	0	+10	+20	+30
Early net							
FMR_{sea}	2000/2900	2200/3100	2500/3300	2700/3400	2900/3600	3200/3800	3400/3900
% sea	2300/3100	2500/3200	2600/3300		2800/3500	3000/3600	3100/3700
Late net							
FMR_{sea}	5000/11400	5600/12000	6100/12600	6700/13200	7300/13800	7800/14400	8400/15000
% sea	5800/12200	6100/12500	6400/12900		7000/13500	7300/13800	7600/NA
Post net							
FMR_{sea}	1100/NA	1300/NA	1400/NA	1500/NA	1600/NA	1700/NA	1800/NA
% sea	1300/NA	1400/NA	1400/NA		1500/NA	1600/NA	1700/NA
Total gross							
FMR_{sea}	9300/17900	10400/19000	11400/20000	12500/21000	13500/22000	14600/23000	15600/24000
% sea	10800/19300	11300/20000	11900/20500		13000/21500	13602/22100	14100/NA

additional energy costs associated with a higher at-sea FMR because we did not initially impose any additional cost for this behavioral change. This assumption is unrealistic when individuals do not have considerable energy stores, especially because the results from the bioenergetic model indicated that changes in at-sea FMR were particularly influential

Fig. 3. Predictions of mean pup growth rate (±SD) of California sea lions as a function of prey availability relative to average conditions assuming that females use 1 of 4 scenarios to compensate for these changes. Reductions in relative prey availability were simulated by reducing the probability of finding prey on any given foraging day. Scenarios are separated based on whether a female increases effort (modelled as an increase in at-sea field metabolic rate) or trip duration; within the effort scenario, the costs associated with increased metabolism are ignored or offset through increasing trip duration or decreasing milk energy delivery to the pup

on energy requirements. We therefore modelled 2 additional scenarios to account for increased energy requirements associated with a higher at-sea FMR. These additional scenarios assumed that the added costs associated with increased effort were met through (1) an increase in trip duration required to acquire these extra costs (energy difference/average daily energy gain), or (2) a reduction in milk energy delivery commensurate with the percentage increase in energy costs (i.e. if a female's costs increased by 5%, then she reduced milk energy delivery by 5%). Under the scenario where females increased trip duration to account for their increased effort, pup growth rates decreased slowly until prey availability was <70% relative to average conditions. After this point, pup growth rates declined rapidly yet still remained positive for all values of relative prey availability (Fig. 3). In contrast, reductions in milk energy delivery to the pup resulted in a rapid decrease in pup growth rate when relative prey availability was <90% and were similar to the scenario where females just increased trip duration to account for reductions in prey availability (Fig. 3).
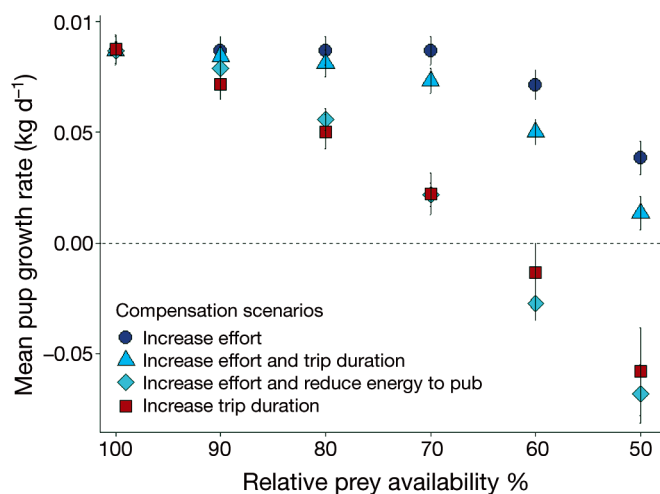
DISCUSSION

