

Energy Demands for Maintenance, Growth, Pregnancy, and Lactation of Female Pacific Walruses (*Odobenus rosmarus divergens*)

Shawn R. Noren^{1,*}

Mark S. Udevitz²

Chadwick V. Jay²

¹Institute of Marine Science, University of California, Santa Cruz, California 95060; ²US Geological Survey, Alaska Science Center, Anchorage, Alaska 99508

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ABSTRACT

Decreases in sea ice have altered habitat use and activity patterns of female Pacific walruses *Odobenus rosmarus divergens* and could affect their energetic demands, reproductive success, and population status. However, a lack of physiological data from walruses has hampered efforts to develop the bioenergetics models required for fully understanding potential population-level impacts. We analyzed long-term longitudinal data sets of caloric consumption and body mass from nine female Pacific walruses housed at six aquaria using a hierarchical Bayesian approach to quantify relative energetic demands for maintenance, growth, pregnancy, and lactation. By examining body mass fluctuations in response to food consumption, the model explicitly uncoupled caloric demand from caloric intake. This is important for pinnipeds because they sequester and deplete large quantities of lipids throughout their lifetimes. Model outputs were scaled to account for activity levels typical of free-ranging Pacific walruses, averaging 83% of the time active in water and 17% of the time hauled-out resting. Estimated caloric requirements ranged from 26,900 kcal d⁻¹ for 2-yr-olds to 93,370 kcal d⁻¹ for simultaneously lactating and pregnant walruses. Daily consumption requirements were higher for pregnancy than lactation, reflecting energetic demands of increasing body size and lipid deposition during pregnancy. Although walruses forage during lactation, fat sequestered during pregnancy sustained 27% of caloric requirements during the first month of lactation, suggesting that walruses use a mixed strategy of capital and income breeding. Ultimately, this model will aid

in our understanding of the energetic and population consequences of sea ice loss.

Introduction

Pacific walruses (*Odobenus rosmarus divergens*) are specialized shallow benthic foragers (Fay 1982), found primarily in the eastern East Siberian Sea to the western Beaufort Sea and southward into the Bering Sea from eastern Kamchatka to Bristol Bay (Fay 1985). This area includes their foraging grounds along the continental shelves of the Chukchi and Bering Seas (Fay and Burns 1988; Jay et al. 2011). However, their summer habitat has been drastically altered by global climate change. The extent of summer sea ice has decreased substantially (Meier et al. 2007), and this trend is expected to continue (Overland and Wang 2007; Douglas 2010; Wang et al. 2012). Because sea ice serves as a platform for Pacific walruses to rest, nurse, and gain access to offshore foraging grounds (Fay 1982), this environmental change may have population-level consequences. Reductions of summer sea ice over the continental shelf in the Chukchi Sea over the past decade have already resulted in increased use of terrestrial haul-outs by adult female and young walruses (Kavry et al. 2008; Jay et al. 2012). As summer sea ice continues to decline, the number of walruses converging on coastal haul-outs and the time they spend ashore are expected to increase (Jay et al. 2011). The ability of the localized food supply in these coastal regions to support large numbers of walruses over the long term is unknown (Ovsyanikov et al. 2008). Changes in access to prey could impact body condition and ultimately impact population growth rates (Jay et al. 2011).

Predicting the responses of walruses to changing Arctic conditions may be facilitated by an understanding of their energetics and food requirements. Direct measurements of field metabolic rate (Acquarone et al. 2006) and observations of foraging (Born et al. 2003) would provide the best information about the energetic requirements and food consumption rates of wild walruses. However, these measurements are difficult to obtain, in part because walruses are difficult to capture and remotely distributed. Several other approaches have been employed to estimate food consumption in marine mammals, including analyses of stomach contents and scat from wild animals as well as bioenergetic modeling (Winship et al. 2006). Bioenergetic modeling has been used to estimate

*Corresponding author; e-mail: snoren@biology.ucsc.edu.

the energy consumption of a variety of marine mammals (e.g., Lavigne et al. 1982; Øritsland and Markussen 1990; Ryg and Øritsland 1991; Olesiuk 1993; Hammill et al. 1997; Stenson et al. 1997; Winship et al. 2002; Winship and Trites 2003; Noren 2011) and was recently applied to female Pacific walrus (Noren et al. 2012).

Noren et al. (2012) constructed a relatively simple bioenergetics model for female walrus because the lack of physiological data for this species did not support a more complex model, although this model did include the bioenergetic costs of molting and reproduction, which had largely been ignored in bioenergetics models for other pinniped species (e.g., Olesiuk 1993; Mohn and Bowen 1996; Stenson et al. 1997). However, the parameters used to characterize the energetic costs of important life-history stages were not derived from data from walrus. The energetic costs of molting and reproduction were derived from data from California sea lions (*Zalophus californianus*; Williams et al. 2007). Likewise, the parameter used to account for the energetic cost of early growth was derived from data from phocid seals (Worthy 1987). A validation exercise made it evident that, at least in some cases, the model overestimated daily energy requirements, which was likely due to the use of data from alternate species to derive some model parameters (Noren et al. 2012). For example, the estimated caloric demand of a lactating, 830-kg, 12-yr-old female walrus was not sustainable within realistic limits for time to forage (Noren et al. 2012). Another shortcoming of the model in Noren et al. (2012) was that uncertainty in model-based estimates of energy requirements was not quantified because the parameters were derived from previously published values. Noren et al. (2012) recommended directed research on walrus to determine how caloric intake and energy stores (body mass) are linked to meet energy requirements, particularly during critical life-history stages such as lactation, when energetic demand may be partially supported by endogenous energy reserves.

Long-term husbandry records from animals in human care can be a valuable source of information about daily caloric intake rates and concurrent fluctuations in body condition (body mass) in relation to important life-history stages. Data on the food consumption of captive pinnipeds have the advantage of being direct measurements (Winship et al. 2006). Nonetheless, in applying studies of captive animals to wild animals, one must ensure that the effects of age, body size, season, and energy density of the food are considered, and it is likely that the energy requirements of captive and wild animals differ (Winship et al. 2006). Although there are concerns regarding the applicability of captive animal feeding rates to wild populations, Williams et al. (2007) demonstrated that data obtained from captive marine mammals can be used to develop reliable indices of the relative energetic costs of important life-history stages. In this study, we acquired historical husbandry records of caloric intake and body mass of female Pacific walrus housed at aquaria and used them in a Bayesian modeling approach that explicitly decoupled caloric intake from caloric demand to estimate energetic costs of

maintenance and activity, growth, pregnancy, and lactation as functions of age and body size. We characterized basal (maintenance) and activity costs for the captive walrus in terms of facility and seasonal effects and then rescaled these to an activity budget characteristic of free-ranging Pacific walrus to estimate energy requirements for free-ranging walrus. This is the first bioenergetic model for walrus that is based on species-specific data for growth, pregnancy, and lactation and also accounts for uncertainty in the parameter estimates.

Methods

Data Acquisition and Processing

Long-term longitudinal husbandry records were obtained for nine female Pacific walrus (*Odobenus rosmarus divergens*) housed in outdoor enclosures that included access to water and land. Six public display facilities participated in this study, including Aquarium du Quebec (Quebec City, Quebec, Canada), Brookfield Zoo (Brookfield, IL), Indianapolis Zoo (Indianapolis, IN), New York Aquarium (Brooklyn, NY), Point Defiance Zoo and Aquarium (Tacoma, WA), and Six Flags Discovery Kingdom (Vallejo, CA). All walrus were obtained from the wild as young orphaned calves, and the majority of the animals were maintained for a minimum of 15 yr. Husbandry records spanned from 0 to 30 yr of age. We considered data for ages ≥ 2 yr old because data for ages < 2 yr old are being used in a concurrent study on nursing walrus calf bioenergetics. The data set included three full-term pregnancies ($n = 2$ individuals) and one 2-yr lactation interval.

The animals were fed a mixed diet consisting primarily of herring, capelin, clams, and squid. Other prey types were occasionally included, such as mackerel, sardines, smelt, shrimp, and trout. Although these prey items may differ somewhat from what walrus typically eat in the wild (Fay et al. 1977; Fay and Lowry 1981; Fay and Stoker 1982a, 1982b; Sheffield and Grebmeier 2009), the digestive efficiency of walrus does not vary with diet (Fisher et al. 1992). The quantity (kg) of each prey type consumed, which was itemized daily by animal care staff, was multiplied by its specific energy density (kcal kg^{-1}) to estimate the associated calories consumed. The caloric content of each prey item was based on the average value obtained from chemical analyses of randomly chosen food items from shipment lots, as determined by local commercial laboratories hired by each aquarium. In some cases, caloric content information was provided by the fish supplier. The ingested calories from all prey types were summed for each day to provide the value for daily caloric intake for each animal. Daily caloric intake was not manipulated for the purpose of this study; rather, it was determined by the husbandry staff based on the perceived requirements and behaviors of the animals.

Body mass was measured at intervals throughout each animal's lifetime by training the walrus to station on scales housed at each of the facilities. For each interval spanning

successive body mass measurements, we calculated average daily energy consumption per day (kcal d⁻¹; fig. 1A), average mass (kg; fig. 1B), and average daily change in mass. Depending on the facility, intervals between successive body mass measurements were typically 1 d to 1 wk; data from intervals greater than 3 wk were excluded.

