

Bioenergetics model for estimating food requirements of female Pacific walruses *Odobenus rosmarus divergens*

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ABSTRACT: Pacific walruses *Odobenus rosmarus divergens* use sea ice as a platform for resting, nursing, and accessing extensive benthic foraging grounds. The extent of summer sea ice in the Chukchi Sea has decreased substantially in recent decades, causing walruses to alter habitat use and activity patterns which could affect their energy requirements. We developed a bioenergetics model to estimate caloric demand of female walruses, accounting for maintenance, growth, activity (active in-water and hauled-out resting), molt, and reproductive costs. Estimates for non-reproductive females 0–12 yr old (65–810 kg) ranged from 16 359 to 68 960 kcal d⁻¹ (74–257 kcal d⁻¹ kg⁻¹) for years with readily available sea ice for which we assumed animals spent 83 % of their time in water. This translated into the energy content of 3200–5960 clams per day, equivalent to 7–8 % and 14–9 % of body mass per day for 5–12 and 2–4 yr olds, respectively. Estimated consumption rates of 12 yr old females were minimally affected by pregnancy, but lactation had a large impact, increasing consumption rates to 15 % of body mass per day. Increasing the proportion of time in water to 93 %, as might happen if walruses were required to spend more time foraging during ice-free periods, increased daily caloric demand by 6–7 % for non-lactating females. We provide the first bioenergetics-based estimates of energy requirements for walruses and a first step towards establishing bioenergetic linkages between demography and prey requirements that can ultimately be used in predicting this population's response to environmental change.

KEY WORDS: Pinniped · Foraging · Metabolism · Energetics · Arctic · Ice · Climate change

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INTRODUCTION

Pacific walruses *Odobenus rosmarus divergens* are gregarious, pagophilic, highly specialized shallow benthic foragers (Fay 1982). Their range is primarily from the eastern East Siberian Sea to the western Beaufort Sea and southward into the Bering Sea from eastern Kamchatka to Bristol Bay (Fay 1985). They forage along the continental shelves of the Chukchi and Bering Seas (Fay & Burns 1988, Jay et al. 2011), and although they feed on a wide variety of organisms, their diets are dominated by clams, snails, and polychaete worms (Fay 1982, Sheffield & Grebmeier

2009). Sea ice is important, because it provides a platform for walruses to rest, nurse, and gain access to offshore foraging grounds (Fay 1982).

The extent of summer sea ice in the Chukchi Sea has decreased substantially in recent decades (Meier et al. 2007), and this trend is expected to continue (Overland & Wang 2007, Douglas 2010). As sea ice retreats off the shallow continental shelf and over deep Arctic Ocean waters, it may become difficult for walruses to feed in proximity to sea ice. The lack of summer sea ice over the continental shelf in the Chukchi Sea over the past decade has resulted in increased use of terrestrial haul-outs by adult female

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and young walruses (Jay & Fischbach 2008, Kavry et al. 2008). As summer sea ice extent continues to decline, it is expected that the number of walruses converging on coastal haul-outs and the time they spend ashore will increase (Jay et al. 2011). However, the ability of the localized food supply in these 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).

Deriving linkages between the responses of walruses to changing Arctic conditions requires 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 quantifications of the energetic requirements and food consumption rates of wild walruses; however, these measurements are difficult to obtain because walruses are remotely distributed and forage along the sea floor. Several other approaches have been employed to estimate food consumption in marine mammals, including analyses of stomach contents and scat from wild animals and observations of feeding by captive animals. Unfortunately, each of these methodologies has inherent errors that could bias estimates of food consumption. For example, errors in food consumption estimates based on analyses of stomach contents (for review see Sheffield et al. 2001) or scat (for review see Arim & Naya 2003) result from disparate digestion rates of remains and the corresponding underrepresentation of soft-bodied prey (Sheffield & Grebmeier 2009). Meanwhile, differences between the activity budgets and environmental demands of captive versus wild animals and the potential for overfeeding (or underfeeding) captive animals limits the applicability of feeding rates from captive animals for estimates of feeding rates for wild populations.

Bioenergetic modeling is an alternate approach that has been used to estimate the energy consumption for a variety of marine mammals (i.e. Lavigne et al. 1982, Øristland & Markussen 1990, Ryg & Øristland 1991, Olesiuk 1993, Hammill et al. 1997, Stenson et al. 1997, Winship et al. 2002, Winship & Trites 2003, Noren 2011), but has yet to be applied to walruses. Bioenergetics models range in detail from simple equations (with few parameters) representing an average individual's annual energy consumption, to detailed energy budgets (with many parameters) for each age- and sex-class and day of the year. A criticism of bioenergetics models is that they often use

inaccurate approximations for parameter values. A complex model requires estimation of several parameters that could result in unanticipated interactions, and each additional parameter has an associated error that may substantially reduce the precision of the model (Stenson et al. 1997). One way to address this is to use fewer parameters estimated with increased precision (Winship et al. 2002), as has been done in several bioenergetics models for marine mammals (i.e. Mohn & Bowen 1996, Stenson et al. 1997). We used this parsimonious approach to develop a bioenergetics model for the Pacific walrus. Our model estimates daily caloric demands of 0 to 12 yr old female walruses based on the metabolic costs of activity (active in-water or hauled-out resting), growth, and molt, and the increased food consumption rates associated with reproduction (pregnancy and lactation). We used the model to (1) estimate annual energy requirements for female walruses as a function of age and reproductive state, (2) estimate changes in energy requirements due to changes in haul-out activity, and (3) determine which bioenergetic parameters have the largest influence on estimates of energy requirements.

MATERIALS AND METHODS

Modeling approach

Our model estimates daily caloric demands of 0 to 12 yr old female Pacific walruses based on mass-specific metabolic costs associated with their haul-out activity budgets (Udevitz et al. 2009) and life history stages (Fay 1982, 1985). Because female walruses achieve full body size at age 12 (Fay 1982), the caloric demands for females >12 yr were assumed to be equivalent to those of 12 yr olds. Activity was categorized as either hauled out (resting) or in water (active). Life history stages included molt, pregnancy, and lactation.

Metabolic costs for each activity and life history stage were expressed as a multiple of Kleiber, where Kleiber is the resting metabolic rate of an animal equivalent to $\text{kcal d}^{-1} = 70 \times \text{mass}^{0.75}$ (Kleiber 1975). The daily proportions for each of these costs were varied throughout the year to reflect changes in activity patterns and life history stages. Additional costs associated with early growth were included in the form of a multiplicative growth premium (Hammill et al. 1997) up to age 6 when female walruses achieve sexual maturity. The total daily metabolic cost was then corrected for digestive efficiency. Thus,

the energetic requirement, $E(t)$, in kcal d^{-1} for a female walrus on day t was given by

$$E(t) = \{ [C_w P_w(t) + C_h P_h(t)] G(t) + C_m P_m(t) + C_p P_p(t) + C_l P_l(t) \} \cdot K_1 M(t)^{K_2} / D \quad (1)$$

where C_w is the cost of being active in water, C_h is the cost of resting while hauled out (includes ice and terrestrial platforms), C_m is the cost of molting, C_p is the cost of pregnancy during the third trimester, and C_l is the cost of lactation, all in kcal d^{-1} . $P_i(t)$ is the proportion of day t associated with cost i . $G(t)$ is the growth premium, a unitless multiplier. $M(t)$ is the mass on day t in kg. K_1 and K_2 are the Kleiber constants ($K_1 = 70$, $K_2 = 0.75$) and D is the digestive efficiency (unitless). Parameter values are described in detail below.

