Received: 25 March 2020 | Accepted: 17 July 2020

DOI: 10.1111/mms.12743

ARTICLE

Marine Mammal Science

Resting and swimming metabolic rates in juvenile walruses (*Odobenus rosmarus*)

David A. S. Rosen[1,2]

[1]Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada

[2]Vancouver Aquarium, Vancouver, British Columbia, Canada

Correspondence
Institute for the Oceans and Fisheries, 2202 Main Mall, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada.
Email: rosen@zoology.ubc.ca

Funding information
Natural Sciences and Engineering Research Council of Canada

Abstract

Changes in Arctic ice conditions have raised concerns regarding potential impacts on energy expenditure and food requirements of walruses. Modeling the repercussions of environmental changes requires accurate species-specific measures of bioenergetic expenditures. This is particularly true for walruses, who have a unique anatomy and foraging ecology from other pinnipeds. This study measured resting metabolic rate (RMR) and subsurface swimming metabolism in two juvenile walruses over a 13-month period. The walruses had relatively low RMR compared to studies of other young pinnipeds. RMR was greater for the male than the female, as expected given its larger size; the reverse was true on a mass-specific basis. There was also considerable variability in RMR for each walrus during the year that could not be accounted for by changes in body mass. Metabolism while swimming was about twice RMR, and locomotor costs were higher than generally predicted for other marine mammals. The lower calculated swimming efficiency may reflect the fact that walruses are not "high velocity" pursuit predators. The estimates of metabolic expenditure obtained in this study for young walruses are invaluable for quantifying the energetic consequences of behavioral changes induced by environmental shifts in the wild.

KEYWORDS

bioenergetics, metabolism, *Odobenus rosmarus*, swimming, walrus

1 | INTRODUCTION

Walruses (*Odobenus rosmarus*) are considered an ice-dependent Arctic species given they rely on this substrate for calving and as a stable platform for hauling out in close proximity to foraging grounds. Recent changes in Arctic ice conditions have raised concerns about the impact of these environmental changes on the rates of energy expenditure of walruses that have to travel further to acquire prey or spend more time in the water (Jay, Marcot, & Douglas, 2011; MacCracken, 2012; Taylor et al., 2018).

The potential effects of environmental changes on the energy balance of individuals can be explored through bioenergetic models, which are simplified mathematical representations of the animal's energy budget. A number of bioenergetic models have been constructed for marine mammals (e.g., Bejarano, Wells, & Costa, 2017; Villegas-Amtmann, Schwarz, Sumich, & Costa, 2015; Winship, Trites, & Rosen, 2002), including the walrus (Noren, Udevitz, & Jay, 2012, 2014, 2016). Such models can be expanded to incorporate the energetic consequences of hypothesized or observed behavioral changes, and can be linked to estimates of individual health and population parameters (New et al., 2014; Pirotta et al., 2018).

For example, Udevitz, Jay, Taylor et al. (2017) modeled the energetic costs of behavioral changes associated with predicted decreases in the extent of summer sea ice cover for adult female walruses in the Chukchi Sea. The model combined general circulation model projections of future ice with observed movement data from tagged walrus (Jay, Taylor, Fischbach, Udevitz, & Beatty, 2017). At the core of the model were individual-based bioenergetic models of walrus energy requirements (Noren et al., 2012, 2014).

Rarely are species-specific data available to fully parameterize these models to the target animal, requiring various levels of substitutions and estimations from other species. The strength and accuracy of any model's predictions rely upon the quality of the underlying data. Given a lack of direct measurements, previous walrus bioenergetic models (Noren et al., 2012, 2014, 2016; Udevitz et al., 2017) have had to extrapolate from either other bioenergetic parameters (e.g., food intake and growth) or other marine mammal species for two key bioenergetic parameters, resting metabolic rate (RMR) and the cost of locomotion (activity).

RMR is a comparative physiological measure of the energy expended by an individual under set conditions: nonactive, awake but quiescent, thermoneutral, and free of the effects of digestion or previous exercise (National Research Council [U.S.], 1981). RMR is elevated in younger animals, partly as a result of the increased cost of growth (both directly and the upregulation of metabolic processes to facilitate somatic growth) (Kleiber, 1975). There is considerable historical debate about whether marine mammals exhibit higher RMR than their terrestrial counterparts (e.g., Lavigne et al., 1986b; Williams, Haun, Davis, Fulman, & Kohin, 2001). To date, there are no published measurements of RMR for walruses, although there are reasons to suspect that it may be lower than that of other pinnipeds given their unique ecological niche (Fay, 1982; Lydersen, 2018).