Energy requirements

Our results indicate that it is energetically expensive to be a female otariid, particularly when compared with the other speciose lineage of pinnipeds,

phocid seals. For example, the mean annual gross energy demand of an adult female California sea lion was 3 to 4 times higher on a mass-specific basis (MJ yr^{-1} $kg^{-0.75}$) than values reported for adult female northern elephant seals *Mirounga angustirostris* (17 500 MJ yr^{-1}; Maresh et al. 2015, J. L. Maresh unpubl. data), grey seals *Halichoerus grypus* (14 000 MJ yr^{-1}; Mohn & Bowen 1996), and harbor seals *Phoca vitulina* (6300 MJ yr^{-1}; Olesiuk 1993). Although many studies show that existence costs of phocids are lower than those of otariids (reviewed in Maresh 2014), the increased cost of being a female otariid also appears to be due to differences in the cost of lactation. For example, the total milk energy consumption of 7 phocid species ranged from 1100 to 5300 MJ (Costa et al. 1986, Tedman & Green 1987, Lydersen & Kovacs 1999); when adjusted for mass at weaning (Worthy & Lavigne 1987, Schulz & Bowen 2004), the costs of a phocid pup ranged from 60 to 250 MJ $kg^{-0.75}$. In comparison, the total mean milk energy consumption of a California sea lion pup was 7200 MJ or 490 MJ $kg^{-0.75}$, which translates to an average per kilogram cost of 4.5 times that of a phocid pup. These increased costs of lactation are likely due to a combination of longer lactation durations and pup growth strategies, as otariid pups receive more protein from their mothers and allocate more energy toward existence costs than phocids (Costa 1991).

Reproductive costs comprised a significant proportion of a female's energy budget, but the majority of these costs were associated with lactation and not gestation. These findings are consistent with general patterns of reproductive energy allocation for mammals (Gittleman & Thompson 1988) and for marine mammals specifically (Kastelein et al. 1993, 2000, 2003, Winship et al. 2002, Williams et al. 2007, Rechsteiner et al. 2013). For California sea lions, the costs associated with nursing a pup were much greater during late than early lactation, comprising almost half of a female's total energy demands during late lactation. Lactating California sea lions held in captivity exhibited a similar trend, with maximum energy intake during peak lactation that was about 2 times higher than energy intake during the first 2 mo of lactation (Williams et al. 2007). The higher cost of a pup during late lactation is due to increases in pup mass and changes in the milk fat composition with pup age, both of which increase the total energy delivered to the pup. This trend has also been found for Steller sea lions *Eumetopias jubatus* (Winship et al. 2002) and likely holds for other otariids, as increases in milk energy consumption with pup age

have been documented for several fur seal species (Arnould et al. 1996, Arnould & Hindell 2002, Donohue et al. 2002). The differences in the percentage of energy needed for lactation during the 2 time periods indicates that the timing of reductions in prey availability may be important, such that females are likely able to adjust to reduced prey availability and maintain sufficient milk energy delivery more readily during early compared with late lactation.

Behavioral changes that affect at-sea FMR or the proportion of time spent at sea have implications for energy requirements of females and energy delivery to pups. These behavioral changes are often associated with reductions in prey availability (Costa 2007), although they may also vary as a result of individual variation in foraging behavior or prey type (Costa & Gentry 1986, Costa & Gales 2000, McHuron et al. 2016). Regardless of the cause, our results indicate that changes in both of these variables affect the energy demands of a female but that changes in effort (at-sea FMR) have a greater impact on energy budgets than changes in the proportion of time spent at sea. This finding is consistent with Winship et al. (2002) and Rechsteiner et al. (2013), who found that estimates of energy requirements were most sensitive to changes in parameters associated with metabolism. Similarly, Noren et al. (2012) found that a 5% increase in the proportion of time at sea only resulted in a 3% increase in the annual energy demands of lactating walruses *Odobenus rosmarus*. In our model, a 30% decrease in the proportion of time spent at sea resulted in a 14% change in annual energy requirements, which is substantial but unlikely to occur in nature. In fact, we did not model a 30% increase because it would have resulted in a female spending >97% of her time at sea. In contrast, measurements of at-sea FMR from free-ranging otariids indicate that a 30% change in this parameter is reasonable (Costa & Gentry 1986, Costa et al. 1991, McHuron 2016), although it is unknown how variable at-sea FMR is throughout the year.