Parameter values

All parameter values were derived from values reported in the literature. We used values specifically reported for walruses when they were available, but

because of difficulties in studying this species, including logistics associated with their remote habitats and their well-developed startle response (stamping and fleeing into the water), few physiological data were available. Thus, where data for walruses were lacking, data from other species of pinnipeds (particularly otariids) were used. Odobenid life history patterns and phylogeny are most similar to otariids. Like otariids, odobenids do not undergo extreme seasonal fasting periods related to breeding, lactating, and molting as do phocids, but rather these events occur over a longer time span and are combined with regular feeding (Fay 1982, Kovacs & Lavigne 1992). Furthermore, recent genetics studies have demonstrated that odobenids are more closely related to otariids than to phocids (Schröder et al. 2009, Agnarsson et al. 2010, Fulton & Strobeck 2010).

At the time of this investigation, the California sea lion *Zalophus californianus* was the only otariid for which the costs of life history stages (molt, pregnancy, and lactation) had been measured directly (Table 1). Activity costs were based on direct measurements of

Table 1. Metabolic and food consumption rate estimates used in our bioenergetics model for female Pacific walruses *Odobenus rosmarus divergens*

Activity or life history stage	Specimen	Data (method)	Conversion into units of Kleiber for model input	Source
Rest hauled-out (C_h)	3 captive non-reproductive female (89.2 ± 0.8 kg) and 2 wild pregnant (98.3 ± 1.6 kg) California sea lions <i>Zalophus californianus</i>	2.2 × Kleiber (open-flow respirometry)	2.2 × Kleiber	Williams et al. (2007)
Active in-water (C_w)	2 wild male walruses <i>O. rosmarus</i> (1250 and 1370 kg)	417.4 and 345 MJ d^{-1} (doubly labeled water)	79.81 kcal $d^{-1} kg^{-1}$ = 6.8 × Kleiber & 60.19 kcal $d^{-1} kg^{-1}$ = 5.2 × Kleiber; Avg = 6 × Kleiber	Acquarone et al. (2006)
Molt (C_m)	3 captive non-reproductive female California sea lions (89.2 ± 0.8 kg)	1.3 times greater than resting metabolic rate during post-molt (open-flow respirometry)	Caloric cost of molt without basal costs = [(1.3 × 2.2) - 2.2] × Kleiber = 0.66 × Kleiber	Williams et al. (2007)
Third trimester of pregnancy (C_p)	2 wild pregnant California sea lions (98.3 ± 1.6 kg)	42% higher than resting metabolic rate (caloric intake)	Caloric cost of pregnancy without basal costs = [(1.42 × 2.2) - 2.2] × Kleiber = 0.924 × Kleiber	Williams et al. (2007)
Lactation (C_l)	2 wild lactating female California sea lions (98.3 ± 1.6 kg)	3.6 times higher than resting metabolic rate (caloric intake)	Caloric cost of lactation without basal costs = [(3.6 × 2.2) - 2.2] × Kleiber = 5.72 × Kleiber	Williams et al. (2007)

metabolism for adults and therefore included basal costs, which are maintenance activities including thermoregulation. Costs associated with life history stages (molt, pregnancy, and lactation) excluded basal costs because maintenance costs were already incorporated into the activity parameters. The initial body mass for each age class was estimated as 65, 195, 270, 345, 420, 495, 570, 645, 725, 755, 785, 810, and 830 kg for 0 to 12 yr old walruses, respectively, from Fay (1982: Fig. 21). The asymptotic mass of female Pacific walruses is 830 kg, which is attained by 12 yr postpartum (Fay 1982). The growth premium multiplier was included in accordance with Hammill et al. (1997) and described in detail by Olesiuk (1993). The growth premium accounts for additional energy required for growth, which for neonatal pinnipeds is 1.8 times predicted adult maintenance requirements (Worthy 1987), and is assumed to converge on adult levels at the onset of sexual maturity at an exponential rate. This gave initial values of 1.8, 1.6, 1.4, 1.3, 1.1, 1.1, and 1.0 for 0, 1, 2, 3, 4, 5, and ≥ 6 (sexually mature) year olds, respectively. The digestive efficiency, which accounts for the energy lost during digestion, is 94.4% for female walruses and did not vary significantly across age class or diet (Fisher et al. 1992). Published values of measured digestive efficiencies for pinniped pups consuming milk were not available, but based on the digestive efficiencies of nursing terrestrial animals, it is assumed that nursing pinniped pups lose 5% of ingested energy in the excretion of urine and feces (Oftedal & Iverson 1987, Donohue et al. 2002, McDonald et al. 2012). Based on this, and for consistency across age classes, we also used the digestive efficiency of 94.4% from Fisher et al. (1992) for milk-dependent pups.

Annual cycle

We estimated daily caloric demands for each day during a year, starting on 1 May (estimated mean birth day based on the range for the birthing period of Pacific walruses described by Fay 1985) and ending on 30 April, corresponding to $t = 1, \dots, 365$. For ages 0 to 11 yr, mass (M) was increased at the start of each day by a daily mass increment, which was 1/365 of the difference between the initial mass for that age class and the initial mass for the next age class (i.e. linear increase). This approach adequately captures annual variability in body mass. Other species of pinnipeds show seasonal variability in body mass (northern fur seals *Callorhinus ursinus*, Trites & Bigg 1996; Steller sea lions *Eumetopias jubatus*, Winship et al.

2001), but we were unable to incorporate seasonal variability in body mass due to the lack of such data for walruses. The growth premium (G), which only has values >1 for ages <6 yr, was calculated on a daily basis for animals <6 yr old in an analogous manner, where G was decreased at the start of each day by a daily growth premium deficit which was 1/365 of the difference between the initial growth premium for that age class and the initial growth premium for the next age class (i.e. linear decrease).

Fay (1982) indicated that the peak annual molting period for Pacific walruses is from July to August and lasts about 1 mo, but that the first postpartum molt occurs in June or July about 1 to 2 mo after birth. We approximated this pattern by setting $P_m(t) = 1$ for $t = 32, \dots, 61$ (30 d, 1 to 30 June) for age 0 and $t = 78, \dots, 107$ (30 d, 17 July to 15 August) for ages >0 . Otherwise, $P_m(t) = 0$.