Accurate estimates of RMR are also important as they serve as the foundation of many bioenergetic models and can therefore have a substantial impact on total calculated energy/food requirements, which are often applied to ecosystem-level questions (e.g., Bowen, 1997; Trites, Christensen, & Pauly, 1997). The effect of inaccurate estimates of RMR can be further exaggerated if certain costs—such as the cost of activity—are incorporated into models as a multiple of RMR. The cost of locomotion is typically the largest “voluntary” cost within an animal's energy budget (Karasov, 1992). Accurate estimates of the cost of locomotion are not just important for accurate bioenergetic models, but are critical for translating observed or predicted behavioral changes into estimates of changes in food requirements. The vast majority of locomotion research in marine mammals has been directed at estimating the costs of diving to depth, which is physiologically distinct from horizontal movement at or near the surface (Fish, 1992; Kooyman, Castellini, & Davis, 1981; Videler & Nolet, 1990). Only a handful of studies have directly measured the costs of swimming in marine mammals, and no studies have measured this in the walrus (see table 3.1 in Williams & Maresh, 2015). The paucity of data among pinnipeds, and the unique anatomy and swimming gait of the walrus (Gordon, 1983; Pierce, Clack, & Hutchinson, 2011), suggest that it is impossible to confidently extrapolate findings from other species to the walrus.

This study used two young walruses under human care to measure RMR while resting in water and the cost of subsurface swimming. It also examined changes in RMR with body mass over the 13-month study period. The data are important for incorporating into bioenergetic models in order to accurately predict the impact of observed or predicted behavioral changes induced by environmental changes in the Arctic on the energy balance and food requirements of young walruses in the wild.

2 | METHODS

2.1 | Study animals

The study used a young male (ZIMS ID #100090) and female (#100089) walrus that had been born in the Aquarium du Québec (Québec City, Canada) in May 2016. The male was a Pacific subspecies (*Odobenus rosmarus divergens*), while the female was the offspring of an Atlantic subspecies mother (*Odobenus rosmarus rosmarus*) and (the same) Pacific subspecies father. The animals were temporarily transferred to the Vancouver Aquarium in December 2017, at about 18 months of age, and remained until November 2019.

Body mass was measured to ±0.1 kg several times per week by having individual animals station on a platform scale prior to the morning meal. Body mass was also recorded within 1 day of metabolic trials. Food intake was allowed to vary naturalistically, with husbandry staff adjusting offered food levels based on animal appetite and behavior. The diet was composed primarily of a mixture of invertebrates (mussels, shrimp, clams) supplemented with fish (herring, capelin, mackerel, hake). The walruses were trained to take part in research activities using positive reinforcement. All research was conducted under Animal Care permits from the Vancouver Aquarium and the University of British Columbia (A18-0056).

2.2 | Measures of oxygen consumption

Measures of oxygen consumption during resting and swimming activities were made using a flow through respirometry system. A 410 L floating respirometry dome was attached to a Sable Systems Flowkit (Sable Systems, North Las Vegas, NV) mass flow generator/controller pulling a constant 400 L/min through the dome. An extended inflow port tube ensured no significant backflow out of the dome during respirations (validated using forced air simulations). The flow was sufficient to maintain instantaneous O_2 concentration > 20.0% and CO_2 concentration < 1%. A subsample of the excurrent air was dried (Dririte) and analyzed for O_2 and CO_2 concentrations using a Sable Systems Field Metabolic System. Gas concentrations were baselined against outside air at the start and end of each trial to correct for potential system drift. Additionally, the entire system was periodically calibrated against known gases and leak-tested using nitrogen dilution. Data were recorded every second to a PC using Expedata software. Environmental and flow temperature and humidity were also recorded through each trial (Vaisala Humicap HM40). Data were subsequently analyzed via LabAnalystX (Mark Chappell, University of California) using appropriate equations from Withers (1977) to convert changes in gas concentrations into rates of instantaneous oxygen consumption over the target period.

2.3 | Resting metabolic rate

The walruses were initially trained over a period of 3 months to remain calm within the floating respirometry dome for increasingly extended sessions. They typically held a vertical position by steadying themselves with their fore-flippers against the side of the pool. This training period was critical for accurate data, as past experience has demonstrated that animals must not only be physically inactive during measurements, but also comfortable (nonstressed).

Data collection occurred between September 4, 2018, and October 10, 2019 (~2.3–3.5 years of age), and were interspersed with reinforcement training sessions. Trials lasted 8–9 min, sufficient to obtain >5 min of stable rates of oxygen consumption. The animals were fasted overnight >16 hr prior to trials to preclude any effects of digestion on metabolism (Rosen & Trites, 1997), but were reinforced throughout the trial with minimal food (<1.0 kg) via a one-way tube to maintain their calm behavior.

2.4 | Swimming trials

Subsurface swimming trials were conducted between October 10 and November 22, 2019, at the end of the study period following a 3-month training period that included several mock (prefasted) trials. The walruses were trained to remain submerged while swimming a set course in a pool, surfacing only within the floating respirometry dome upon completion of the task. With the aid of target poles submerged ~1.2 m below the surface, the walruses swam from next to the respirometry dome directly to the diagonal corner of the research pool and back three times, for a total swimming distance of 110 m. The time to transit each of the six segments was recorded on a digital stopwatch, allowing the calculation of average swimming speed from total swimming time (including the minimal time required to change direction). After completing the three laps without breathing, the animals surfaced in the respirometry dome, and remained there until instantaneous rates of oxygen consumption reached a stable level for 2 min (generally starting between 5–8 min after surfacing). This was deemed the postexercise resting level, as it was not possible to obtain pretrial RMR measurements. However, the values were not dissimilar from measures of RMR obtained during the latter portion of the study.