Modeling Energy Consumption

We used a hierarchical Bayesian framework to model caloric consumption as a function of metabolic costs and changes in mass. The form of the model was

$$E_c(ij) \sim \text{Normal}(\mu_c(ij), \sigma_c^2), \quad (1)$$

where $E_c(ij)$ is the average energy (kcal) consumed per day by walrus i during interval j , with variance σ_c^2 and mean $\mu_c(ij)$, comprised of a metabolic component ($\mu_m(ij)$) and a storage component ($\mu_s(ij)$), so that $\mu_c(ij) = \mu_m(ij) + \mu_s(ij)$. The metabolic component includes metabolic costs due to basal metabolism, activity, and life-history stage (growth, pregnancy, and lactation) and also includes a random effect to account for repeated measures on individual walruses. Metabolic costs were expressed as multiples of Kleiber, which was assumed to be the resting metabolic rate, equivalent to $70 \times \text{mass}^{0.75}$ kcal d⁻¹ (Kleiber 1975). A correction factor to account for digestive efficiency was also included. Although the heat increment of feeding may also reduce the amount of energy available from the diet, we did not consider this factor because we were comparing data from this study to our previous theoretical model that did not include this factor (Noren et al. 2012). Thus, the metabolic component is given by

$$\mu_m(ij) = \frac{[A(ij) + C_g I_g(ij) + C_p I_p(ij) + C_l I_l(ij) + W_i] K_1 m_{ij}^{K_2}}{D}, \quad (2)$$

where $A(ij)$ represents base per-day metabolic cost (basal plus activity) for walrus i during interval j . C_g represents the additional metabolic costs of growth (growth premium) for animals $< a_g$ years old, with $I_g(ij)$ as an indicator variable having a value of 1 for a walrus $< a_g$ years old. To determine the maximum age that accrues this additional metabolic cost of growth, we considered a series of models with a_g ranging from 2 (i.e., no growth increment) to 14, in increments of 1 yr. The final value for a_g was selected based on a comparison of the deviance information criterion (DIC) for these models (Spiegelhalter et al. 2002). C_p and C_l represent the metabolic costs of pregnancy and lactation, respectively, with corresponding indicator variables for pregnancy ($I_p(ij) = 1$) or lactation ($I_l(ij) = 1$). We did not include a metabolic cost for molt because the molts of the walruses in this study were protracted compared to those of free-ranging walruses and exploratory analyses did not indicate additional costs during the molting interval. $W_i \sim \text{Normal}(0, \sigma_w^2)$ is a random effect that accounts for repeated measurements on walrus i . $K_1 = 70$ and $K_2 = 0.75$ are the

Kleiber constants (Kleiber 1975), m_{ij} is the average mass (kg) for the walrus during the interval, and D is digestive efficiency (0.944; Fisher et al. 1992).

Direct information on activity was not available for the walruses in this study, but preliminary analyses indicated that differences in activity could be accounted for by annual cycles that varied among facilities. Therefore, we represented base metabolic costs as

$$A(ij) = f_i + \alpha \cos\left(\frac{2\pi d_j}{365}\right) + \beta \sin\left(\frac{2\pi d_j}{365}\right), \quad (3)$$

where $A(ij)$ is the per-day cost at facility i during interval j and d_j is the number of days in the year up to the last day of the interval. The value 365 was replaced by 366 in leap years.

The storage component of the model represents energy that is stored in or drawn from body reserves when consumption is greater or less than daily caloric requirements, respectively. We assumed changes in mass provided an index to this storage and use of energy, so the storage component is given by

$$\mu_s(ij) = [C_{\delta+} I_{\delta+}(ij) + C_{\delta-} I_{\delta-}(ij)] \delta_{ij}, \quad (4)$$

where δ_{ij} is the average daily change in mass (kg) for walrus i during interval j and $I_{\delta+}(ij)$ and $I_{\delta-}(ij)$ are indicators for whether δ_{ij} is positive or negative, respectively. Multiplying by $C_{\delta+}$ or $C_{\delta-}$ transforms changes in mass to equivalent amounts of consumed energy. Adding this term allowed us to estimate the parameters in the metabolic component of the model while explicitly accounting for energy used to accumulate mass as a result of a surplus in consumption and energy released as a result of a deficit in consumption. Unlike effects in the metabolic component, effects in the storage component depend only on the magnitude of the change in mass; they do not depend on the total mass of the animal.

Preliminary analyses indicated that δ_{ij} values calculated from a smoothed time series of mass values might provide a better index to storage and use of energy than values based directly on observed mass values. Therefore, we considered a series of models that used δ_{ij} values calculated from unsmoothed values and from a range of less smoothed values of mass, differing in the amount of smoothing as specified by the smoothing degrees of freedom (df; Hastie and Tibshirani 1990). The amount of smoothing did not have a large effect on other model parameters but primarily affected $C_{\delta+}$ and $C_{\delta-}$, with more smoothing resulting in higher estimates. Preliminary analyses also indicated that, for a fixed set of covariates, the DIC values for a series of models based on different amounts of smoothing had a concave pattern with a minimum that could be located by plotting DIC as a function of trial values of df. Therefore, we started by fixing the maximum age for the growth increment at $a_g = 12$ (age at full growth; Fay 1982) and found the smoothing df that gave the minimum DIC for this value of a_g . We then fixed the smoothing df at this

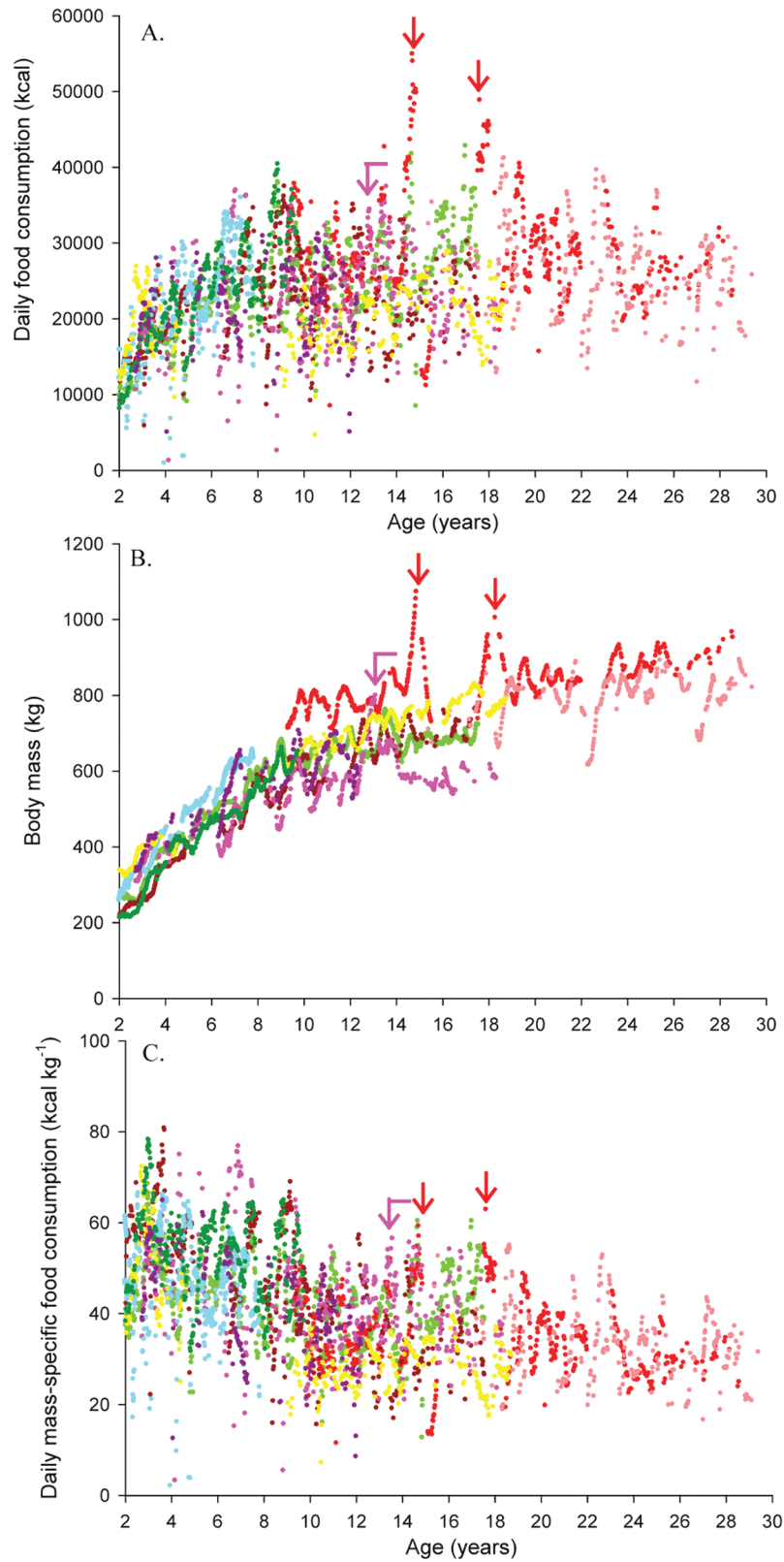


Figure 1. Daily food consumption (A), body mass (B), and mass-specific food consumption (C) in relation to age for nine Pacific walrus (*Odobenus rosmarus divergens*) housed at six aquaria. Values are daily averages for each interval spanning successive body mass measurements as described in “Methods.” Data for each individual are denoted by a unique color. Arrows denote pregnancies (all full term), and the bar denotes a 2-yr lactation interval; colors of the arrows and bar are coordinated with the color of the data for those particular walrus.

value and found the a_g value that minimized DIC for this df. Finally, we confirmed that this smoothing df still gave the minimum DIC value for this value of a_g .