Females appear to ovulate principally in January to February; implantation of the blastocyst is delayed until June to July, and calves are born 10–11 mo later, mainly from April to mid-June (Fay 1985). We had no information about the energetic costs of early pregnancy, but most of the costs of pregnancy for an otariid were incurred during the last trimester (Williams et al. 2007). Thus, for females with an embryo in diapause on Day 1, we set $P_p(t) = 1$ for $t = 260, \dots, 365$ (15 January to 30 April), which represented the duration of the last trimester of pregnancy (106 d) and otherwise let $P_p(t) = 0$. Walruses nurse their young for up to 2 yr post parturition (Fay 1985), and thus we set $P_l(t) = 1$ for $t = 1, \dots, 365$ for individuals nursing on Day 1 and $P_l(t) = 0$ for individuals that were not nursing. Walruses may still be nursing their last calf while they are in their last trimester of pregnancy (Fay 1985). Therefore, we considered cases where females were pregnant on Day 1 but not nursing, nursing but not pregnant, and both pregnant and nursing.

Activity

We were also interested in exploring how changes in haul-out activity associated with variable sea ice states might impact energetic costs. Udevitz et al. (2009) found that Pacific walruses in the Bering Sea spent about 83% of their time in water during April. This is consistent with values observed for Atlantic and other Pacific walruses during October to January (Born et al. 2005) and July to September (Born & Knutsen 1997, Gjertz et al. 2001, Jay et al. 2001, Born et al. 2005, Acquarone et al. 2006, Lydersen et al. 2008), although there are no published data on proportion of

time in water for walruses at other times of year. Therefore, we used the value from Udevitz et al. (2009) as a base rate, setting $P_w(t) = 0.83$ and $P_h(t) = 1 - P_w(t) = 0.17$, $t = 1, \dots, 365$, to represent behavior when sea ice is available throughout the year (Scenario 1), as was the case for sea ice in previous decades (Douglas 2010). We also considered scenarios where sea ice was not available ('ice-free') for periods of 46 d (Scenario 2; $t = 116, \dots, 161$, 24 August to 8 October) and 92 d (Scenario 3; $t = 93, \dots, 184$, 1 August to 31 October). The 46 d period represents an intermediate value while the 92 d period is based on models that indicate shelf waters of the Chukchi Sea will be ice-free during at least August, September, and October by the end of the century (Douglas 2010). It was hypothesized that during ice-free periods, walruses may spend more time transiting in water to reach productive foraging areas (Jay et al. 2011). We investigated the cost of this change in behavior by allowing $P_w(t)$ to range as high as 0.93, the maximum proportion of time in water observed for a free-ranging walrus in the Bering Sea (Udevitz et al. 2009).

Validation

For our model to be plausible, it must allow walruses to meet their estimated energetic demands by consuming enough prey, given realistic limits to time available for foraging and realistic limits to ingestion. Due to a lack of data for walruses, we were not able to address how mobilization of internal energy stores could support daily energetic demand. The proportion of time required to forage must be considerably less than 83% of the time (or less than 93% during ice-free periods) because the proportion of time in water includes all aquatic activity (transit time, other activities, and foraging time). The ingestion rate should be approximately 5–7% of body mass d^{-1} to be in agreement with consumption estimates based on stomach contents (Fay 1982) and observations of foraging (Born et al. 2003) for walruses. We assumed the maximum possible rate of ingestion was 15–20% of body mass d^{-1} based on observed upper limits to food consumption by Steller sea lions (Rosen 2009). Our estimates of foraging time and biomass consumption were calculated from data based on observations of free-ranging Atlantic walruses *Odobenus rosmarus rosmarus* (Born et al. 2003). These walruses consumed an average of 8 clams (comprised of 72% *Mya truncata*, 21% *Hiatella arctica*, and 7% *Serripes groenlandicus*) per minute of dive cycle (dive duration plus subsequent surface duration; Born et al.

2003). Based on the energy content of the bivalves collected from the walruses' feeding sites, this consumption rate was equivalent to 92.57 kcal (conversion: 4.184 kJ = 1 kcal) or 87.68 shell-free g wet weight per minute of dive, or 11.57 kcal and 10.96 shell-free g wet weight per bivalve consumed (energy density = 1.06 kcal g^{-1} or 4.42 kJ g^{-1} ; Born et al. 2003). Although the diet of Pacific walruses is more diverse (Sheffield & Grebmeier 2009) than we assumed for validation, walruses are highly selective for bivalves (Fay et al. 1977, Fay & Lowry 1981, Fay & Stoker 1982a,b), and the energy contents of diverse taxa of marine benthic invertebrates from the Canadian Arctic are similar (Wacasey & Atkinson 1987). Nonetheless, the bivalves sampled by Born et al. (2003) were collected in August, the time of peak reproductive activity in Arctic waters (Wacasey & Atkinson 1987). Thus, the caloric densities may be at the high end of the range (Wacasey & Atkinson 1987), with the result that the calculated number of clams required to meet energetic demands may represent a minimum number of bivalves. Counteracting this, however, is the possible increase in foraging time required by a strict clam diet. This is because the handling time required for clams may be greater than other soft-bodied benthic invertebrates because walruses must extract the clams from their shells before consuming them. Thus, our foraging time estimates may represent maximum effort.

Elasticity

We assessed the relative effects of potential errors in parameter values used in the model by calculating the elasticity (e) of mean daily energy requirement to each of these parameters. These elasticities expressed the change in estimated mean daily energy requirement that would result from a given proportional change in each of the parameters. Elasticities were calculated analytically according to Caswell (2001) as:

$$e_{\theta} = \frac{\theta}{\bar{E}} \frac{\delta \bar{E}}{\delta \theta} \quad (2)$$

where θ is the parameter under consideration and $\bar{E} = (\sum_{t=1}^{365} E(t)) / 365$ is the mean daily energy requirement for a given age and reproductive class of walrus. For parameters with elasticities that depended on the proportion of time in water, we used a value of $P_w(t) = 0.83$. For parameters that are constant, the resulting elasticity values are the proportional changes in mean daily energy requirement that would result from changing the given parameters by 1%. For $\theta = M(t)$ or $G(t)$, the values are the proportional change

resulting from changing these parameters by 1% of their average values for the year.