The total cost of swimming during a trial was estimated by integrating the instantaneous oxygen consumption rate over the entire postswim surface interval, and subtracting the measured postexercise resting levels over the entire "recovery" period. In theory, the "extra" oxygen consumed postexercise above resting levels represents the oxygen used during the submerged swimming portion of the trial. This measure could also be converted into rate of oxygen consumption while swimming at a given speed by dividing by the total submergence time.

This method of estimating the cost of activity while breath-holding is the same as that used for estimating the costs of individual dives (e.g., Hastie, Rosen, & Trites, 2007; Young, Rosen, Hindle, Haulena, & Trites, 2011), but different from studies that estimate metabolism over a "dive cycle" (e.g., Castellini, Kooyman, & Ponganis, 1992; Fahlman, Svard, Rosen et al., 2008). It assumes that the costs of swimming and resting are strictly additive, and that the animals are fully recovered from their exercise during the immediate postsurfacing interval. While violation of these assumptions may lead to underestimates of true costs, it is a standard method of determining swimming and diving costs that allows valid comparisons to other studies and species.

2.5 | Statistical tests

Measures of RMR and RMR_M were compared between the male and female walrus using a Welch's two-way unpaired *t*-test, with $\alpha = .05$. Given the small sample size of the male for the surface swimming trials, no statistical comparisons were performed and results are reported as means with standard deviations.

3 | RESULTS

3.1 | Resting metabolic rate

Resting metabolic rate (RMR) was measured as milliliters of oxygen consumed per minute, which can be converted into MJ d^{-1} with a few reasonable assumptions on fuel use (1 L O_2 = 20.1 kJ). RMR for both walruses generally increased over the study period. Overall, RMR was higher for the male than the female ($t(32) = 2.7$, $p = .009$). RMR ranged from 35.2 to 68.3 MJ d^{-1} for the male and 30.0 to 55.8 MJ d^{-1} for the female (Figure 1). Body mass generally

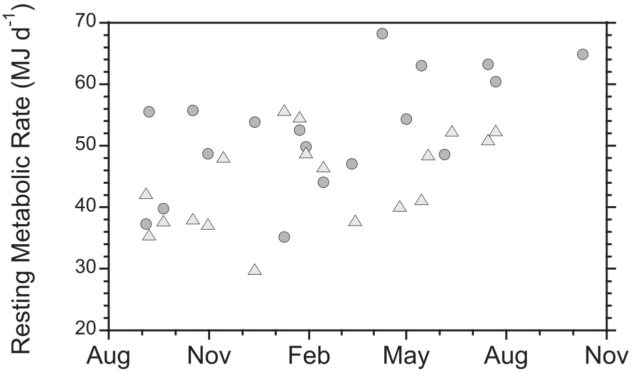

FIGURE 1 Measures of resting metabolic rate (RMR; MJ d^{-1}) for the male (dark circles) and female (light triangles) walrus over the 13-month study. Rates of measured oxygen consumption while resting in water were converted into rates of energy consumption.

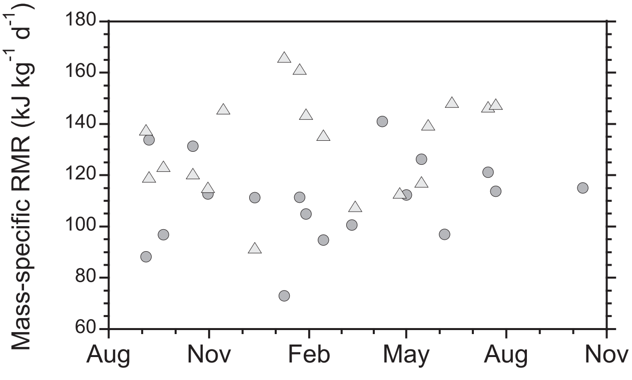

FIGURE 2 Measures of mass-specific resting metabolic rate (RMR$_M$; kJ kg^{-1} d^{-1}) for the male (dark circles) and female (light triangles) walrus over the 13-month study.

increased through the study, although growth was not constant. Mass for the male ranged between 410.5 kg and 601.5 kg, while mass for the female ranged from 298.0 to 383.2 kg. The general increase in RMR was not surprising given the growth of both animals over the study period, and the greater RMR of the male would similarly be expected given his greater mass.

Generally, larger individuals will tend to have higher metabolic rates, but the exact means of controlling for this effect—in order to discern changes not related to mass, such as seasonal rheostatic changes—are open to considerable debate (Glazier, 2005; Nagy, 1987). For simplicity I chose to express rates of energy consumption per kg body mass measured at the time RMR was measured (RMR$_M$; kJ kg^{-1} d^{-1}). However, to aid comparisons to other studies, I also expressed metabolism as a multiple of the basal metabolic rate (BMR) predicted by Kleiber's (1975) interspecific allometric equation for mature mammals ($\text{BMR} = 293\ M^{0.75} = 1 \times$ predicted metabolism), despite the fact that this scaling does not reflect developmental changes.