For a fully grown, nonreproductive walrus, the expected value of daily change in mass (δ_{ij}) is 0, so energy requirements are entirely represented by the metabolic component of the model, which increases with the mass of the animal. For a growing walrus, the expected value of δ_{ij} is positive, and the storage component accounts for additional energy required to increase body size. This occurs up to about age 12, when the asymptote for mature body mass is obtained in wild Pacific walruses (Fay 1982). These requirements are in addition to the growth-related metabolic costs accounted for by the growth premium for walruses $<a_g$ yr old ($C_g K_1 m_{ij}^{K_2}/D$). During pregnancy, the expected value of δ_{ij} is also positive, and the storage component accounts for the energy required for fetal growth and storage of energy reserves to be used in the subsequent lactation period. These requirements are in addition to the pregnancy-related metabolic costs that accrue during pregnancy ($C_p K_1 m_{ij}^{K_2}/D$). During lactation, energy requirements are given by the metabolic component of the model, which accounts for the additional lactation-related metabolic costs as $C_l K_1 m_{ij}^{K_2}/D$. The expected value of δ_{ij} is negative during this period, and the storage component of the model accounts for energy mobilized from stored mass to supplement consumption in fueling lactation.

Estimating Model Parameters

We estimated posterior distributions for each of the parameters in the full model (1) with each combination of smoothing df and a_g values, using Markov chain Monte Carlo (MCMC; Gelman et al. 1997) and standard, noninformative prior distributions. In each case, we used three separate chains of at least 30,000 iterations. We assessed convergence by examining the trace for each parameter over the iterations within chains (Spiegelhalter et al. 2003) and Gelman-Rubén statistics for comparisons among chains (Brooks and Gelman 1998). The final 5,000 iterations from each chain were combined to give 15,000 iterations for estimating posterior distributions of parameters and derived quantities. Models were compared with DIC as described above. Final parameter estimates and subsequent analyses were based on the model with the lowest DIC value.

We assessed the fit of the model to the data from individual captive walruses during their growth periods (ages 2–9) by estimating the model-based expected consumption and comparing this to observed caloric consumption totaled over all intervals with adequate data (i.e., with consumption data and no more than 3 wk between successive mass measurements) for the walrus during the period. We also assessed the fit of the model to data from individual captive walruses during pregnancy and lactation periods by comparing model-based estimates of expected consumption to observed caloric consumption, totaled over all intervals with adequate data for these periods.

Estimating Energy Requirements

In general, we estimated energy requirements as

$$\hat{E}(ij) = \frac{[\hat{A}(ij) + \hat{C}_g I_g(ij) + \hat{C}_p I_p(ij) + \hat{C}_l I_l(ij)] K_1 m_{ij}^{K_2}}{D} + [\hat{C}_{\delta+} I_{\delta+}(ij) + \hat{C}_{\delta-} I_{\delta-}(ij)] \delta_{ij}, \quad (5)$$

using the posterior distributions of the parameter estimates and either actual or calculated (as described below) values for m_{ij} and δ_{ij} .

We estimated daily and average daily energy requirements for an 830-kg, static-mass female at each facility by assuming $m_{ij} = 830$ and $\delta_{ij} = 0$ and equated this to the proportion of time a free-ranging walrus would spend active in water (vs. hauled-out and resting) based on the relation

$$A(ij) = 6.0P_w(ij) + 2.2[1 - P_w(ij)], \quad (6)$$

where $P_w(ij)$ is the proportion of the time walrus i spends in water during interval j . Equation (6) is based on the assumption used by Noren et al. (2012) that periods active in water are associated with a metabolic cost of $6 \times$ Kleiber (Acquarone et al. 2006) and periods hauled-out resting are associated with a metabolic cost of $2.2 \times$ Kleiber (Williams et al. 2007). This gives the proportion of time in water as $P_w(ij) = [A(ij) - 2.2]/3.8$.

To estimate energy requirements for free-ranging walruses, we set $P_w = 0.83$ based on observed activity budgets of free-ranging walruses in the Bering Sea (Udevitz et al. 2009), which was also assumed by Noren et al. (2012). This gave a value of $A(ij) = 5.4$ for free-ranging walruses. We estimated average mass-at-age values for a free-ranging female walrus, using least squares regression to fit a logistic model of the form

$$m_{ij} = \frac{\theta_1}{1 + \exp(\theta_2 + \theta_3 a_{ij})} \quad (7)$$

to mass (m_{ij}) at age (a_{ij}) values obtained from Fay (1982, fig. 11). These values were used for m_{ij} to calculate corresponding daily changes in mass (δ_{ij}) and to estimate caloric requirements using equation (5). We partitioned requirements into the component due to basal plus activity costs (associated with $A(ij)$), the component due to the metabolic cost of growth (associated with C_g), and the component due to mass gain (associated with $C_{\delta+}$).

We estimated the pattern of mass gain during pregnancy by fitting a hierarchical logistic model to data from the two pregnancies with consistently recorded data. We defined pregnancy as the time from implantation of the blastocyst to birth of the calf (assumed to be 334 d, approximately 11 mo). The model had the form

$$M_{ij} \sim \text{Normal}(m_{ij}, \sigma_M^2), \quad (8)$$

where M_{ij} is the mass gain of walrus i on day j of the pregnancy and m_{ij} is the same as equation (7) except that a_{ij} now represents the number of days into the pregnancy ($a_{ij} = 1, \dots, 334$), $\theta_1 \sim \text{Normal}(\mu_1, \sigma_1^2)$, $\theta_2 \sim \text{Normal}(\mu_2, \sigma_2^2)$, and $\theta_3 \sim$

Normal(μ_3 , σ_3^2). Posterior estimates of the model parameters were obtained using MCMC as described above for the consumption model. We used the hierarchical median of M_{ij} added to a starting mass of 830 kg for the m_{ij} to calculate the corresponding δ_{ij} and to estimate the associated caloric requirements using equation (5) with $A(ij) = 5.4$ for a free-ranging 12-yr-old walrus during pregnancy. We partitioned requirements into components due to basal plus activity costs (associated with $A(ij)$), metabolic cost of pregnancy (associated with C_p), and mass gain (associated with $C_{\delta+}$). Energy requirements during pregnancy included mass that was stored to be used during the subsequent lactation period.

We had lactation data for only a single walrus. The additional weight gained by this walrus during pregnancy was lost by the end of the first year of the lactation period. Based on this, we approximated the mass of a lactating walrus as

$$m_{ij} = 830 + 195 \exp(-0.017a_{ij}), \quad (9)$$

where a_{ij} represents number of days into lactation ($a_{ij} = 1, \dots, 730$), 830 kg is the mass of a mature female walrus from Fay (1982, fig. 11), and 195 kg is the model-based median weight gain during pregnancy for the two pregnancies in our data set less the mean weight of a newborn calf and placenta (based on mass measurements from two newborns and one placenta from the study animals). This function exponentially declines from the initial postpartum weight of 1,025 kg to an asymptotic weight of 830 kg approximately 1 yr after lactation commences. We used the values from equation (9) for m_{ij} to calculate the corresponding δ_{ij} and to estimate caloric requirements (based on eq. [5] with $A(ij) = 5.4$) for a free-ranging 12-yr-old walrus during lactation. We partitioned requirements into components due to basal plus activity costs (associated with $A(ij)$), metabolic cost of lactation (associated with C_l), and mass loss (associated with $C_{\delta-}$). Energy consumption requirements for lactation excluded energy that was gained from mass loss because this represents caloric intake that was already accounted for during the pregnancy period.

We also estimated energy requirements for the case where a free-ranging 12-yr-old walrus becomes pregnant while she is still nursing a calf and gives birth at the end of the 2-yr lactation interval for the first calf. Values for m_{ij} were obtained by combining model (8) and equation (9), and these were then used to calculate the corresponding δ_{ij} and to estimate caloric requirements based on equation (5). Requirements were partitioned into components as described above for pregnancy and lactation.

Validation

For our model to be plausible, walrus must be able to meet estimated energetic requirements within realistic limits for foraging time and ingestion capacity. The proportion of time required to forage must be less than the assumed activity level (83% of the time active in water) because the time in water

must also include transit and search time. The required ingestion rate should be approximately 5%–7% of body mass per day to be in agreement with consumption estimates based on stomach contents (Fay 1982), and observations of foraging (Born et al. 2003) for walrus but could be as high as 15%–20% of body mass per day, based on observed upper limits to food consumption by Steller sea lions (*Eumetopias jubatus*; Rosen 2009).