RESULTS

Model

Across age and reproductive classes, daily caloric needs ranged from 16 359 to 137 576 kcal d⁻¹ during ice-available years, with larger animals having greater overall daily energetic needs (Fig. 1). The influence of increasing body mass on daily caloric demand was particularly evident in the age-0 class, which had the fastest growth rate and largest change in caloric demand over the year (Fig. 1). On a mass-specific basis, the youngest age classes (particularly the 0–5 yr olds subject to a growth premium multiplier) had the greatest energetic demand (Table 2). The energetic demand of the molt was apparent on Days 32 to 61 for the young of the year and Days 78 to 107 for 1–12 yr olds, where there was a 7–12% increase in daily caloric requirements for non-lactating females (Fig. 1). Reproductive females had the greatest caloric require-

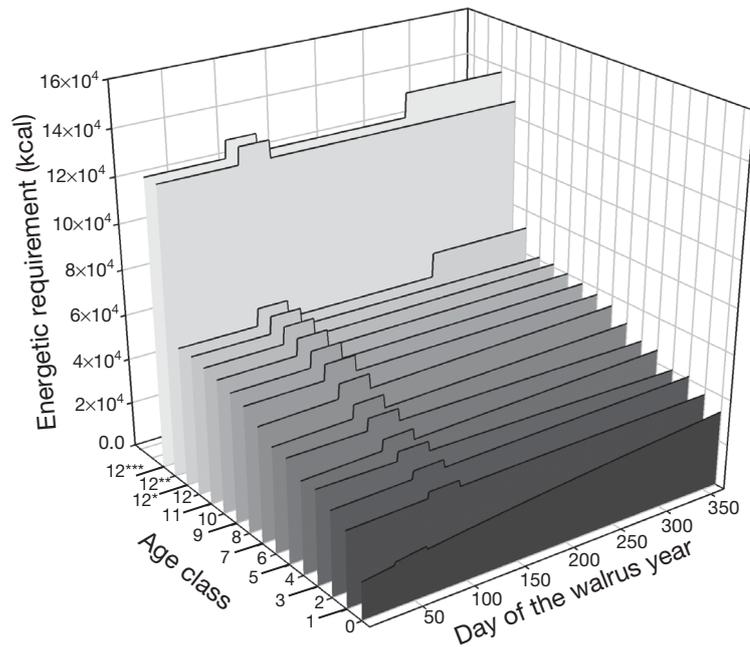


Fig. 1. *Odobenus rosmarus divergens*. Daily energetic requirements (kcal) of 0 to 12 yr old female Pacific walrus throughout the year when sea ice is available. Energetic demand was based on an activity budget of 83% of the time active in water and 17% of the time resting hauled-out, where Day 1 of the walrus year is 1 May (birth date of the animals) and Day 365 is 30 April. The energetic demand of their 30 d molt is represented by $t = 32, \dots, 61$ (1 to 30 June) for the young of the year and by $t = 78, \dots, 107$ (17 July to 15 August) for ages >0 . The 12 yr age class is represented by 4 different cases, 12 (non-reproductive), 12* (pregnant), 12** (lactating), and 12*** (simultaneously pregnant and lactating), where the energetic demand of pregnancy is during the third trimester ($t = 260, \dots, 365$, 15 January to 30 April) and the energetic demand of lactation occurs throughout 2 yr postpartum

Table 2. *Odobenus rosmarus divergens*. Estimated annual and daily energetic needs for female Pacific walrus spending 83% of the time in water year-round (Scenario 1). NA: not applicable; P: pregnant; L: lactating

Age class (mass range in kg)	Annual energetic demand (kcal)	Daily energetic demand (kcal)	Daily mass-specific energetic demand (kcal kg ⁻¹)	Daily clams consumed to meet energetic demand	Daily clams consumed as % body mass to meet energetic demand	% of day foraging to meet energetic demand
0 (65–95)	9 368 313	16 359–33 113	170–257	NA	NA	NA
1 (95–270)	12 976 911	33 147–37 349	137–175	NA	NA	NA
2 (270–345)	14 443 101	37 022–41 881	120–145	3200–3620	13–15	28–31
3 (345–420)	15 127 583	40 522–45 426	97–126	3502–3926	9–12	30–34
4 (420–495)	15 903 034	40 517–46 799	93–106	3502–4045	9–10	30–35
5 (495–570)	17 007 992	45 830–51 389	81–100	3961–4442	8–10	34–39
6 (570–645)	17 903 102	46 314–53 507	79–91	4003–4625	8–9	35–40
7 (645–725)	19 590 718	50 813–58 612	77–88	4392–5066	7–8	38–44
8 (725–755)	20 765 514	55 470–62 869	76–86	4794–5434	7–8	42–47
9 (755–785)	21 393 870	57 183–64 787	75–85	4942–5600	7–8	43–49
10 (785–810)	21 964 971	58 878–66 595	74–84	5089–5756	7–8	44–50
11 (810–830)	22 428 648	60 279–68 074	74–84	5210–5884	7–8	45–51
12 (830)	22 635 120	61 392–68 960	74–83	5306–5960	7–8	46–52
12 P (830)	23 758 190	61 392–71 987	74–87	5306–6222	7–8	46–54
12 L (830)	46 575 105	126 981–134 549	153–162	10 975–11 629	15	95–101
12 P&L (830)	47 698 175	126 981–137 576	153–166	10 975–11 891	15–16	95–103