Mass-specific RMR (RMR$_M$) for the female (91.7–166.1 kJ kg^{-1} d^{-1}) was greater than that of the male (73.1–141.0 kJ kg^{-1} d^{-1}; $t(33) = 3.6$, $p = .001$; Figure 2). However, it is not possible to determine how much of this difference is the result of the scaling employed. Expressed in comparison to Kleiber's predicted BMR for mature terrestrial mammals, the range of metabolism of the male and female were almost identical (1.2–2.3 and 1.3–2.4 times predicted metabolism, respectively).

3.2 | Swimming metabolic rate

I successfully measured swimming metabolic rate eight times with the female walrus and four times with the male prior to their return to the Aquarium du Québec. Successful trials were those that met the criteria of completing all laps underwater without surfacing, with no behavioral hesitations or drifting from the set course, and where post-exercise metabolism was measured with calm animals until rates of oxygen consumption had stabilized for the defined interval.

The rate of total energy expenditure during submerged swimming for the male and female walrus while swimming at a very consistent average speed of 1.6 ± 0.1 and 2.1 ± 0.1 m s^{-1} averaged 145.5 ± 37.1 and 121.7 ± 27.1 kJ min^{-1}, respectively (Figure 3A). As with most measures of metabolism, there are numerous ways to express the cost of swimming. The corresponding mass-specific rates of metabolic expenditure for the male and female walrus while swimming were 242.9 ± 60.0 and 336.6 ± 84.4 J kg^{-1} min^{-1}, respectively. Alternately, the energy required to move 1 kg of body mass one meter (by incorporating appropriate swimming speeds) can be defined as the total cost of transport (COT_{TOT}; Schmidt-Nielsen, 1972). In the present study the COT_{TOT} for the male and female walrus were 2.6 ± 0.8 and 2.7 ± 0.6 J kg^{-1} m^{-1}, respectively (Figure 3B). However, all of these previously described estimates of the cost of swimming combine, by definition, the cost of physical activity and the underlying cost of maintenance. Therefore, the "additional" cost of moving 1 kg of body mass 1 m (net cost of transport; Schmidt-Nielsen, 1972) can be expressed as locomotor costs (LC; J kg^{-1} m^{-1}) by subtracting mass-specific resting metabolic rate from swimming costs (COT_{TOT}; Williams, 1989). For the male and female walrus, LC was 1.8 ± 0.6 and 1.7 ± 0.9 J kg^{-1} m^{-1}, respectively (Figure 3C).

4 | DISCUSSION

Numerous studies have measured RMR in pinnipeds, leading to a continuing debate on whether this taxonomic group has an elevated energy budget, and therefore higher prey requirements and potential ecological impact (Bowen, 1997; Smith, Link, Cadrin, & Palka, 2015; Trites et al., 1997). Past studies have also measured the cost of swimming in several pinnipeds and found energetic efficiencies similar to terrestrial runners (Williams, 1999). Walruses, however, are different in many respects from other pinnipeds. Unlike most marine mammals for which data are available, walruses are not "high velocity" pursuit predators, feeding primarily by grazing on mollusks and other sessile prey (Fay, 1981; Sheffield & Grebmeier, 2009). Walrus are among the largest of all pinnipeds, and their flipper anatomy and "rotund body shape" is also notably different than most other pinnipeds (Gordon, 1983; Kastelein, 2009; Pierce et al., 2011; Reidenberg, 2007). As a consequence, bioenergetic values measured in other pinnipeds cannot necessarily be used to substitute for those of walruses in predictive models.

In our study, average RMR of young, 2–3-year-old walruses ranged between 1.2–2.4-fold that predicted for adult terrestrial mammals of a similar size (Kleiber, 1975). This is similar to the 1.4–2.8-fold range reported for RMR of adult marine mammals in most interspecific comparisons (Hunter, 2005; Lavigne, Innes, Worthy, & Kovacs, 1986a; Smith, 1986; Williams et al., 2001), which is surprising given that mass-specific RMR of young mammals is usually elevated compared to adults (Kleiber, 1975; McNab, 1999; Poczopko, 1979). In fact, the values for RMR in the walruses in this study are notably lower than those reported for other young pinnipeds, although most studies have focused on relatively young pups (e.g., Davydov & Marakova, 1965; Donohue, Costa, Goebel, & Baker, 2000; Rea & Costa, 1992; Thompson, Ono, Oftedal, & Boness, 1987).