Because of a lack of data for Pacific walrus, we estimated foraging and consumption rates based on observations of free-ranging Atlantic walrus *Odobenus rosmarus rosmarus* (Born et al. 2003). The approach is described in detail by Noren et al. (2012). Briefly, we estimated that walrus consume eight clams per minute of dive cycle (dive duration plus subsequent surface duration), which is equivalent to 92.57 kcal or 87.68 shell-free grams wet weight per minute of dive, or 11.57 kcal and 10.96 shell-free grams wet weight per bivalve consumed (energy density = 1.06 kcal g⁻¹ or 4.42 kJ g⁻¹; Born et al. 2003). Admittedly, we oversimplified this system. First, the feeding rates from Born et al. (2003) are for adult walrus, but young walrus, like other immature pinnipeds, could have limited foraging capabilities due to naïveté, small body size, and underdeveloped diving physiology (for review, see Noren et al. 2005). Thus, our estimates of foraging times for immature walrus likely represent minimum values. Second, the diets of Pacific walrus are more diverse than strictly clams (Sheffield and Grebmeier 2009). Nonetheless, walrus are highly selective for bivalves (Fay et al. 1977; Fay and Lowry 1981; Fay and Stoker 1982a, 1982b), and the energy contents of diverse taxa of marine benthic invertebrates from the Canadian Arctic fall within a relatively narrow range (Wacasey and Atkinson 1987). Even with these limitations, we feel that this approach provides adequate approximations for assessing model plausibility.

Results

For comparison to Noren et al. (2012), the energetic requirements of walrus determined in this study are reported in kilocalories, but these values can be converted to kilojoules according to the following conversion factor: 1 kcal = 4.184 kJ. The daily caloric intake for the female Pacific walrus in this study varied with body size, facility, and season and ranged from 0 to 56,298 kcal d⁻¹ for 210–1,085-kg, 2.0–30.4-yr-old walrus. Older animals tended to have greater daily caloric intake and lower mass-specific caloric intake, consistent with the scaling of metabolism with body mass (fig. 1). Body mass increased during pregnancy, as did caloric intake, while during lactation, body mass decreased, as did caloric intake (fig. 1A, 1B). Interestingly, mass-specific food consumption changed little during reproductive events (fig. 1C), suggesting that a large portion of the elevated caloric intake during pregnancy and early lactation (fig. 1A) was due to the larger body sizes of the animals (fig. 1B) because of the scaling of metabolism with body mass (Kleiber 1975).

Model Parameters and Base Energy Requirements

The lowest DIC model for energy consumption used δ values calculated from a 46 df loess smooth of observed mass values and applied the metabolic cost of growth (growth increment) for ages $<a_g = 10$ yr. Estimated metabolic costs for growth and pregnancy were each about half of the estimated metabolic cost of lactation (table 1). The relative effects of these costs on required consumption were moderated by the additional costs of mass accumulation during growth and pregnancy and by energy gained from mass depletion during lactation. During periods of weight gain, mass was acquired at an estimated rate of 1 kg per $C_{\delta+} = 6,813$ kcal consumed (table 1). During periods of weight loss, required consumption was offset at an estimated rate of $C_{\delta-} = 8,103$ kcal per kg lost (table 1).

Estimated daily energy requirements varied across facilities, tending to be higher and more constant at the northernmost facilities and lower with stronger seasonal patterns at the more southerly and coastal facilities (fig. 2). Mean daily energy requirements at all facilities corresponded to activity levels that were low relative to observed averages for free-ranging walruses (Udevitz et al. 2009). Estimated energy requirements for an 830-kg female at the northernmost facilities were equivalent to requirements for a free-ranging

walrus active only 11%–15% of the time, while requirements at the southern and coastal facilities were equivalent to requirements for a free-ranging walrus active only up to 3% of the time.

Energetic Cost of Growth

The logistic growth model fit the mass-at-age values from Fay (1982) very closely. Least squares estimates of the growth model parameters were $\theta_1 = 833$ (SE = 3.3), $\theta_2 = 1.78$ (SE = 0.062), and $\theta_3 = -0.45$ (SE = 0.014). Energy requirements were mainly associated with base (basal and activity) costs, though a smaller but important portion was attributable to the metabolic cost of growth and the energetic demand of adding mass for ages <10 yr (fig. 3). The combined costs of growth (metabolic and mass accumulation) increased to a maximum of 7% of total requirements at about 5.5 yr and then declined, becoming negligible ($<1\%$ of total requirements) at age 10, when the metabolic cost of growth no longer accrued (fig. 3). The posterior mean estimate of the total energy requirement for the early growth period (ages 2–5) was 57,830,000 kcal (95% credibility interval [CI] = 57,430,000–58,250,000). The posterior mean estimate of the total energy

Table 1: Parameter estimates for the model of daily caloric consumption by female Pacific walruses

Parameter	Description	Mean	SD	95% CI	
				Lower limit	Upper limit
f_1	Base metabolic cost at facility 1 ^a	2.62	.12	2.37	2.88
f_2	Base metabolic cost at facility 2 ^a	1.99	.17	1.65	2.36
f_3	Base metabolic cost at facility 3 ^a	2.79	.13	2.55	3.06
f_4	Base metabolic cost at facility 4 ^a	2.30	.10	2.09	2.49
f_5	Base metabolic cost at facility 5 ^a	2.20	.12	1.95	2.46
f_6	Base metabolic cost at facility 6 ^a	2.63	.18	2.24	2.97
α_1	Cosine component of seasonal metabolic cost at facility 1 ^a	.01	.02	-.04	.05
α_2	Cosine component of seasonal metabolic cost at facility 2 ^a	-.13	.03	-.19	-.07
α_3	Cosine component of seasonal metabolic cost at facility 3 ^a	.03	.02	-.01	.07
α_4	Cosine component of seasonal metabolic cost at facility 4 ^a	-.05	.02	-.09	-.01
α_5	Cosine component of seasonal metabolic cost at facility 5 ^a	-.14	.03	-.21	-.07
α_6	Cosine component of seasonal metabolic cost at facility 6 ^a	-.01	.02	-.05	.04
β_1	Sine component of seasonal cost at facility 1 ^a	.06	.02	.02	.10
β_2	Sine component of seasonal cost at facility 2 ^a	.10	.03	.04	.16
β_3	Sine component of seasonal cost at facility 3 ^a	-.07	.02	-.10	-.03
β_4	Sine component of seasonal cost at facility 4 ^a	-.10	.02	-.14	-.07
β_5	Sine component of seasonal cost at facility 5 ^a	-.03	.04	-.10	.05
β_6	Sine component of seasonal cost at facility 6 ^a	.08	.02	.04	.13
C_g	Metabolic cost of growth ^b	.23	.02	.19	.27
C_p	Metabolic cost of pregnancy ^b	.26	.04	.18	.34
C_l	Metabolic cost of lactation ^b	.60	.06	.48	.72
$C_{\delta-}$	Energy mobilization coefficient ^c	8,103	293	7,530	8,678
$C_{\delta+}$	Energy storage coefficient ^c	6,813	231	6,361	7,268

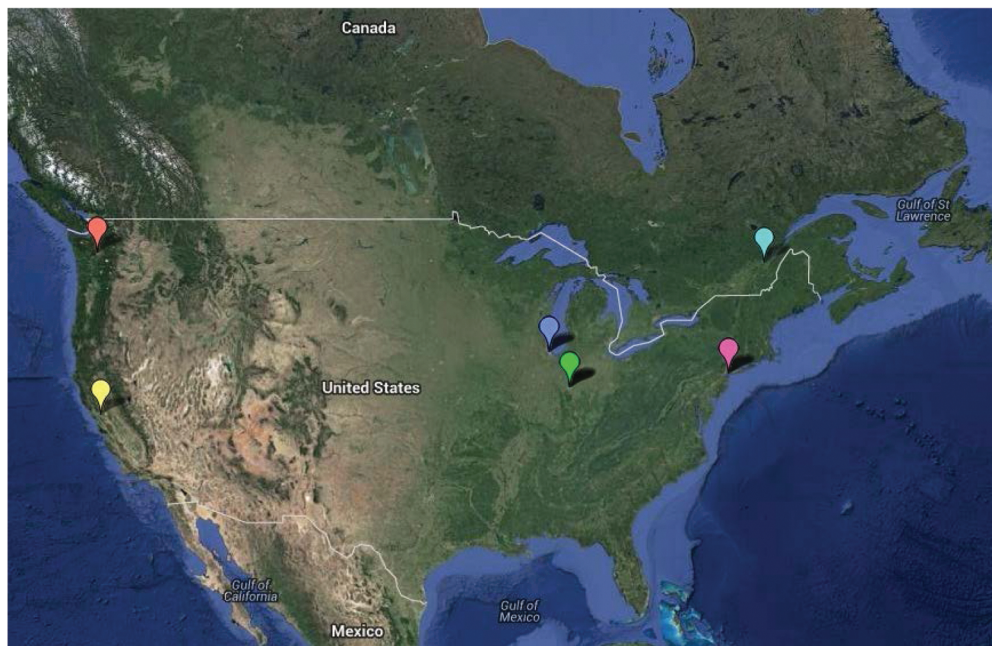
Note. CI = credibility interval.