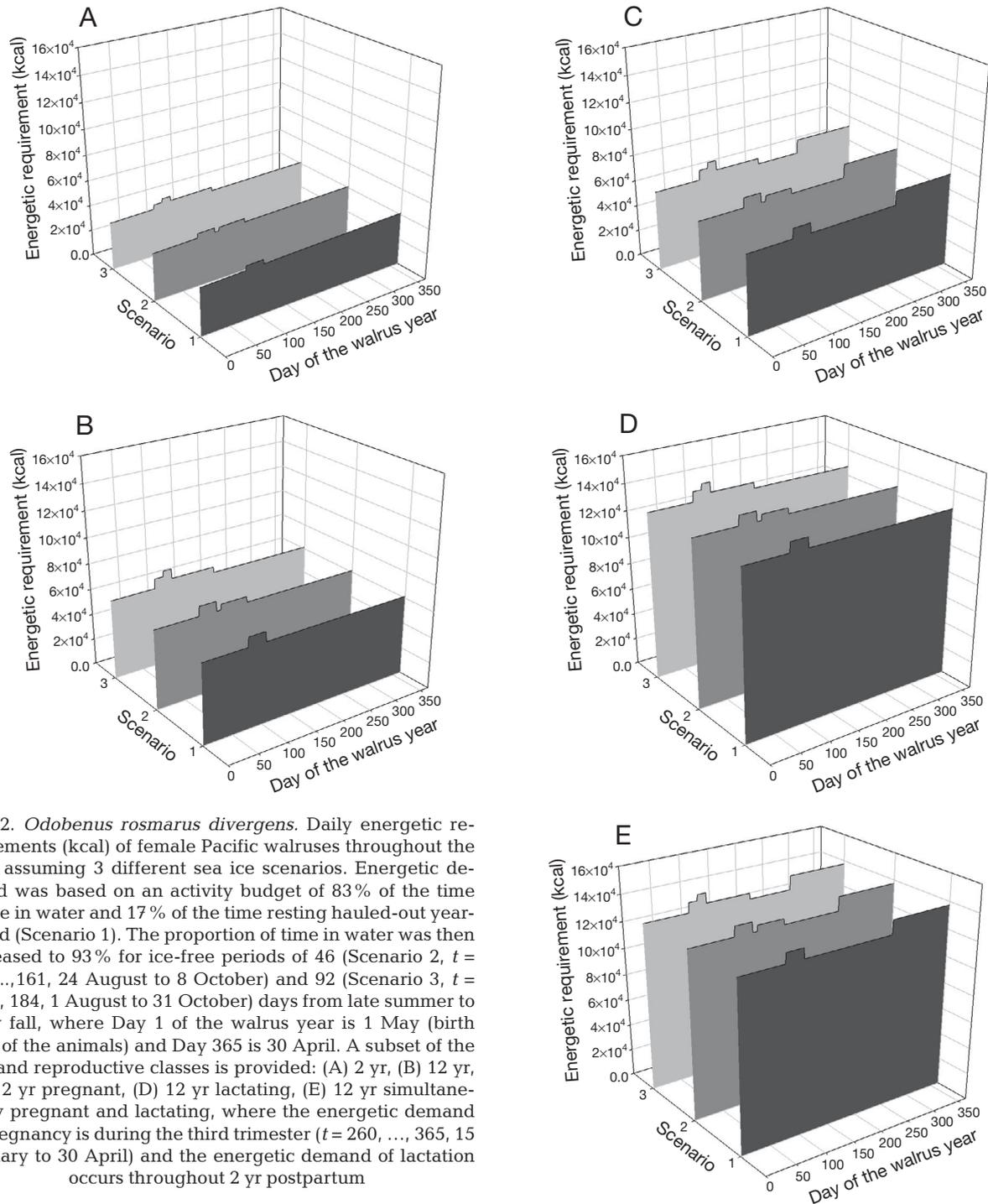


Fig. 2. *Odobenus rosmarus divergens*. Daily energetic requirements (kcal) of female Pacific walrus throughout the year assuming 3 different sea ice scenarios. Energetic demand was based on an activity budget of 83% of the time active in water and 17% of the time resting hauled-out year-round (Scenario 1). The proportion of time in water was then increased to 93% for ice-free periods of 46 (Scenario 2, $t = 116, \dots, 161$, 24 August to 8 October) and 92 (Scenario 3, $t = 93, \dots, 184$, 1 August to 31 October) days from late summer to early fall, where Day 1 of the walrus year is 1 May (birth date of the animals) and Day 365 is 30 April. A subset of the age and reproductive classes is provided: (A) 2 yr, (B) 12 yr, (C) 12 yr pregnant, (D) 12 yr lactating, (E) 12 yr simultaneously pregnant and lactating, where the energetic demand of pregnancy is during the third trimester ($t = 260, \dots, 365$, 15 January to 30 April) and the energetic demand of lactation occurs throughout 2 yr postpartum

ments, with the third trimester of pregnancy and lactation in 12 yr old walrus resulting in a 17 and 107% increase in daily caloric requirements from non-reproductive levels, respectively (Fig. 1).

Changes in the duration of the ice-free period, and hence the proportion of time in water, also impacted daily caloric requirements (Fig. 2). Although there was less than a 1% difference in annual energy

demand across the 3 ice scenarios (Tables 2 to 4), daily energy requirements increased by 6–7% for 0 to 12 yr old non-lactating females when the proportion of time in water increased from 83 to 93% of the time during 24 August to 8 October (Scenario 2) and 1 August to 31 October (Scenario 3; Fig. 2). The caloric demand of lactation minimized the signal associated with variable activity budgets; daily caloric

Table 3. *Odobenus rosmarus divergens*. Estimated annual and daily energetic needs for female Pacific walrus spending 83% of the time in water when sea ice is available and 93% of the time in water for 46 d of the year when sea ice is not available (24 August to 8 October) (Scenario 2). NA: not applicable; P: pregnant; L: lactating

Age class (mass range in kg)	Annual energetic demand (kcal)	Daily energetic demand (kcal)	Mass-specific energetic demand (kcal kg ⁻¹)	Daily clams consumed to meet energetic demand	Daily clams consumed as % body mass to meet energetic demand	% of day foraging to meet energetic demand
0 (65–95)	9 446 267	16 359–33 113	170–257	NA	NA	NA
1 (95–270)	13 091 047	33 147–37 714	137–175	NA	NA	NA
2 (270–345)	14 569 826	37 022–41 881	120–145	3200–3620	13–15	28–31
3 (345–420)	15 262 378	40 522–45 426	97–126	3502–3926	9–12	30–34
4 (420–495)	16 041 934	40 517–46 799	93–106	3502–4045	9–10	30–35
5 (495–570)	17 158 637	45 830–51 389	81–100	3961–4442	8–10	34–39
6 (570–645)	18 059 900	46 314–53 507	79–91	4003–4625	8–9	35–40
7 (645–725)	19 762 394	50 813–58 612	77–88	4392–5066	7–8	38–44
8 (725–755)	20 948 727	55 470–62 869	76–86	4794–5434	7–8	42–47
9 (755–785)	21 582 657	57 183–64 787	75–85	4942–5600	7–8	43–49
10 (785–810)	22 158 926	58 878–66 595	74–84	5089–5756	7–8	44–50
11 (810–830)	22 626 821	60 279–68 074	74–84	5210–5884	7–8	45–51
12 (830)	22 835 542	61 392–68 960	74–83	5306–5960	7–8	46–52
12 P (830)	23 958 612	61 392–71 987	74–87	5306–6222	7–8	46–54
12 L (830)	46 775 527	126 981–134 549	153–162	10 975–11 629	15	95–101
12 P&L (830)	47 898 597	126 981–137 576	153–166	10 975–11 891	15–16	95–103

Table 4. *Odobenus rosmarus divergens*. Estimated annual and daily energetic needs for female Pacific walrus spending 83% of the time in water when sea ice is available and 93% of the time in water for 92 d of the year when sea ice is not available (1 August to 31 October) (Scenario 3). NA: not applicable; P: pregnant; L: lactating

Age class (mass range in kg)	Annual energetic demand (kcal)	Daily energetic demand (kcal)	Mass-specific energetic demand (kcal kg ⁻¹)	Daily clams consumed to meet energetic demand	Daily clams consumed as % body mass to meet energetic demand	% of day foraging to meet energetic demand
0 (65–95)	9 524 080	16 359–33 113	170–257	NA	NA	NA
1 (95–270)	13 205 142	33 147–39 804	137–185	NA	NA	NA
2 (270–345)	14 696 536	37 022–44 608	120–154	3200–3856	13–16	28–34
3 (345–420)	15 397 148	40 522–48 359	97–133	3502–4180	9–13	30–36
4 (420–495)	16 180 829	40 517–49 785	93–113	3502–4303	9–11	30–37
5 (495–570)	17 309 268	45 830–54 660	81–106	3961–4724	8–10	34–41
6 (570–645)	18 216 691	46 314–56 888	79–96	4003–4917	8–9	35–43
7 (645–725)	19 934 069	50 813–62 315	77–93	4392–5386	7–9	38–47
8 (725–755)	21 131 945	55 470–66 841	76–91	4794–5777	7–9	42–50
9 (755–785)	21 771 432	57 183–68 880	75–90	4942–5953	7–9	43–52
10 (785–810)	22 352 884	58 878–70 803	74–89	5089–6120	7–9	44–53
11 (810–830)	22 824 996	60 279–72 375	74–89	5210–6255	7–8	45–54
12 (830)	23 035 964	61 392–73 317	74–88	5306–6337	7–8	46–55
12 P (830)	24 159 034	61 392–73 317	74–88	5306–6337	7–8	46–55
12 L (830)	46 975 949	126 981–138 906	153–167	10 975–12 006	15–16	95–104
12 P&L (830)	48 099 019	126 981–138 906	153–167	10 975–12 006	15–16	95–104

demand of 12 yr old lactating females only increased by 3% as the proportion of time in water increased (Fig. 2). Nonetheless, the timing and duration of the sea ice-free period was important because increased energetic demands associated with increased time in water is additive when it overlaps with other ener-

getically demanding life history stages, particularly the molt and lactation (Fig. 2). Effects on annual caloric demand became more important as the duration of the ice-free period increased and the proportion of time spent in the water increased to its maximum potential value (Fig. 3).