A lower than expected measured RMR has important implications for modeled energy requirements. For example, Noren et al. (2012) built a detailed bioenergetics model for 0–12 year old female walruses that, through a lack of species-specific data, required them to use estimates from California sea lions (*Zalophus californianus*) for their RMR parameter. The model estimated a RMR_M of ~2.8–3.0× Kleiber for a young, growing walrus in the same age group as our study animals. For a 335 kg, 2–3- year-old female, applying the lower RMR_M measured in our study model would result (all other parameters held equal) in a ~ 15% decrease (~24,500 kJ d^{-1}) in total daily energy expenditure than what was estimated from the Noren et al. (2012) model. A follow-up model based on walrus energy intake records (which was unable to disentangle metabolic costs of maintenance and activity) lowered the previous energy intake estimate for young walrus by ~6%, partly due to a reduction in the estimated cost of growth (Noren et al., 2014).

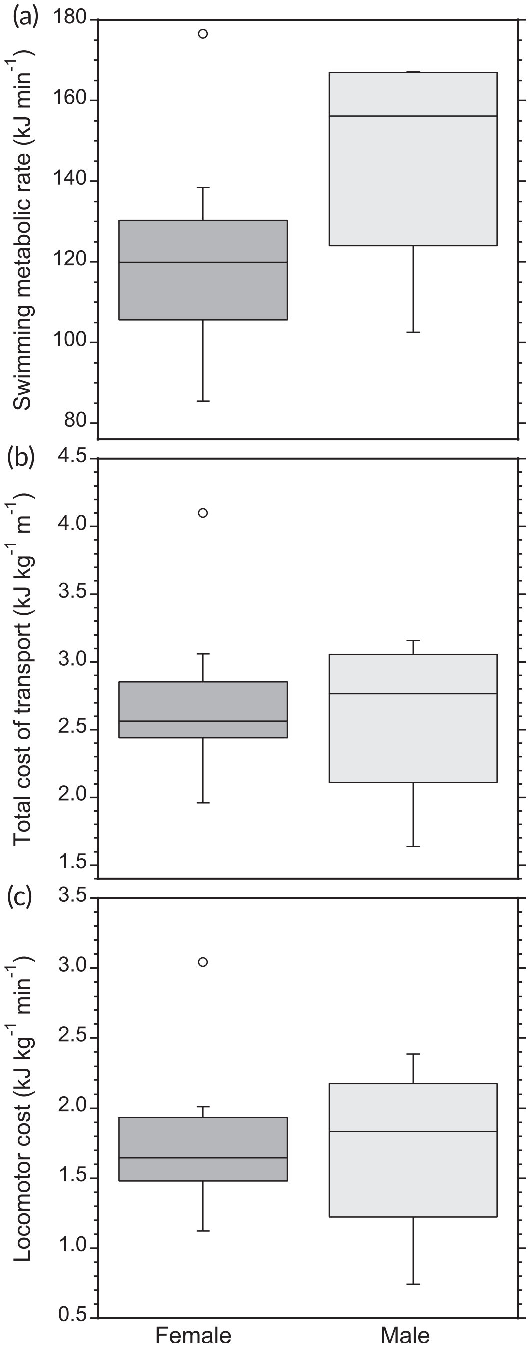

FIGURE 3 Metabolic expenditure of the female and male walrus expressed as: (3A, top) total metabolic cost (kJ min^{-1}); (3B, middle) total cost of transport (COT_{TOT}; kJ kg^{-1} m^{-1}), a measure of energy expended to move 1 kg of body mass 1 m; and (3C, bottom) locomotor cost (LC; kJ kg^{-1} m^{-1}), which estimates the additional costs of locomotion above resting levels. The boxplots define the median and the upper and lower quartiles; the whiskers represent the quartile ±1.5*IQD.

Both models were subsequently used to predict the effect of changing sea ice conditions on the health of Pacific walruses (Udevitz et al., 2017), where RMR values had a direct impact on estimated food requirements under different environmental conditions.

It is notable that RMR of the walruses in our study was not constant across the year, despite very rigorous behavioral testing criteria. While some of the variation was undoubtedly due to changes in body mass, there was also a two-fold difference in RMR_M that was independent of these changes. It is unclear from the present study whether this represents a regular seasonal cycle; seasonal shifts in RMR have been well documented in many pinniped species, and usually become more pronounced with maturity (e.g., Boily & Lavigne, 1997; Dalton, Rosen, & Trites, 2015; Hart & Irving, 1959; Renouf & Gales, 1994; Rosen & Renouf, 1998). Strong seasonal signals were also seen in the food intake of captive walrus (Kastelein, Schooneman, & Wiepkema, 2000; Noren et al., 2014). Seasonality is an aspect of walrus energetics that should be studied in more depth, particularly considering the possible role in defining vulnerable periods to environmental perturbations.