^aFrom equation (3).

^bFrom equation (2).

^cFrom equation (4).

A.



B.

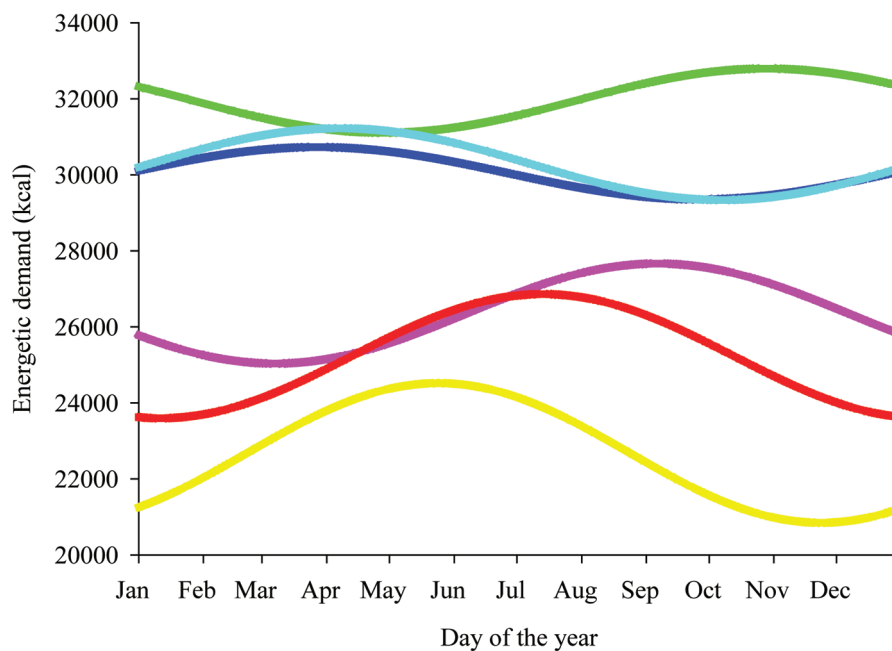


Figure 2. Map showing the locations of the facilities (A) and graph showing the estimated total energetic demand per day for 1 yr for a hypothetical, nonreproductive, 830-kg, static-mass, 12-yr-old female at each of the six facilities (B). The color for the facility and that for the modeled animal from that facility are coordinated. Energetic demands tended to be higher in regions that experience lower air temperatures.

requirement for the later growth period (ages 6–9) was 83,810,000 kcal (95% CI = 83,230,000–84,410,000). Differences between model-based estimates of expected total consumption during the entire growth phase (>2 to <10 yr of age) ranged from 1% to 10% of the observed value, but 75% of the

differences were less than 4% and consumption was not consistently over- or underestimated. By age 10, requirements were primarily due to basal and activity costs for nonreproductive animals (fig. 3) and achieved an asymptote of about 61,500 kcal d⁻¹ (fig. 3; table 2). At a consumption rate of 92.57 kcal min⁻¹

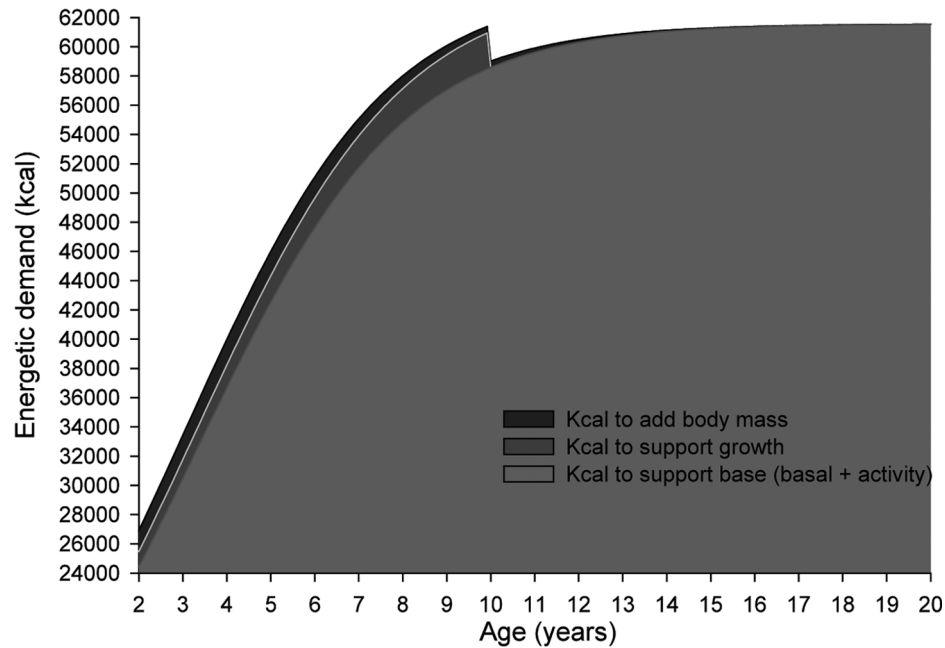


Figure 3. Estimated energetic demand throughout the life of a nonreproductive, free-ranging female Pacific walrus over 20 yr, assuming an activity budget of 83% of the time active in water and 17% of the time hauled-out resting. The height of the shaded area represents the total energetic demand on a given day, partitioned into calories required for early growth, adding body mass, and base (basal plus activity).

(Born et al. 2003), 2–5-, 6–9-, and ≥ 10 -yr-old walruses must forage 20%–35%, 38%–45%, and 44%–46% of the day, respectively, to meet these requirements. Assuming a clam diet, where a gram of shell-free wet weight has an energy density of 1.06 kcal (calculated from Born et al. 2003), 2–5-, 6–9-, and ≥ 10 -yr-old walruses could support energetic requirements by consuming 9%–10%, 7%–8%, and 7% of body mass d^{-1} , respectively.

Energetic Costs of Reproduction

There were two full-term pregnancies with consistently recorded data for estimating the pattern of weight gain during pregnancy. Estimates of the posterior medians of the weight gain model parameters were $\mu_1 = 281$ (95% CI = 258–318), $\mu_2 = 5.63$ (95% CI = 2.58–9.03), and $\mu_3 = 0.0247$ (95% CI = –0.1016 to 0.1457). This gave a pattern of weight gain that began increasing rapidly about halfway through the pregnancy to a total of 256 kg by the end of the period (fig. 4). Energy requirements increased during pregnancy as a result of the increasing mass of the walrus and the metabolic cost associated with C_p , which also increased with mass (table 3; fig. 5A). However, there was also a substantial energy requirement for accumulating mass (associated with C_{s+}), some of which went to growth of the fetus and placenta but most of which (195 kg) was apparently stored for use during the subsequent lactation (fig. 5B). The energy required for accumulating mass increased to a maximum of 14% of total requirements at about day 220 of the pregnancy and then began decreasing, accounting for 3% of total requirements by the end of the pregnancy (fig. 5A). The

additional metabolic requirements of pregnancy accounted for a relatively constant 4%–5% of total requirements throughout the pregnancy period (fig. 5A). The posterior mean estimate of total energy required during the 11-mo pregnancy period was 24,950,000 kcal (95% CI = 24,640,000–25,260,000). Differences between model-based estimates of expected total consumption during the two pregnancy periods were 3% less than the observed value in one case and 13% greater than the observed value in the other case. Based on consumption rates for walruses consuming clams (from Born et al. 2003), the estimated peak energy requirements during pregnancy (month 9 of pregnancy) could be met by a walrus foraging for 64% of the day and consuming 8% of body mass per day.

Total energy requirements during the lactation interval decreased throughout the first year (table 4; fig. 5B), which was associated with the decreasing mass of the walrus; mass decreased exponentially from an initial weight of 1,025 kg to an asymptotic weight of approximately 830 kg. Total energy requirements leveled off after the first year of lactation to a value about 11% higher than that required for a nonlactating walrus of comparable size. The posterior mean estimate of total energy consumption required during the 2-yr lactation period was 48,930,000 kcal (95% CI = 47,930,000–49,940,000). This does not include the estimated 1,580,000 kcal (95% CI = 1,470,000–1,690,000) derived from utilizing mass during lactation, which was acquired and stored during the preceding pregnancy period. The estimated peak energy consumption period for the 2-yr lactation interval occurred during months 6–24, once onboard energy reserves were exhausted (table 4). The model-based estimate of expected to-

Table 2: Estimated daily energy requirement on day 1 for each age class for nonreproductive, free-ranging female Pacific walruses, assuming an activity budget of active in water for 83% of the time and hauled-out resting for 17% of the time

Age class	Body mass (kg)	Daily requirement (kcal)	95% CI	
			Lower limit	Upper limit
2	243	26,900	26,700	27,100
3	326	33,410	33,170	33,650
4	418	39,960	39,670	40,250
5	509	45,990	45,660	46,320
6	592	51,080	50,720	51,440
7	661	55,060	54,680	55,450
8	714	58,000	57,590	58,410
9	753	60,060	59,640	60,490
10	780	59,010	58,980	59,030
11	798	59,900	59,880	59,920
12	810	60,490	60,480	60,500
13	818	60,870	60,870	60,880
14	824	61,120	61,120	61,130
15	827	61,280	61,280	61,290
16	829	61,390	61,380	61,390
17	831	61,450	61,450	61,450
18	832	61,490	61,490	61,500
19	832	61,520	61,520	61,520
20	833	61,540	61,540	61,540

Note. CI = credibility interval.

tal consumption was within 1% of observed consumption for the single lactation period in this study. Assuming a consumption rate of $92.57 \text{ kcal min}^{-1}$, the peak energy consumption period during lactation could be met by a walrus foraging for 51% of each day at a rate of $92.57 \text{ kcal min}^{-1}$. Based on a clam diet (energy density = 1.06 kcal g^{-1}), this translates to consuming 8% of body mass per day. By utilizing onboard stores to support 27% of the energetic demands of lactation, females during the first month of lactation could meet energetic needs by foraging for only 42% of the day and consuming only 5% of body mass per day (based on consumption rates for walruses consuming clams from Born et al. 2003). Surprisingly, this level of consumption and foraging effort is lower than what we estimated for mature, nonreproductive females.