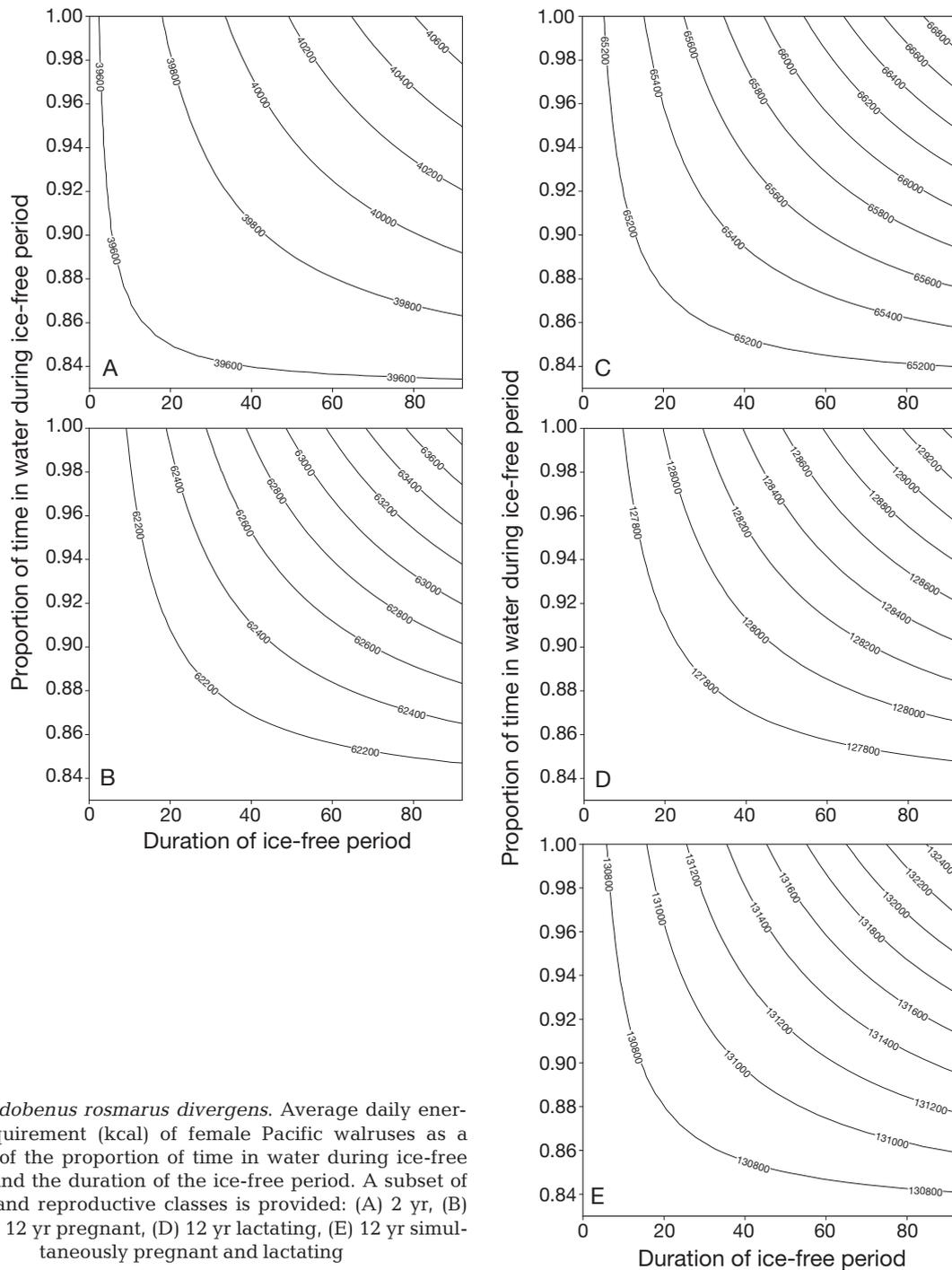


Fig. 3. *Odobenus rosmarus divergens*. Average daily energetic requirement (kcal) of female Pacific walruses as a function of the proportion of time in water during ice-free periods and the duration of the ice-free period. A subset of the age and reproductive classes is provided: (A) 2 yr, (B) 12 yr, (C) 12 yr pregnant, (D) 12 yr lactating, (E) 12 yr simultaneously pregnant and lactating

Validation

The predicted energetic requirements of mature (≥ 6 yr old), 570–830 kg non-reproductive walruses were in agreement with estimates from other studies. Daily energy requirements during an ice-available year (46 314–68 960 kcal d^{-1}) fell within the range of calories consumed (22 500–70 300 kcal d^{-1}) by 250–

1200 kg captive walruses (Fay 1982, Gehrich 1984, Fisher et al. 1992, Kastelein et al. 2000). In contrast, the estimated daily energy requirements for the young of the year (age-0 class; 16 359–33 113 kcal d^{-1}) were nearly double that of a 10–12 mo old captive walrus fed formula (approximately 11 000–14 000 kcal d^{-1} estimated from Figs. 4 & 5 in Kastelein et al. 2003) and the estimated energy requirements for 2–4 yr

olds were more than 10 000 kcal d⁻¹ over intake rates for a captive female walrus followed longitudinally from 2 to 4 yr postpartum (Gehrich 1984).

Nonetheless, the estimated daily caloric requirements (range: 37 022–73317 kcal d⁻¹) for milk-independent, non-reproductive female walrus aged 2–12 yr across all 3 sea ice scenarios could be met within our assumed limits to proportion of time foraging (<83–93%) and ingestion rate (≤15–20% of body mass d⁻¹) based on a clam diet. Daily energetic demands were met by foraging 28–55% of the day and consuming 7–16% of body mass in clams per day (Tables 2 to 4). In fact, ingestion rates (7–9% of body mass d⁻¹) for sexually mature walrus ≥6 yr were similar to previous estimates for wild mature Atlantic (Born et al. 2003) and Pacific (Fay 1982) walrus based on underwater observations of clam consumption and analyses of stomach contents, respectively. We did not estimate foraging time or clam consumption for the 0 and 1 yr age classes (Tables 2 to 4) because these animals are milk-dependent to varying degrees through 2 yr postpartum (Fay 1985), and without empirical data we cannot estimate the contribution of clams to their daily caloric need.