The potentially large impact of these parameters, mainly at-sea FMR, on the output of our bioenergetic model indicates that the mean energy requirements of female California sea lions depend on the distribution and abundance of prey. These factors should therefore be taken into consideration when applying the values from our bioenergetic model to understand the relationships between energy requirements, population dynamics, and prey availability. The at-sea FMR data we used to parameterize the model were collected during late lactation in 2014, when pup growth rates were much lower than the

average (<0.02 kg d^{-1}; Leising et al. 2015) and strandings of emaciated young of the year were high, suggesting that females were struggling to acquire sufficient energy to meet their needs and those of their pups. Thus, the results of our bioenergetic model using the original parameter values are most representative of the energy that would be required by an adult female to meet her needs and sustain a pup at the average growth rate (if applicable) during a period of reduced prey availability. Energy requirements during a year of adequate prey availability are more likely represented by the scenarios where at-sea FMRs are 20 to 30% lower than those used in our analysis (Table 2).

Model uncertainty

Bioenergetic models are a useful tool for quantifying energy demands, but it is important to recognize that the resulting estimates are affected by the values assigned to input parameters. It is difficult to empirically measure many of these input parameters for free-ranging marine mammals, but we were able to parameterize our bioenergetic model using data collected from free-ranging sea lions for most input parameters and used a distribution of values for some parameters to account for the fact that many of these parameters are dynamic. There were several factors that we did not account for or assumptions that were made that could have influenced our results, but these likely would have had minimal impact on our estimates of annual energy requirements. First, we assumed that growth of adult animals was negligible because sea lions exhibit asymptotic growth and length (Laake et al. 2016) and do not deposit large fat stores to support reproduction. Growth may be an important factor affecting energy requirements for capital or mixed capital breeders (Noren et al. 2014), but it does not appear to comprise a large proportion of the energy budgets of income breeders (Winship et al. 2002). We also assumed that at-sea FMR did not differ among time periods or with reproductive status, and there is no clear indication from available data to suggest otherwise (Costa & Gentry 1986, Costa et al. 1991, McHuron 2016). We did not explicitly include the costs associated with molting for adult females or pups in our model, but molting does not appear to affect metabolic rates of reproductive females (Williams et al. 2007) or milk energy delivery to pups (Donohue et al. 2002). Non-reproductive adult females had resting metabolic rates that were 1.3 times greater during molt (Williams et al. 2007),

which may indicate that energy requirements for non-reproductive females during the 3 mo of molt are slightly higher than predicted.

Prey requirements

Daily at-sea estimates of prey requirements indicate that during years of reduced prey availability, an 80 kg pregnant, lactating female California sea lion would need to consume an average of 14 to 25% of her body mass per day at sea. These consumption estimates decreased to 12 to 21% of body mass under a 30% reduction in metabolic rate, which is likely more representative of consumption during favorable conditions for sea lions. Prey consumption estimates of free-ranging female sea lions during late lactation using measurements of water influx indicated they consumed between 9.5 and 23% of their body mass per day (McHuron 2016), providing validation that our estimates of food consumption are feasible. Food intake data collected from captive female sea lions indicated that the average daily food consumption was considerably lower at only 5 to 6% of body mass (Kastelein et al. 2000), but estimates of maximum energy (78 MJ d^{-1}; Williams et al. 2007) and prey intake (16 kg d^{-1}; Kastelein et al. 2000) were within the range of our estimates for free-ranging sea lions. Captive animals typically consume less prey than that estimated for free-ranging animals (Rechsteiner et al. 2013), which is not particularly surprising given they are fed daily and likely have reduced locomotion and foraging costs. Estimates of maximum stomach capacity for pinnipeds indicate values that range from 7 to 16% of body mass, depending on age and feeding frequency (Kastelein et al. 1990, Trumble et al. 2003), with daily estimates of food consumption as high as 26% of body mass (Rosen & Trites 2004). This ability to consume large quantities of prey in 1 feeding event coupled with digestive passage rates of <5 h (Helm 1984) likely enable free-ranging marine mammals to acquire enough prey to meet energy requirements, even when foraging is interspersed with fasting, as is the case for lactating otariids.