The additional energy requirements due to pregnancy were added to those of lactation for a walrus assumed to become pregnant during the lactation interval (table 5; fig. 5C). The maximum energy requirement occurred when lactation overlapped the last half of the pregnancy period. The posterior mean estimate of total energy required during a 2-yr lactation period that included an 11-mo pregnancy was 53,560,000 kcal (95% CI = 52,440,000–54,710,000). The peak energy consumption period across all age classes and reproductive statuses occurred for females that are simultaneously lactating and are 9 mo into pregnancy. This peak energy consumption period for a simultaneously pregnant and lactating female walrus could be met by foraging for 70% of each day, which

translates to consuming 9% of body mass per day (based on consumption rates for walruses consuming clams from Born et al. 2003).

Discussion

The only previously available bioenergetics model for walruses was developed by Noren et al. (2012), but that model had to be relatively simple because the lack of physiological data for this species did not support a more complex model. For example, the energetic cost of adding mass was accounted for only by including a growth multiplier that accounted for the elevated metabolic rate of immature animals <6 yr old, even though mature body size is not attained in female Pacific walruses until they are 12 yr old (Fay 1982). In addition, body mass was kept static during reproductive events (pregnancy and lactation), though blubber thickness (and hence body mass) has been observed to vary with the reproductive condition of female walruses (Fay 1985). Perhaps more important, Noren et al. (2012) did not attempt to explore the linkage between caloric intake and energy stores (body mass), which can allow energy consumption and demand to be uncoupled during critical life-history stages. These types of limitations led, for example, to the unreasonable implication that a lactating walrus would need to forage 95%–101% of its time to meet energetic requirements (Noren et al. 2012). By explicitly accounting for accumulation and depletion of energy stores and by conducting focused research on walruses

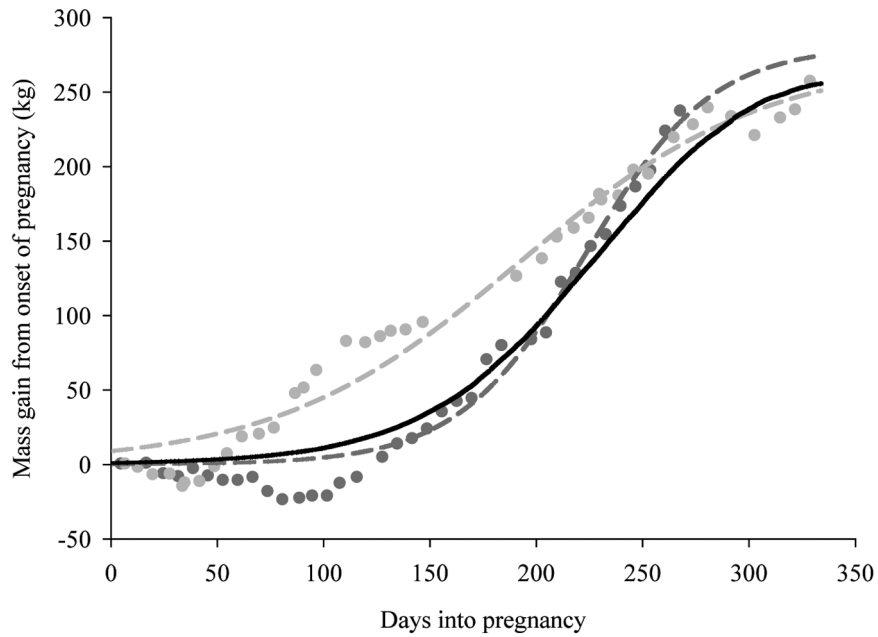


Figure 4. Gain in body mass from the onset of pregnancy for two Pacific walruses. Observed and model-based estimates of mass for the two individual walruses are denoted by light gray and dark gray, respectively. The median body mass gain function across the two walruses is represented by the black line.

in aquaria to develop walrus-specific estimates for model parameters, we have been able to address many of the limitations of the model developed by Noren et al. (2012).

Base (Basal and Activity) Requirements

The amount of food consumed by captive animals is generally lower than what bioenergetic models predict for wild animals

(Winship et al. 2006). Compared to free-ranging walruses in the Arctic, walruses in aquaria are likely to have relatively low base (basal and activity) energetic demands because in aquaria, at least in temperate regions, thermoregulatory demands are lower. Also, because the captive walruses do not need to forage for their food or avoid predators, their activity demands are undoubtedly lower. Caloric intakes observed for the nonreproductive captive walruses in this study ranged

Table 3: Estimated mean daily energy requirements by month of pregnancy after implantation of the blastocyst for a free-ranging female Pacific walrus, assuming an activity budget of active in water for 83% of the time and hauled-out resting for 17% of the time

Month	Mean body mass (kg)	Mean daily requirement (kcal)	95% CI	
			Lower limit	Upper limit
1	831	64,720	63,820	65,610
2	833	65,010	64,110	65,900
3	836	65,720	64,830	66,610
4	843	67,250	66,370	68,130
5	856	69,950	69,080	70,840
6	881	74,370	73,450	75,290
7	919	79,580	78,580	80,580
8	969	83,680	82,620	84,750
9	1,018	85,400	84,340	86,470
10	1,057	84,090	83,050	85,140
11	1,080	81,810	80,750	82,860

Note. CI = credibility interval.