The effect of changes in RMR on total energy requirements may be overshadowed by changes in locomotion activity, the largest component of most mammalian energy budgets (Schmidt-Nielsen, 1972; Tucker, 1970). In this study, RMR of the walruses ranged from 25% to 55% of the total cost of swimming among all trials, similar to the range reported among other marine mammals (22%–77%; Williams, 1999) and similar to what can be extrapolated from field metabolic rates of walrus (Acquarone, Born, & Speakman, 2006; Noren et al., 2012). The COT_{TOT} for the walruses measured in our study (2.6–2.7 J kg^{-1} m^{-1}) was greater than that predicted by the interspecific relationship for marine mammals, including a number of pinniped species (Williams, 1999). This may have been because the animals may not have been swimming at optimal swimming speeds where costs are at a minimum (Fish, 2000), although the highly consistent preferred speeds of the two walrus were not too dissimilar from those predicted by the general equation proposed by Videler and Nolet (1990). More importantly, the higher COT_{TOT} of the walruses was at least partly due to the fact that, as young animals, they have higher underlying maintenance costs. COT_{TOT} values for young Steller sea lions *Eumetopia jubata* (Rosen & Trites, 2002) are similarly greater than what would be predicted from the general marine mammal equation.

Calculating the locomotor costs (LC) has been proposed as an alternate way of expressing the costs of movement, by controlling for differences in maintenance costs (Schmidt-Nielsen, 1972). Even after accounting for differences in RMR, LC in the walruses in this study was still elevated compared to what would be predicted for other marine mammals of a similar mass (fig. 2 in Williams, 1999). Again, the reasons are unclear, but may relate to the general observations that, as grazers, walruses generally swim at relatively low velocities for their size (Born et al., 2014; Kastelein, 2009), are not very streamlined (Fish, 2000), and have an intermediate or mixed form of aquatic locomotion compared to other pinnipeds (Pierce et al., 2011).

Regardless of the root of these differences, this is the first study to directly measure the costs of subsurface swimming in the walrus, and the results can be directly incorporated into bioenergetic disturbance models (Udevitz et al., 2017). However, it is important to note that not all types of activity have a similar cost. Additional studies that estimate the costs of diving, as well as the energy expended foraging at depth, will greatly improve overall accuracy in quantifying behavior changes into energetic consequences. This is also the first study to measure RMR in young walrus. However, additional studies are required to measure whether there are significant differences in energy expenditure between walrus resting in the water or in air, and explore the effect of season and age on bioenergetic demands. Together, these types of data are invaluable for building more accurate bioenergetic models to predict the consequences of environmental shifts in the wild.

ACKNOWLEDGMENTS

The author would like to thank the Marine Mammal Husbandry team at the Vancouver Aquarium for their expertise in training the walruses for this study, and the continued support of Ocean Wise Conservation Association. This work was partly supported by an NSERC Discovery grant. This manuscript was improved by discussions with Andreas Fahlman (Oceanographic, Valencia) and the valuable feedback of three anonymous reviewers.

AUTHOR CONTRIBUTIONS

David Rosen: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; validation; visualization; writing-original draft; writing-review and editing.

ORCID

David A. S. Rosen https://orcid.org/0000-0003-2931-9608

REFERENCES

Acquarone, M., Born, E. W., & Speakman, J. R. (2006). Field metabolic rates of walrus (*Odobenus rosmarus*) measured by the doubly labeled water method. *Aquatic Mammals*, *32*, 363–369.

Bejarano, A. C., Wells, R. S., & Costa, D. P. (2017). Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. *Ecological Modelling*, *356*, 162–172.

Boily, P., & Lavigne, D. M. (1997). Developmental and seasonal changes in resting metabolic rates of captive female grey seals. *Canadian Journal of Zoology*, *75*, 1781–1789.

Born, E., Stefansson, E., Mikkelsen, B., Laidre, K. L., Andersen, L. W., Rigét, F., … Bloch, D. (2014). A note on a walrus' European odyssey. *NAMMCO Scientific Publications*, *9*, 75–91.

Bowen, W. D. (1997). Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, *158*, 267–274.

Castellini, M. A., Kooyman, G. L., & Ponganis, P. J. (1992). Metabolic rates of freely diving Weddell seals: Correlations with oxygen stores, swim velocity and diving duration. *Journal of Experimental Biology*, *165*, 181–194.

Dalton, A. J. M., Rosen, D. A. S., & Trites, A. W. (2015). Resting metabolic rate and activity: Key components of seasonal variation in daily energy expenditure for the northern fur seal (*Callorhinus ursinus*). *Canadian Journal of Zoology*, *93*, 635–644.

Davydov, A., & Marakova, A. (1965). Changes in heat regulation and circulation in newborn seals on transition to aquatic form of life. *Federation Proceedings*, *24*, 563–566.

Donohue, M. J., Costa, D. P., Goebel, M. E., & Baker, J. D. (2000). The ontogeny of metabolic rate and thermoregulatory capabilities of northern fur seal, *Callorhinus ursinus*, pups in air and water. *Journal of Experimental Biology*, *203*, 1003–1016.

Fahlman, A. L., Svard, C., Rosen, D. A. S., Jones, D. R., & Trites, A. W. (2008). Metabolic costs of foraging and the management of O_2 and CO_2 stores in Steller sea lions. *Journal of Experimental Biology*, *211*, 3573–3580.

Fay, F. H. (1981). Walrus - *Odobenus rosmarus*. In S. H. Ridgway & R. J. Harrison (Eds.), *Handbook of marine mammals* (pp. 1–23). London, UK: Academic Press.