The ability of reproductive female walrus to meet caloric requirements within our criteria was dependent on the stage of reproduction. Across all 3 sea ice scenarios, 12 yr old pregnant females met daily caloric demand by foraging 46–55% of the time and consuming 7–8% of body mass in clams per day (Tables 2 to 4). Lactating and simultaneously pregnant and lactating females, however, required consumption rates approaching our upper limit to ingestion (15–16% of body mass in clams per day) and required 95–104% of the time for foraging to meet daily energetic needs, which is not possible.

Elasticity

Elasticities to model parameters spanned nearly 2 orders of magnitude, ranging from <0.01 to 1.00 (Table 5). For non-reproductive walrus, elasticities to digestive efficiency (D), growth premium ($G[t]$), and cost of activity in water (C_w) had values close to unity and were larger than elasticities to any other parameters. Elasticity to mass ($M[t]$) was also relatively high. Elasticities to D and $M[t]$ remained unchanged for reproductive walrus, but elasticity to C_w was reduced during lactation, when elasticities to both C_w and C_l were about half the elasticity to D . Elasticities to the other metabolic cost parameters (C_h , C_p , and C_m) were relatively negligible regardless of reproductive status.

Table 5. *Odobenus rosmarus divergens*. Elasticities of mean annual energy requirements to bioenergetic parameters for walrus where D is the digestive efficiency, $M(t)$ is the mass on day t , C_l is the cost of lactation, $G(t)$ is the growth premium, C_w is the cost of being active in water, C_h is the cost of resting while hauled out, C_p is the cost of pregnancy, and C_m is the cost of molting

Parameter	Elasticity	
	Non-reproductive	Pregnant and nursing
D	1.00	1.00
$M(t)$	0.75 ^a	0.75
C_l	–	0.50
$G(t)$	0.99	–
C_w	0.92	0.44
C_h	0.07	0.03
C_p	–	0.02
C_m	0.01	0.00

^aMean value for ages 0–12; this was the only parameter with age-dependent elasticities (see 'Results')

DISCUSSION

Estimating the daily energy requirements of marine mammals is difficult. Metabolic rates are influenced by activity level, age (and hence growth), body size, molt (for pinnipeds), reproductive status, and environmental conditions (Kleiber 1975, Costa et al. 1986, Costa 2002, Noren 2002, Williams et al. 2007). Bioenergetic modeling is a flexible technique for estimating food consumption of wild pinnipeds because it can account for the influence of some of these factors (Winship et al. 2006). Here we present a bioenergetics model that provides estimates of the energetic demands of female Pacific walrus per a given age and reproductive class. This model estimates the metabolic costs of growth and activity (active in water or hauled-out resting) based on walrus-specific field metabolic rates (direct measurement of whole animal metabolism; Acquarone et al. 2006) and observed activity budgets of walrus in the Bering Sea (Udevitz et al. 2009).

We assessed the relative effects of potential errors in the parameter values used in the model (see parameter value section in the 'Materials and methods' and Table 1) by calculating the elasticity of mean daily energy requirement to each of these parameters. This elasticity analysis indicated that potential errors in values for digestive efficiency (D), the growth premium ($G[t]$, for juveniles), and cost of activity in water (C_w) would have the most serious effects on our estimates of energy requirements (Table 5). Nonetheless, the value we used for D was based on direct measurements of digestive efficiency

in female walruses, which did not vary by diet or age (Fisher et al. 1992), and is consistent with the high efficiencies reported for various carnivorous mammals (see Table 3.5 in Blaxter 1989; see Table 4 in Lavigne et al. 1982), as well as for other pinniped species, which ranged from 90.4 to 97% when fed diets of clams, squid, or various fish (see Table 3 in Rosen & Trites 2000). Values for $G(t)$ were based on direct measurements of metabolism from immature harp *Phoca groenlandica* and gray *Halichoerus grypus* seals (Worthy 1987) because this type of data was not available for immature odobenids or otariids. Future research should focus on obtaining walrus-specific measurements of metabolism throughout ontogeny, even though errors in this parameter will only affect caloric requirement estimates for walruses <6 yr old. The parameters C_h and C_w entered the model symmetrically; elasticity to C_h was less than the elasticity to C_w only because we set the proportion of time in water, $P_w(t) = 0.83$ for these analyses. Elasticity to C_h would increase with a corresponding decrease in the elasticity to C_w as the proportion of time in water decreased. Errors in values for these parameters will be most important for non-lactating females. In any case, the value we used for C_w was based on direct field metabolic rate measurements from walruses (Acquarone et al. 2006), and this value as well as the value for C_h (Table 1) were within the range of field (5–6 times Kleiber-predicted basal metabolic rate [BMR]; Costa et al. 1991, Costa & Williams 1999, Costa 2002) and maintenance (1.4–2.8 times Kleiber-predicted BMR; for review see Williams et al. 2001) metabolisms measured directly from a range of pinniped species, which suggests they are robust. Elasticities to mass ($M(t)$) and lactation costs (C_l) were lower than those to D and $G(t)$, but still non-negligible relative to elasticities associated with other parameters. Values for $M(t)$ were based on data from Pacific walruses (Fay 1982), but do not reflect seasonal fluctuations. However, because energy gained during one period is expended in another (Winship et al. 2002), this should not affect estimates of annual energy requirements. Our value for C_l was based on food consumption of wild, lactating California sea lions temporarily under human care (Williams et al. 2007), but this value is also consistent with levels of intake reported for other lactating mammals, including domestic dogs *Canis familiaris* (Case 1999), free-ranging African lions *Panthera leo* (Schaller 1972), and Antarctic fur seals *Arctocephalus gazella* (Costa et al. 1989).

As would be expected due to the mass-related scaling of metabolism and the influence of growth on

metabolism (Kleiber 1975), daily energy demand on average over the year across non-reproductive walruses was approximately 2 times greater in the oldest (largest) walruses compared to age-0 walruses, while mass-specific daily energy demand was nearly 3 times greater for age-0 walruses compared to ≥ 6 yr old age classes that were approaching the asymptote for mature body mass. Daily consumption of clams on average over the year declined with the size of the walrus from 14 to 7% of body mass d^{-1} for non-reproductive 2–12 yr old females. These differences highlight the vulnerability of the youngest age classes during food-limited periods because they must acquire proportionally greater amounts of prey. At the same time, the youngest age classes of walruses may be similar to other young pinnipeds in that small body size combined with underdeveloped diving physiology limits foraging capabilities (for review see Noren et al. 2005). These factors combined may explain the disproportionate deleterious effects on juveniles during prey-limited periods (DeLong et al. 1991).