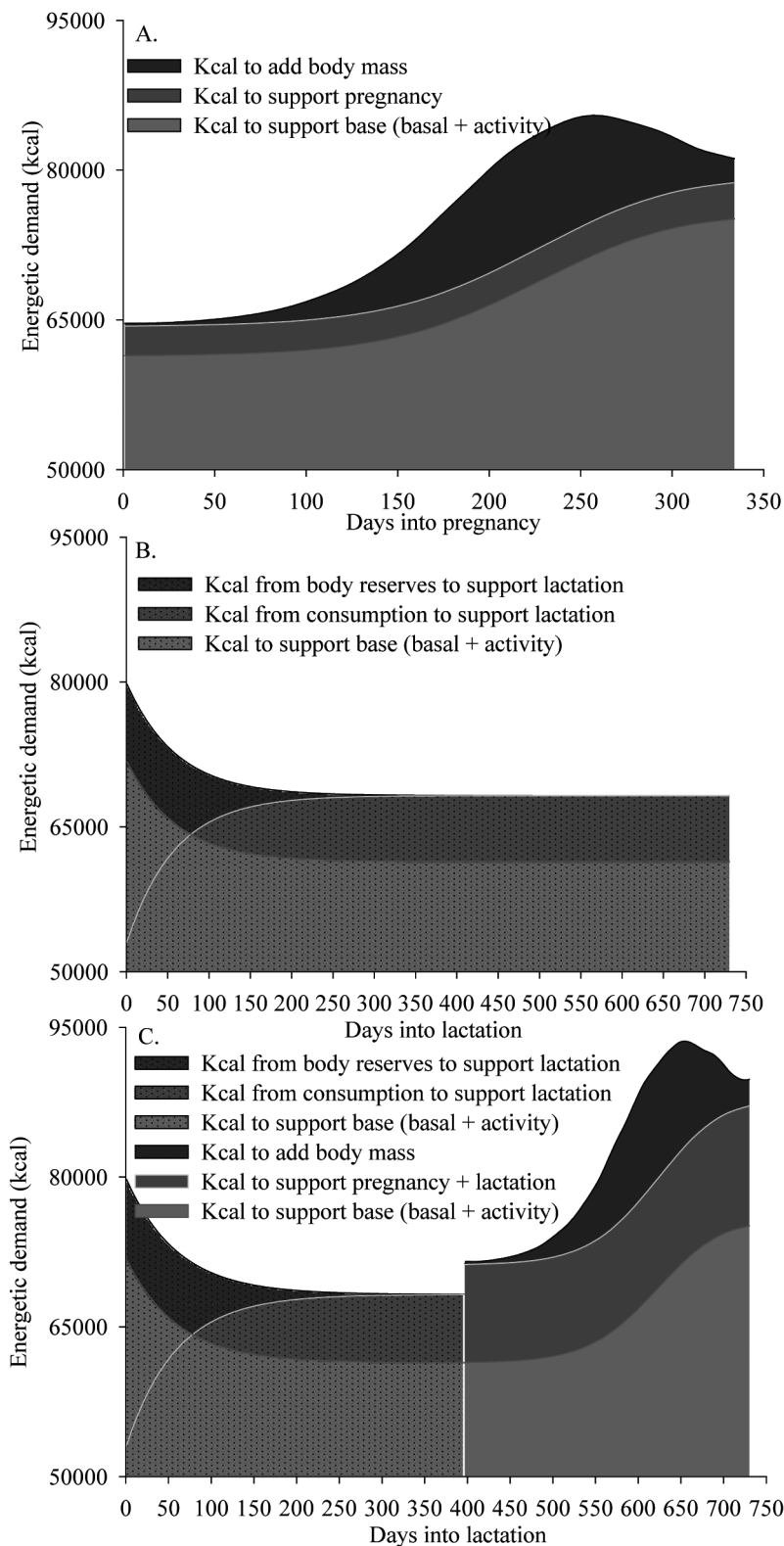


Figure 5. Estimated daily energy demand during reproductive events for a 12-yr-old free-ranging female walrus. The animal's initial body mass was assumed to be 830 kg, with a weight gain of 256 kg during the pregnancy period. Estimates for a walrus that is pregnant, lactating, and simultaneously lactating and pregnant are shown in A, B, and C, respectively. The height of the shaded area represents the total caloric demand on a given day, which is partitioned into calories associated with the energy of adding body mass or the energy released from depleting body mass and the energy required for base (basal plus activity) and reproduction (pregnancy, lactation, or both). Dotted shading represents periods when a portion of the calories required to support energetic demands is coming from depletion of body mass, as during lactation.

Table 4: Estimated mean daily energy requirements, via consumption and from body stores, by month of lactation for a free-ranging female Pacific walrus, assuming an activity budget of active in water for 83% of the time and hauled-out resting for 17% of the time

Month	Mean body mass (kg)	Mean daily requirement from consumption (kcal) ^a	95% CI		Mean daily requirement from stores (kcal)	95% CI	
			Lower limit	Upper limit		Lower limit	Upper limit
1	983	56,330	54,210	58,510	21,050	19,580	22,530
2	921	61,140	59,440	62,880	12,640	11,760	13,530
3	884	64,030	62,520	65,560	7,530	7,000	8,060
4	862	65,740	64,330	67,180	4,480	4,170	4,800
5	849	66,750	65,380	68,150	2,670	2,480	2,860
6	841	67,360	66,000	68,730	1,590	1,480	1,700
7	837	67,710	66,360	69,070	950	890	1,020
8	834	67,930	66,580	69,280	570	530	610
9	832	68,050	66,710	69,410	340	310	360
10	831	68,130	66,780	69,480	200	190	220
11	831	68,180	66,830	69,530	120	110	130
12	831	68,200	66,860	69,560	70	70	80
13	830	68,220	66,870	69,570	40	40	50
14	830	68,230	66,880	69,580	30	20	30
15	830	68,230	66,890	69,590	20	10	20
16	830	68,240	66,890	69,590	10	10	10
17	830	68,240	66,890	69,590	10	10	10
18	830	68,240	66,900	69,590	0	0	0
19	830	68,240	66,900	69,590	0	0	0
20	830	68,240	66,900	69,590	0	0	0
21	830	68,240	66,900	69,590	0	0	0
22	830	68,240	66,900	69,590	0	0	0
23	830	68,240	66,900	69,590	0	0	0
24	830	68,240	66,900	69,590	0	0	0

Note. CI = credibility interval.

from 0 to 56,298 kcal d⁻¹ (fig. 1A), which corresponded to estimated activity levels of up to only 15% of the time active in water. This activity level is dramatically lower than the average 83% of the time active in water observed for free-ranging walruses in the Bering Sea (Udevitz et al. 2009).

Based on this assessment, we used estimates from Noren et al. (2012) for base (basal and activity) energy requirements of wild walruses, and we recommend that these continue to be used in the absence of new data. The estimates were based on the average proportions of time spent active and resting by free-ranging Pacific walruses (Udevitz et al. 2009), with periods of activity and rest requiring a metabolism of 6 times basal metabolic rate (BMR; based on measured field metabolisms of free-ranging male Atlantic walruses *Odobenus rosmarus rosmarus*; Born et al. 2003) and 2.2 times BMR (measured for resting California sea lions *Zalophus californianus*; Williams et al. 2007), respectively. These estimates are in the range of field (5–6 times BMR; Costa et al. 1991; Costa and Williams 1999; Costa 2002) and maintenance (1.4–2.8 times BMR; for review, see Williams et al. 2001) metabolisms measured directly from a range of pinniped species. As with the captive walruses (fig. 2), there may be seasonal variations in

energy requirements and consumption in wild walruses, but a lack of physiological data from wild walruses precluded us from characterizing these. The simplification of maintaining base energetic costs at a consistent mean level throughout the year should not affect estimates of annual energy requirements (Noren et al. 2012) but should be considered when inferring the magnitude of seasonal variations in energy requirements and consumption in wild walruses.

Growth Requirements

Consistent with the mass-related scaling of metabolism (Kleiber 1975), observed caloric intake increased with walrus age (fig. 1A), as did estimated caloric intake requirements (fig. 3). However, our estimates for 2–5-yr-old immature walruses were lower than the estimates of Noren et al. (2012). As a result, newly weaned 2-yr-old female walruses require 1.3 h less foraging time per day than previously estimated by Noren et al. (2012). Overall, the posterior mean estimate of the total energy requirement for this 4-yr early growth period was 6% less than the estimate based on the Noren et al. (2012) model. This discrepancy between the models arises

Table 5: Estimated mean daily energy requirement, via consumption and from body stores, by month of lactation for a free-ranging female Pacific walrus, assuming an activity budget of active in water for 83% of the time and hauled-out resting for 17% of the time

Month	Mean body mass (kg)	Mean daily requirement from consumption (kcal)	95% CI		Mean daily requirement from stores (kcal) ^a	95% CI	
			Lower limit	Upper limit		Lower limit	Upper limit
1	981	56,330	54,210	58,510	21,050	19,580	22,530
2	921	61,140	59,440	62,880	12,640	11,760	13,530
3	884	64,030	62,520	65,560	7,530	7,000	8,060
4	862	65,740	64,330	67,180	4,480	4,170	4,800
5	849	66,750	65,380	68,150	2,670	2,480	2,860
6	841	67,360	66,000	68,730	1,590	1,480	1,700
7	837	67,710	66,360	69,070	950	890	1,020
8	834	67,930	66,580	69,280	570	530	610
9	832	68,050	66,710	69,410	340	310	360
10	831	68,130	66,780	69,480	200	190	220
11	831	68,180	66,830	69,530	120	110	130
12	831	68,200	66,860	69,560	70	70	80
13	830	68,220	66,870	69,570	40	40	50
14	831	71,490	69,820	73,190	-310	-340	-290
15	833	71,860	70,170	73,580	-480	-510	-450
16	836	72,590	70,900	74,310	-1,000	-1,070	-930
17	843	74,150	72,450	75,880	-2,120	-2,260	-1,980
18	856	76,900	75,180	78,660	-4,010	-4,280	-3,750
19	880	81,350	79,580	83,190	-6,940	-7,400	-6,480
20	919	86,890	85,020	88,810	-10,040	-10,710	-9,380
21	968	91,320	89,370	93,340	-11,420	-12,170	-10,660
22	1,018	93,370	91,360	95,440	-10,400	-11,090	-9,710
23	1,057	92,340	90,310	94,420	-6,990	-7,460	-6,530
24	1,079	90,180	88,140	92,280	-3,470	-3,700	-3,240

Note. In this case, at month 14, the animal becomes pregnant, so she is simultaneously lactating and pregnant. CI = credibility interval.

^aPositive values indicate energy coming from stores; negative values indicate energy going into stores.

primarily because, lacking specific information about growth in odobenids, or more closely related otariids (Schröder et al. 2009; Agnarsson et al. 2010; Fulton and Strobeck 2010), Noren et al. (2012) based their estimates for the energetic demand of growth on data from phocids (Worthy 1987). However, compared to odobenids, phocids have a greater rate of mass gain early in life (for review, see Ferguson 2006), which is sustained by relatively high caloric intake, as the milk produced by phocids is higher in fat and energy content than that of odobenids (for review, see Riedman 1990; Ferguson 2006). This difference in life-history patterns results in lower energy requirements for walruses during the early growth period.