Fay, F. H. (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North American Fauna*, *74*, 1–279.

Fish, F. E. (1992). Aquatic locomotion. In T. E. Tomasi & T. H. Horton (Eds.), *Mammalian energetics: Interdisciplinary views of metabolism and reproduction* (pp. 34–63). Ithaca, NY: Comstock Publishing Associates.

Fish, F. E. (2000). Biomechanics and energetics in aquatic and semiaquatic mammals: Platypus to whale. *Physiological and Biochemical Zoology*, *73*, 683–698.

Glazier, D. S. (2005). Beyond the '3/4-power law': Variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews*, *80*, 611–662.

Gordon, K. R. (1983). Mechanics of the limbs of the walrus (*Odobenus rosmarus*) and the California sea lion (*Zalophus californianus*). *Journal of Morphology*, *175*, 73–90.

Hart, J. S., & Irving, L. (1959). The energetics of harbor seals in air and in water with special consideration of seasonal changes. *Canadian Journal of Zoology*, *37*, 447–457.

Hastie, G. D., Rosen, D. A. S., & Trites, A. W. (2007). Reductions in oxygen consumption during dives and estimated submergence limitations of Steller sea lions (*Eumetopias jubatus*). *Marine Mammal Science*, *23*, 272–286.

Hunter, A. M. J. (2005). *A multiple regression model for predicting the energy requirements of marine mammals* (M.Sc. thesis). University of British Columbia, Vancouver, Canada.

Jay, C. V., Marcot, B. G., & Douglas, D. C. (2011). Projected status of the Pacific walrus (*Odobenus rosmarus divergens*) in the twenty-first century. *Polar Biology*, *34*, 1065–1084.

Jay, C. V., Taylor, R. L., Fischbach, A. S., Udevitz, M. S., & Beatty, W. S. (2017). Walrus haul-out and in water activity levels relative to sea ice availability in the Chukchi Sea. *Journal of Mammalogy*, *98*, 386–396.

Karasov, W. H. (1992). Daily energy expenditure and the cost of activity in mammals. *American Zoologist*, *32*, 238–248.

Kastelein, R. A. (2009). Walrus: *Odobenus rosmarus*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 1212–1217). San Diego, CA: Elsevier.

Kastelein, R., Schooneman, N., & Wiepkema, P. (2000). Food consumption and body weight of captive Pacific walruses (*Odobenus rosmarus divergens*). *Aquatic Mammals*, *26*, 175–190.

Kleiber, M. (1975). *The fire of life: An introduction to animal energetics*. New York, NY: Robert E. Krieger Publishing.

Kooyman, G. L., Castellini, M. A., & Davis, R. W. (1981). Physiology of diving in marine mammals. *Annual Review of Physiology*, *43*, 343–356.

Lavigne, D. M., Innes, S., Worthy, G. A. J., & Kovacs, K. M. (1986a). Metabolic rate—body size relations in marine mammals. *Journal of Theoretical Biology*, *122*, 123–124.

Lavigne, D. M., Innes, S., Worthy, G. A. J., Kovacs, K. M., Schmitz, O. J., & Hickie, J. P. (1986b). Metabolic rates of seals and whales. *Canadian Journal of Zoology*, *64*, 279–284.

Lydersen, C. (2018). Walrus: *Odobenus rosmarus*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd. ed., pp. 1045–1048). San Diego, CA: Elsevier.

MacCracken, J. G. (2012). Pacific walrus and climate change: Observations and predictions. *Ecology and Evolution*, *2*, 2072–2090.

McNab, B. K. (1999). On the comparative ecological and evolutionary significance of total and mass-specific rates of metabolism. *Physiological and Biochemical Zoology*, *72*, 642–644.

Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs*, *57*, 111–128.

National Research Council (U.S.). (1981). *Nutritional energetics of domestic animals & glossary of energy terms*. Washington, DC: National Academy Press.

New, L. F., Clark, J. S., Costa, D. P., Fleischman, E., Hindell, M. A., Klanjscek, T., … Harwood, J. (2014). Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Marine Ecology Progress Series*, *496*, 99–108.

Noren, S., Udevitz, M. S., & Jay, C. (2012). Bioenergetics model for estimating food requirements of female Pacific walruses *Odobenus rosmarus divergens*. *Marine Ecology Progress Series*, *460*, 261–275.

Noren, S. R., Udevitz, M. S., & Jay, C. V. (2014). Energy demands for maintenance, growth, pregnancy, and lactation of female Pacific walruses (*Odobenus rosmarus divergens*). *Physiological and Biochemical Zoology*, *87*, 837–854.

Noren, S. R., Udevitz, M. S., & Jay, C. V. (2016). Sex-specific energetics of Pacific walruses (*Odobenus rosmarus divergens*) during the nursing interval. *Physiological and Biochemical Zoology*, *89*, 93–109.