In addition to the influence of body size and growth on caloric requirements, certain life history stages induce additional energetic demands. One of these stages for pinnipeds is the molt. Until recently, the cost of pinniped molting was considered to be low (Ashwell-Erickson & Elsner 1981, Worthy et al. 1992), and as a result these costs were not included in most bioenergetics models (i.e. Olesiuk 1993, Mohn & Bowen 1996, Stenson et al. 1997, Winship et al. 2002). However, a recent study on California sea lions demonstrated that resting metabolism increased by 1.3 times during the molt (Williams et al. 2007). Using this value in our model, we estimated that the annual 30 d molt (Fay 1982) of a 12 yr old female costs a total of 227040 extra kilocalories. Although this only accounts for 1% of the animal's total annual energetic requirements, it translates into an energetic demand of nearly 20000 extra clams to sustain the cost of the molt. Although walruses in captivity generally consume less during the molt than at other times (Gehnrich 1984, Dittrich 1987, Kastelein et al. 2000), radio-tracking of Pacific walruses indicates that foraging behavior is ongoing during the molt period (USGS, Alaska Science Center unpubl. data). If endogenous reserves (i.e. blubber) are not increased outside of the molting period to compensate for this increased energetic burden, aggregations of highly gregarious molting walruses may have a negative short-term impact on localized prey resources.

Reproduction has also been largely ignored in bioenergetic estimates for pinnipeds (Olesiuk 1993,

Mohn & Bowen 1996, Stenson et al. 1997) with the exception of a bioenergetics model for Steller sea lions (Winship et al. 2002). Although measurements of resting metabolism were similar for non-lactating and lactating fur seals (Costa & Gentry 1986) as well as for non-reproductive, pregnant, and lactating California sea lions (Williams et al. 2007), food consumption was greater in the lactating fur seals (Costa et al. 1989) and later-stage pregnant and lactating California sea lions (Williams et al. 2007) compared to their non-reproductive counterparts. For example, food consumption increased substantially within the first few days of lactation and was maintained at a consistently high level until 2 wk after weaning (Williams et al. 2007, T.M. Williams pers. comm.). Indeed, food intake was 11% (Costa et al. 1991) and 5% (Winship et al. 2006) of body mass d^{-1} for lactating and non-lactating California sea lions, respectively. Thus, during reproduction there can be a mismatch where an increase in food consumption is not reflected by the measured metabolism (Williams et al. 2007). Pinnipeds are similar to other mammals, where there is little additional metabolic cost to milk synthesis but lactation is fueled by greater caloric intake (Hammond & Diamond 1992). As with other pinnipeds, marked increases in food consumption have been observed for pregnant and lactating captive walruses. Females consumed 30–40% more food when pregnant and 50–101% more food when lactating compared to non-reproductive periods, while simultaneously lactating and pregnant females were estimated to increase food consumption by 90–130% (Gehrich 1984, Kastelein et al. 2000).

In our model, the effect of reproduction had a pronounced impact on estimated caloric requirements (Fig. 1) and the time that the animal must allocate to foraging to meet these demands (Table 2). For example, during each day of the last trimester, an 830 kg 12 yr old female had an extra energetic burden of 10595 kcal d^{-1} . For walruses, the third trimester lasts approximately 106 d, thus the total energetic burden of pregnancy (assuming there are no costs during the first and second trimesters) for a 12 yr old female is 1123070 kcal, equivalent to nearly 100000 clams. The caloric demand of a lactating 12 yr old walrus during an ice-available year (83% of time in water year-round) doubled from non-reproductive levels, with the result that corresponding clam consumption doubled from 7–8% to 15% of body mass d^{-1} and the estimated proportion of time required to forage increased from 46–52% to 95–101% of the time (or 95–103% of the time when the animal was simultaneously pregnant and lactating; Table 2). Clearly,

proportions of time spent foraging >83% are not possible, given our baseline assumption that walruses only spend a total of 83% of their time in the water. Undoubtedly some of the energetic demand of lactation is met by utilizing endogenous energy reserves (e.g. blubber), which is consistent with the observation that blubber thickness varies with reproductive condition in female walruses (Fay 1985). Changes in lipid stores and the blubber layer have also been associated with the demands of lactation in California sea lions (Williams et al. 2007).

Walruses likely undergo periods of weight gain to build up energy stores and subsequently lose weight during other periods, such as during the breeding season and molt as is evident in other pinnipeds, particularly phocids (Chabot et al. 1996). Captive female walruses have been observed to fast briefly, and their food consumption rates are known to vary seasonally (Kastelein et al. 2000). It has been suggested that Pacific walruses eat little on their northward spring migration (Fay 1982) while summer (July to September) and autumn (October to December) migrations are marked by high food intake (Fay 1985). However, recent radio-tracking studies indicate that walruses do forage during the spring migration (USGS, Alaska Science Center unpubl. data). Detailed data on the body condition of female walruses across reproductive stages and seasons are not available, thus further research is necessary before we can allocate differential food intake rates across seasons. If there are intermittent periods of fasting and subsequent periods of excessive consumption to bolster lipid storage, food consumption and caloric requirements may be uncoupled on a daily basis such that daily calories consumed will be more variable than those estimated by our model. Nonetheless, on an annual basis, food consumption must equal caloric requirements because energy gained during one period is expended in another (Winship et al. 2002).

Although caloric requirements associated with basic physiology of walruses are unlikely to change, caloric requirements may change as behavior is altered in response to environmental change. For example, environmentally induced changes in haul-out behavior could alter energy requirements of walruses (Fay & Ray 1968). If walruses continue to increase utilization of terrestrial haul-outs as seasonal sea ice availability in the Chukchi Sea decreases (Douglas 2010), they may spend greater amounts of time in water actively transiting to productive foraging areas (Jay et al. 2011). In our model, when the proportion of time in water was increased from 83 to 93% of the time during ice-free periods, daily energy

requirements increased by 6–7% for 0–12 yr old non-lactating female walruses (Tables 2 to 4). The timing of the sea ice-free period is also important because the increased energetic demands of increased time in water associated with ice-free periods can overlap with energetically costly life history stages, such as the molt, pregnancy, and lactation. Considering that walruses are gregarious on terrestrial haul-outs, the increased energetic requirement at the population level could have an impact on localized prey resources, where they might not be able to sustain the energetic demands of walruses during sea ice-free periods.

Our model provides the first bioenergetics-based estimates of energy requirements for Pacific walruses, and includes an estimate of the effect on energetic requirements that could result from potential haul-out behavior changes in response to seasonal reductions in sea ice. Unlike most bioenergetics models for pinnipeds (e.g. Olesiuk 1993, Mohn & Bowen 1996, Stenson et al. 1997), ours incorporates costs of reproduction and molting, which can be substantial. Still, the model is, of necessity, relatively simple because of the lack of data on walrus physiology required to support a more complex model. Estimates of parameters in the current model may be improved by obtaining species-specific data on seasonal variation in food consumption and body condition to support extensions to account for seasonal variations in the acquisition, use, and storage of energy by walruses. These types of extensions, in combination with more detailed accounts of the variation in activity throughout the year (proportion of time in water and time hauled out), could support bioenergetic linkages between prey distribution and walrus demography that can ultimately be used for predicting population responses to their changing environment.

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