Although our estimates of daily caloric requirements of young walruses are lower than estimates in Noren et al. (2012), 2–5-yr-olds still must consume proportionately greater quantities of food than 6–20-yr-olds. Our estimates suggest that the youngest animals must consume 9%–10% of their body mass on a daily basis, while older animals need to consume only 7%–8% of their body mass. The need for immature ani-

mals to consume proportionately more food than larger conspecifics is in agreement with the empirical data collected from the walruses in aquaria (fig. 1C) and observations from other pinniped species (for review, see Winship et al. 2006). In addition, our estimate of the quantity of food consumed per day by older walruses is in agreement with previous estimates for free-ranging adult walruses (5%–7% of body mass per day; Fay 1982; Born et al. 2003). The difference in mass-specific caloric requirements with age increases the vulnerability of immature pinnipeds during food-limited periods because they must acquire proportionately greater amounts of prey. This may in part explain the disproportionate deleterious effects on juveniles during prey-limited periods (DeLong et al. 1991).

Our approach to explicitly account for the cost of accumulating mass (storage component in the model) and our data-based model selection indicated that both the mass accumulation and metabolic costs associated with growth extend beyond the 4-yr growth period (2–5-yr-olds) considered by Noren et al. (2012). Our estimate of the total energy re-

quirement for the later growth period for 6–9-yr-olds was 6% greater than the estimate based on the Noren et al. (2012) model, which did not include energy requirements of growth for animals ≥ 6 yr old. By age 10, as female walruses approach the asymptote for mature body size (Fay 1982), caloric consumption requirements of nonreproductive females in our model and that of Noren et al. (2012) are essentially the same since they are primarily due to basal and activity costs. By using empirical data from walruses in aquaria, estimates for the energetic demands of growth presented here more closely reflect the life-history patterns of free-ranging walruses than those presented in Noren et al. (2012).

Reproduction Requirements

The walruses in this study showed marked increases in daily caloric intake during pregnancy and lactation (fig. 1A). This is consistent with previous studies on captive female walruses, where the animals consumed 30%–40% more food when pregnant, 50%–101% more food when lactating, and 90%–130% more food while simultaneously lactating and pregnant (Gehrich 1984; Kastelein et al. 2000). Elevated food consumption has also been observed in wild and captive pregnant and lactating otariids (Costa et al. 1989, 1991; Williams et al. 2007), yet these potentially significant reproductive costs have been largely ignored in previous bioenergetic models for pinnipeds (Olesiuk 1993; Mohn and Bowen 1996; Stenson et al. 1997). Although the model in Noren et al. (2012) incorporated costs of reproduction for female Pacific walruses, it used the oversimplifying assumption that body mass was static during reproductive events.

We found large increases in body mass during pregnancy and subsequent mass loss during lactation (fig. 1B). Our bioenergetics model enabled us to account for alterations in caloric requirements associated with changes in body size due to the scaling of metabolism with size (Kleiber 1975) and, importantly, allowed us to uncouple caloric intake and demand during reproductive events (fig. 5; tables 3–5). This is important for pinnipeds because they sequester and deplete large quantities of lipids throughout their lifetimes, particularly during reproduction. Some of the energetic demand of lactation in walruses is undoubtedly met by utilizing endogenous energy reserves (e.g., blubber) accumulated during pregnancy, which is consistent with the observation that blubber thickness varies with reproductive condition in female walruses (Fay 1985). Our estimate of the amount of energy recovered per kilogram of body mass is slightly lower than the energy found in lipid (9,386.805 kcal kg⁻¹; Schmidt-Nielsen 1997), suggesting that walruses likely also metabolize some protein during periods of energy deficit, which for Stellar sea lions (*Eumatopias jubatus*) can represent up to 31.2% of the caloric contribution from body reserves (Rea et al. 2007).

Our more comprehensive approach to modeling energy requirements during pregnancy differed from that of Noren et al. (2012) in several respects. For example, based on data

from an otariid, Noren et al. (2012) only ascribed a cost of pregnancy during the last trimester. However, the empirical data from the walruses in this study indicated that, even though the per-day metabolic cost for pregnancy ($C_p = 0.26$) was lower than the otariid-based value ($C_p = 0.92$) used by Noren et al. (2012), the cost accrued throughout the entire pregnancy. In addition, there was a cost due to the scaling of metabolism with the increasing mass of the walrus, and there was a substantial energy requirement for accumulating mass, some of which went to growth of the fetus and placenta but most of which (76%) was apparently stored mass (e.g., lipid) for use during the subsequent lactation (fig. 5B). Neither of these requirements was accounted for by Noren et al. (2012). As a result, the posterior mean estimate of total energy required during the 11-mo pregnancy period was 15% greater than the estimate based on the Noren et al. (2012) model. Nonetheless, our estimated daily caloric requirements of pregnant walruses are plausible. At the height of their energetic demand, pregnant walruses could meet caloric requirements by consuming 7,831 clams per day, which would require them to forage for only 64% of the day (based on foraging efficiency estimates in Born et al. 2003).

A substantial proportion of the energetic requirements for lactation is supported by consumption and storage of lipid during the pregnancy period. Our estimate of total energy consumption required during the 2-yr lactation period was 47% less than the estimate based on the Noren et al. (2012) model, partly because we accounted for an estimated 1,580,000 kcal derived from mass that was acquired and stored during the preceding pregnancy period, though this was offset somewhat by the cost of maintaining the additional mass until it was depleted. Most of the difference, however, was due to our walrus-specific estimate of the metabolic cost of lactation ($C_l = 0.6$), which was substantially lower than the otariid-based value ($C_l = 5.72$) used by Noren et al. (2012). Our posterior mean estimate of total energy consumption required during the 2-yr lactation period and 11-mo pregnancy was 43% less than the estimate based on the model in Noren et al. (2012). During the most energetically taxing life-history stage (simultaneously pregnant and lactating), caloric requirements could be met by foraging 70% of the day. This coarse estimate of foraging requirements is more reasonable than the estimates of Noren et al. (2012), which indicated caloric requirements during lactation could not be sustained by foraging.

Noren et al. (2012), lacking information specific to walruses, derived estimates of energetic costs for reproduction using data from an otariid (California sea lions *Zalophus californianus*; Williams et al. 2007) because odobenid phylogeny (Schröder et al. 2009; Agnarsson et al. 2010; Fulton and Strobeck 2010) and life-history patterns (Fay 1982; Kovacs and Lavigne 1992) are similar in some respects to those of otariids. Odobenids, like otariids, forage throughout their prolonged lactation interval (for review, see Riedman 1990; Bowen 1991; Costa 1991). In addition, the milk of odobenids

and otariids is comparatively lower in energy content than the milk of phocids (for review, see Reidman 1990). However, odobenids are much larger than otariids, and body size has a large impact on lactation traits (Ferguson 2006). According to Costa (1991), a larger female can devote a greater proportion of body stores to its offspring because metabolic overhead (the energy expended to support the basal and activity costs of the female; Fedak and Anderson 1982) scales with body size ($M^{0.75}$) at a lower rate than the amount of energy stored as adipose tissue ($M^{1.19}$; Calder 1984). This suggests that it may be more energetically efficient for walrus to undergo weight gain during pregnancy to build up energy stores to support lactation, as has been observed in phocids (Chabot et al. 1996). Although the lactation intervals of otariids are partially supported by lipid reserves (i.e., California sea lions *Zalophus californianus*; Williams et al. 2007), the larger walrus can theoretically support a greater proportion of the energetic demands of lactation through lipid reserves than the comparatively smaller otariid.

Much of the accumulated mass of the captive walrus during pregnancy was probably lipid, since the combined average mass for a full-term fetus and placenta was only 24% of the estimated mass gained during pregnancy. The observation that blubber thickness varies with reproductive condition in free-ranging female walrus (Fay 1985) supports the assumption that the energetic demands of lactation in walrus are partially met by utilizing endogenous energy reserves (fig. 5B). This attribute is a hallmark of capital breeders (provision offspring using energy stores accumulated at an earlier time), but, except for perhaps several days during estrus and a week or so at parturition, walrus feed during lactation (Fay 1985), which would classify them as income breeders (provision offspring using energy gained concurrently). Thus, it seems that walrus straddle these two lactation strategies. This is consistent with the recommendation of Houston et al. (2007) that capital and income breeding should not be thought of as dichotomous strategies because some pinnipeds may adopt a mixture of the two lactation strategies. By shifting some of the energetic costs of lactation into the pregnancy period, walrus are able to reduce caloric intake requirements during the first few months of lactation. This may be especially important for walrus, because unlike otariids, walrus are accompanied by their offspring while they forage (Fay 1985), which could impact the female's foraging success.

Conclusion

Our extension of the Noren et al. (2012) model, incorporating new walrus-specific data, represents a substantial improvement in quantifying energy requirements of key life-history stages (growth and reproduction) for Pacific walrus. More generally, this work demonstrates the utility of food consumption and body mass data acquired from animals in aquaria for elucidating the bioenergetics of wild conspecifics. By decoupling daily caloric intake from daily caloric de-

mand, we were able to improve our understanding of how female walrus sequester and deplete body reserves throughout their lifetime. This approach revealed new information about the basic biology of walrus, including the apparent use of a mixed reproductive strategy of capital and income breeding. Moreover, our bioenergetics model provides a basis for quantifying how energy deficits can manifest in mass loss and reduced body condition in female walrus. It also provides the linkage required for understanding energetic consequences of the changes in walrus behavior and prey accessibility that are resulting from changes in sea ice availability. This type of information will be essential for predicting Pacific walrus population responses to the changing Arctic environment.

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