Pierce, S., Clack, J., & Hutchinson, J. (2011). Comparative axial morphology in pinnipeds and its correlation with aquatic locomotory behaviour. *Journal of Anatomy*, *219*, 502–514.

Pirotta, E., Booth, C. G., Costa, D. P., Fleishman, E., Kraus, S. D., Lusseau, D., … Harwood, J. (2018). Understanding the population consequences of disturbance. *Ecology and Evolution*, *8*, 9934–9946.

Poczopko, P. (1979). Metabolic rate and body size relationships in adult and growing homeotherms. *Acta Theriologica*, *24*, 125–136.

Rea, L. D., & Costa, D. P. (1992). Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiological Zoology*, *65*, 97–111.

Reidenberg, J. S. (2007). Anatomical adaptations of aquatic mammals. *The Anatomical Record*, *290*, 507–513.

Renouf, D., & Gales, R. (1994). Seasonal variation in the metabolic rate of harp seals: Unexpected energetic economy in the cold ocean. *Canadian Journal of Zoology*, *72*, 1625–1632.

Rosen, D. A. S., & Renouf, D. (1998). Correlates to seasonal changes in metabolism in Atlantic harbour seals (*Phoca vitulina concolor*). *Canadian Journal of Zoology*, *76*, 1520–1528.

Rosen, D. A. S., & Trites, A. W. (1997). Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. *Comparative Biochemistry and Physiology A*, *118*, 877–881.

Rosen, D. A. S., & Trites, A. W. (2002). Cost of transport in Steller sea lions, *Eumetopias jubatus*. *Marine Mammal Science*, *18*, 513–524.

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying and running. *Science*, *177*, 222–228.

Sheffield, G., & Grebmeier, J. M. (2009). Pacific walrus (*Odobenus rosmarus divergens*): Differential prey digestion and diet. *Marine Mammal Science*, *25*, 761–777.

Smith, E. V. (1986). Metabolic rates of seals and whales. *Canadian Journal of Zoology*, *64*, 279–284.

Smith, L. A., Link, J. S., Cadrin, S. X., & Palka, D. L. (2015). Consumption by marine mammals on the Northeast US continental shelf. *Ecological Applications*, *25*, 373–389.

Taylor, R. L., Udevitz, M. S., Jay, C. V., Citta, J. J., Quakenbush, L. T., Lemons, P. R., & Snyder, J. A. (2018). Demography of the Pacific walrus (*Odobenus rosmarus divergens*) in a changing Arctic. *Marine Mammal Science*, *34*, 54–86.

Thompson, S. D., Ono, K. A., Oftedal, O. T., & Boness, D. J. (1987). Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups. *Physiological Zoology*, *60*, 730–736.

Trites, A. W., Christensen, V., & Pauly, D. (1997). Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fisheries Science*, *22*, 173–187.

Tucker, V. A. (1970). Energetic cost of locomotion in animals. *Comparative Biochemistry and Physiology A*, *34*, 841–846.

Udevitz, M. S., Jay, C. V., Taylor, R. L., Fischbach, A. S., Beatty, W. S., & Noren, S. R. (2017). Forecasting consequences of changing sea ice availability for Pacific walruses. *Ecosphere*, *8*, e02014.

Videler, J. J., & Nolet, B. A. (1990). Cost of swimming measured at optimum speed: Scale effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. *Comparative Biochemistry and Physiology A*, *97*, 91–99.

Villegas-Amtmann, S., Schwarz, L. K., Sumich, J. L., & Costa, D. P. (2015). A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere*, *6*, 1–19.

Williams, T. M. (1989). Swimming by sea otters: Adaptations for low energetic cost locomotion. *Journal of Comparative Physiology A*, *164*, 815–824.

Williams, T. M. (1999). The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. *Philosophical Transactions*, *Royal Society of London B*, *354*, 193–201.

Williams, T. M., & Maresh, J. L. (2015). Exercise energetics. In M. A. Castellini & J.-A. Mellish (Eds.), *Marine mammal physiology: Requisites for ocean living* (pp. 47–68). Boca Raton, FL: CRC Press.

Williams, T. M., Haun, J., Davis, R. W., Fuiman, L. A., & Kohin, S. (2001). A killer appetite: Metabolic consequences of carnivory in marine mammals. *Comparative Biochemistry and Physiology A*, *129*, 785–796.

Winship, A. J., Trites, A. W., & Rosen, D. A. S. (2002). A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska. *Marine Ecology Progress Series*, *229*, 291–312.

Withers, P. C. (1977). Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology*, *42*, 120–123.

Young, B. L., Rosen, D. A. S., Hindle, A. G., Haulena, M., & Trites, A. W. (2011). Dive behaviour impacts the ability of heart rate to predict oxygen consumption in Steller sea lions (*Eumetopias jubatus*) foraging at depth. *Journal of Experimental Biology*, *214*, 2267–2275.

How to cite this article: Rosen DAS. Resting and swimming metabolic rates in juvenile walruses (*Odobenus rosmarus*). *Mar Mam Sci*. 2021;37:162–172. https://doi.org/10.1111/mms.12743