It is important to recognize that estimated prey requirements from our bioenergetic model may not always represent prey consumption, particularly during periods when sea lions increase effort to compensate for changes in the abundance and distribution of prey. First, the relationship between FMR and prey intake is likely asymptotic, such that at some point, further increases in the rate of energy expenditure do

not result in any additional energy gain. Second, during periods of reduced prey availability, sea lions may have difficulty finding prey despite increased effort, and even when they find prey, their ability to meet energy demands may be hindered by the physical inability to consume enough prey. Under these scenarios, a female's inability to balance her energy budget likely results in reduced energy delivery to the pup, which is consistent with the decreased pup growth rates and increased pup mortality observed for otariids during periods of reduced prey availability, such as El Niño events (Trillmich & Limberger 1985, Soto et al. 2004, Leising et al. 2015). The physical limitations of stomach capacity and processing time are likely to be an issue when reductions in prey availability also correspond with reductions in energy content of available prey. Recent oceanographic changes in the CCE have favored an increase in market squid and rockfish in southern and central California (McClatchie et al. 2016); these species have a relatively low energy content compared with northern anchovy and sardine (Costa et al. 1991, Glaser 2010). Thus, female California sea lions likely have a limited ability to offset increased costs by switching to energy-rich prey, meaning that prey consumption required to sustain a pup at the average growth rate during periods of reduced prey availability are likely closer to our maximum estimates. Although the available data suggest it may be feasible for some females to physically consume >20% of their body mass per day, further increases in at-sea FMR would likely make it physically impossible to meet energy requirements when the available prey is of low energy content.

Effects of prey availability on pup growth

The effect of reductions in prey availability were not linearly related to changes in pup growth rates and also varied depending on the mechanism by which females compensated for reductions in available prey. When faced with relatively small changes in prey availability, female otariids should largely be able to maintain average pup growth rates irrespective of their compensatory mechanism. This was not the case when faced with greater prey reductions (<90%), where it was more detrimental to the pup if a female just increased her trip duration or increased her effort but compensated for the added cost by reducing milk energy delivery. The similar trends in pup growth rates for females using these 2 scenarios indicate that increasing effort is not always a better

strategy, as the way that females compensate for these additional costs strongly impacts pup growth rates. Increasing effort is clearly the best strategy when females are able to offset the additional metabolic costs through body reserves or by switching to more energy-rich prey, which is consistent with empirical evidence from northern fur seals (Costa & Gentry 1986, Costa 2007). For California sea lions, prey switching is unlikely to be an option as discussed in the previous paragraph; therefore, increases in effort may co-occur with decreases in female body mass and/or increases in trip duration, depending on how quickly a female finds prey while at sea and her intrinsic qualities (e.g. foraging efficiency, metabolic rate). Morphometric and behavioral data from 2014 support this prediction; most satellite-tracked females lost varying amounts of mass across a foraging trip to sea, but only some of these females had trip durations that were longer than the average (McHuron 2016). There are not enough empirical data on prey biomass in the southern and central CCE to accurately validate the quantitative predictions from our model, but the range of growth rates from the scenario most likely used by California sea lions is similar to mean daily growth rates of California sea lion pups between 1997 and 2014 (Leising et al. 2015). These empirical data indicate that even during severe El Niño events, the average pup growth rate approaches but never falls below zero, a trend that is also reflected in our model.

CONCLUSIONS

The results of our study provide quantitative estimates of energy and prey requirements for female California sea lions, which are necessary to better understand the impact of this abundant predator on prey populations, and the relationship between prey availability and recent poor reproductive success of California sea lions. Our results indicate that it is energetically expensive to be a sea lion, in terms of both metabolism and the costs associated with lactation. Metabolic costs likely increase during years of reduced prey availability, which may result in greater energy requirements if a female does not reduce milk energy delivery to her pup. It is therefore important to consider behavioral responses to environmental conditions when applying results from bioenergetic models to understand the relationships between energy requirements, population dynamics, and prey availability, particularly as these strategies have clear energetic and reproductive implications.

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Energy and prey requirements of California sea lions under variable environmental conditions

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Description of Negative Binomial model used to predict the effects of reduced prey availability on pup growth rates

To examine the effects of changes in prey availability on pup growth rates, we developed a relatively simple model that accounted for the two behavioral strategies female otariids use to cope with environmental change (Costa 2008). To do so, we assumed that pup growth rates could be predicted based on the length of the maternal cycle, which consists of a foraging trip to sea and energy delivery to the pup onshore. Because California sea lions do not appear to alter the amount of time spent ashore in response to trip duration (McHuron et al. 2016), changes in the length of the maternal cycle are primarily driven by trip duration. Thus, we used the Negative Binomial Distribution (NB) to predict the average duration of a foraging trip under varying prey availability by altering the probability of finding food (Mangel 2006). Parameter values used in the model described below can be found in Table S1.

A foraging trip can be decomposed into its two main components, travel time (τ) and time spent finding and acquiring prey. We assumed that a female did not terminate a foraging trip until she acquired enough energy to meet a predetermined energetic target that was based on her own energy needs and those of her pup. This assumption was based on the finding by Costa et al. (1989) that female Antarctic fur seals (*Arctocephalus gazella*) stayed at sea until they achieved a substantial proportional change in body mass, even though extending the duration of the trip resulted in reduced growth rate of their pup. The average energetic target for a female of mass M whose pup needs are N_{pup} (kJ day^{-1}) and who spends the average number of days at sea and on land are

$$\overline{N} = \frac{\left(\overline{d}_{sea} FMR_{sea} M^{0.75} + \overline{d}_{land} FMR_{land} M^{0.75} + (\overline{d}_{sea} + \overline{d}_{land}) N_{pup} \right)}{P_{metabolized}} \quad (1)$$

The average trip duration at sea can be further decomposed into

$$\overline{d}_{sea} = \overline{s} + \overline{k} + 2\overline{\tau} \quad (2)$$

where $\overline{s}$ is the average number of days of successful foraging, $\overline{k}$ is the average number of days of unsuccessful foraging, and $\overline{\tau}$ is the average travel time to a foraging ground. The average number of successful days of foraging ($\overline{s}$) is a function of the average daily energy value of food ($\overline{Y}$) and the average energetic target, such that

$$\overline{s} = \frac{\overline{N}}{\overline{Y}} \quad (3)$$

We parameterized $\overline{N}$ (based on an 80 kg female with a 15 kg pup), $\overline{s}$, $\overline{\tau}$, and $\overline{Y}$ using the behavior and energetics data described for the bioenergetic model. Specifically, we estimated (1) $\overline{s}$ based on the proportion of time at sea spent diving combined with estimates of the maximum consumption rate

based on the kg of prey needed to meet $\overline{N}$, (2) $\overline{\tau}$ based on existing tracking data, and (3) $\overline{Y}$ by rearranging Eqn 8. The values of female and pup mass were arbitrarily chosen for illustrative purposes.

The appropriate probability distribution for the number of unsuccessful days of foraging (k) is the NB distribution (Mangel 2006), which describes the probability of waiting for a fixed number of successes. In particular, we set

$$p(k \mid s, \lambda) = \Pr\{k \text{ days of unsuccessful foraging before the } s^{th} \text{ day of successful}$$
$$\text{foraging given that the probability of success on a day is } \lambda\} \tag{4}$$

The NB distribution for k is

$$p(k \mid s, \lambda) = \binom{s+k-1}{k} \lambda^s (1-\lambda)^k = \frac{(s+k-1)!}{k!(s-1)!} \lambda^s (1-\lambda)^k \tag{5}$$

The terms in Eqn 10 can be evaluated iteratively without having to compute the factorials by noting that $p(0 \mid s, \lambda) = \lambda^s$ and for $k \geq 0$

$$p(k+1 \mid s, \lambda) = \binom{k+s}{k+1}(1-\lambda) p(k \mid s, \lambda) \tag{6}$$

In principle, k can be unbounded, but both in nature and computationally it cannot. Thus, we chose a maximum value for k, K_{max}, so that $\sum_{k=0}^{K_{max}} p(k \mid s, \lambda)$ was close to 1 (i.e., 0.999) and then renormalized so that it was equal to 1. When k follows the NB distribution given in Eqn 11, its average value is $\overline{k} = \dfrac{\overline{s}(1-\overline{\lambda})}{\overline{\lambda}}$. Consequently, Eqn 7 can be rewritten as

$$\overline{d}_{sea} = \overline{s} + \frac{\overline{s}(1-\overline{\lambda})}{\overline{\lambda}} + 2\overline{\tau} = \frac{\overline{s}}{\overline{\lambda}} + 2\overline{\tau} \tag{7}$$

and inverted to obtain the average daily probability of foraging success given the average trip length and average number of successful foraging days needed to match energy demands

$$\overline{\lambda} = \frac{\overline{s}}{\overline{d}_{sea} - 2\overline{\tau}} \tag{8}$$

We introduced environmental variability by multiplying $\overline{\lambda}$ by a value between 0 and 1, representing the proportion reduction in food relative to "average" conditions. To account for the ability of females to increase effort to offset this reduction, we assumed that if the current probability of finding food was λ, a female increased her effort by ε so that

$$(1+\varepsilon)\lambda = \overline{\lambda} \tag{9}$$

We assumed that females were only able to increase their effort by 50% ($\varepsilon_{max} = 0.5$) so that there are situations in which environmental conditions are so poor that she will not be able to reach $\overline{\lambda}$ through increases in effort alone. We denoted the probability of finding food given λ and ε as λ_{adj}.

The daily pup growth rate (G) for each value of k was calculated by converting the milk delivery rate in MJ day^{-1} to growth rate in kg day^{-1} using the equations in Oftedal et al. (1987) where

$$\text{Milk delivery rate} = \frac{N_{pup}}{\overline{s} + \overline{k} + 2\overline{\tau} + \overline{d}_{land}} \qquad (10)$$

The expected pup growth rate is then

$$E\{G\} = \sum_{k=0}^{k_{max}} p(k \mid \overline{s}, \lambda_{adj})G(k) \qquad (11)$$

with variance

$$V\{G\} = \sum_{k=0}^{K_{max}} G(k)^2 p(k \mid \overline{s}, \lambda_{Adj}) - E\{G\}^2 \qquad (12)$$

We set a maximum limit on growth rate assuming that females would not allocate all surplus energy to the pup if they were unusually successful. We calculated expected pup growth rates assuming that (1) females increased effort before trip duration, or (2) that females only increased trip duration to account for changes in prey availability. Under this framework, expected growth rates of pups is predicted to increase during better than average foraging conditions because females reach $\overline{N}$ faster than expected; thus the same amount of milk energy is being delivered over a shorter time interval. The opposite occurs under poor environmental conditions when trip durations increase because the same amount of energy (or potentially less) is being delivered over a longer time interval than expected.

Table S1. Description and values of parameters used to model the effects of prey availability on pup growth.

Variable	Description	Value	In-text equation	Data Source
$\overline{N}$	Energy needs per foraging trip	305 MJ	Equation 6	See Table 1
M	Female mass	80 kg		
FMR_{sea}	Mass-specific at-sea field metabolic rate	1.35 MJ day^{-1}		See Table 1
$\overline{d}_{sea}$	Duration of foraging trip	4.5 days	Equation 7	McHuron et al. 2016
$\overline{\tau}$	Travel time to foraging patch	0.5 days		Estimated from empirical data
$\overline{s}$	# successful foraging days	2.5 days		
$\overline{k}$	# unsuccessful foraging days	1 day		
FMR_{land}	Mass specific onshore field metabolic rate	0.60 MJ day^{-1}		See Table 1
$\overline{d}_{land}$	Time on land	1.5 days		McHuron et al. 2016
N_{pup}	Energy needs of pup	114 MJ		
M_{pup}	Pup mass	15 kg		See Table 1
$Milk\ intake$	Mass-specific milk intake rate	1.38 MJ day^{-1}		
$P_{metabolized}$	Metabolizable energy	0.87		See Table 1
$\overline{Y}$	Daily energy gain from successful foraging	122 MJ	Equation 8	Calculated
G_{max}	Maximum allowed pup growth rate	0.11 kg day^{-1}		Leising et al. 2015

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