

RESEARCH ARTICLE

Subsurface swimming and stationary diving are metabolically cheap in adult Pacific walrus (*Odobenus rosmarus divergens*)

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ABSTRACT

Walrus rely on sea-ice to efficiently forage and rest between diving bouts while maintaining proximity to prime foraging habitat. Recent declines in summer sea ice have resulted in walrus hauling out on land where they have to travel farther to access productive benthic habitat while potentially increasing energetic costs. Despite the need to better understand the impact of sea ice loss on energy expenditure, knowledge about metabolic demands of specific behaviours in walrus is scarce. In the present study, 3 adult female Pacific walrus (*Odobenus rosmarus divergens*) housed in professional care participated in flow-through respirometry trials to measure metabolic rates while floating inactive at the water surface during a minimum of 5 min, during a 180 s stationary dive, and while swimming ~90 m horizontally underwater. Metabolic rates during stationary dives ($3.82 \pm 0.56 \text{ l O}_2 \text{ min}^{-1}$) were lower than those measured at the water surface ($4.64 \pm 1.04 \text{ l O}_2 \text{ min}^{-1}$), which did not differ from rates measured during subsurface swimming ($4.91 \pm 0.77 \text{ l O}_2 \text{ min}^{-1}$). Thus, neither stationary diving nor subsurface swimming resulted in metabolic rates above those exhibited by walrus at the water surface. These results suggest that walrus minimize their energetic investment during underwater behaviours as reported for other marine mammals. Although environmental factors experienced by free-ranging walrus (e.g. winds or currents) likely affect metabolic rates, our results provide important information for understanding how behavioural changes affect energetic costs and can be used to improve bioenergetics models aimed at predicting the metabolic consequences of climate change on walrus.

KEY WORDS: Metabolic rate, Energetics, Diving, Swimming, *Odobenus rosmarus*, Walrus

INTRODUCTION

The Pacific walrus (*Odobenus rosmarus divergens*) inhabits a region of the Arctic that is experiencing some of the most rapid loss of summer sea ice (Laidre et al., 2015; Markus et al., 2009). The sea ice is a critical habitat for this species as it provides a location for

resting between foraging bouts and immediate access to their benthic offshore foraging habitat (Fay, 1982). The sea ice platform is also used for breeding, and females and young walrus usually haul out onto sea ice throughout the year, while adult males haul out on sea ice primarily during winter and spring (Fay, 1982). In recent years, sea ice has retreated beyond the continental shelf in the eastern Chukchi Sea in the autumn (Markus et al., 2009). In response, female and young walrus are hauling out in large numbers on land during the summer where they either forage for nearshore prey, or travel farther to more productive benthic habitats in offshore areas (Jay et al., 2012). Walrus with only access to land in the summer spend more time in water while not foraging, and less time hauled out resting as compared with walrus with access to sea ice habitats (Jay et al., 2017). In addition, walrus hauling out on land on the northwest coast of Alaska have been documented to migrate to the coast of northern Chukotka in September and October when sea ice is sometimes preserved (Jay et al., 2012). This migration occurs with minimal foraging activity but provides the opportunity to maintain offshore locations (Jay et al., 2012). Migration and extended trips to maintain access to feeding habitat may increase energetic costs while decreasing energy intake, which could have implications for individual health, survival and breeding success (MacCracken, 2012). For instance, female walrus increase body size and lipid deposition during pregnancy to support early lactation, but only 27% of caloric requirements during lactation are met by body reserves (Noren et al., 2014). Thus, foraging during lactation is critical for calf survival and walrus population dynamics are known to be sensitive to successful calf survival (Udevitz et al., 2013). Furthermore, projections of female walrus behaviour with continued sea ice loss suggest that these activity patterns (less time invested on resting and foraging) will become more common in the future (Udevitz et al., 2017).

Understanding the implications of changing behavioural patterns for walrus energetic balance requires information on the energetic demands or metabolic rates associated with individual behaviours. Satellite radio tags deployed on walrus can record location, pressure and conductivity, which together identify whether a walrus is likely in water (foraging or not foraging) or hauled out (Fischbach and Jay, 2016; Jay et al., 2006). This information was recently used in combination with estimated metabolic rates of different behaviours to develop a bioenergetic model for female walrus (Noren et al., 2012; Udevitz et al., 2017). This bioenergetic model allowed prediction of how changes in behaviour in response to sea ice loss or other factors might affect walrus energetic costs. However, model outcomes were most sensitive to estimates of the cost of activity in water (Noren et al., 2012; Udevitz et al., 2017), which has not been directly measured in adult walrus. Data on metabolic rates of walrus are currently limited to a study that reported field metabolic rate (FMR) in two free-ranging adult males (Acquarone et al., 2006) and a study that measured metabolic rates

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List of symbols and abbreviations

%kJ _{tot}	percentage of energy intake in relation to the total daily intake for the days of the experiments
ADL	aerobic dive limit, or maximum diving time exclusively using the available O ₂ stores
BMR	basal metabolic rate
BMR _{est}	predicted basal metabolic rate
BV	blood volume
cADL	aerobic dive limit calculated from estimated body oxygen stores and diving metabolic rate during subsurface swimming
DMR	diving metabolic rate
DMR _{Stationary}	metabolic rate measured during stationary dives
DMR _{Swim}	metabolic rate measured during subsurface swimming
FMR	field metabolic rate
f _R	respiratory frequency
Hg	haemoglobin
kJ _{est}	estimated energy intake
M _b	body mass
Mg	myoglobin
MR _{Surface}	metabolic rate measured while floating at the water surface
RER	respiratory exchange ratio
RMR	metabolic rate measured at rest
sDMR _{Stationary}	mass-specific metabolic rate measured during stationary dives
sDMR _{Swim}	mass-specific metabolic rate measured during subsurface swimming
sMR _{Surface}	mass-specific metabolic rate measured while floating at the water surface
STP	standard temperature and pressure conditions
STPD	standard temperature and pressure dry conditions
TLC _{est}	estimated total lung capacity
\dot{V}_{CO_2}	carbon dioxide production rate
\dot{V}_{O_2}	oxygen consumption rate

of juveniles while resting in water or during horizontal subsurface swimming (Rosen, 2020). FMR in the two free-ranging adult male Atlantic walrus was measured using doubly labelled water, which provided estimates of the total energetic costs, but not the energetic costs associated with individual behaviours (Acquarone et al., 2006). More recently, Rosen (2020) reported the first data of activity-associated energetic costs in two trained juvenile walrus. Although these first studies have provided important information to help understand the energetic requirements in this species, we still lack direct measurements of the metabolic cost of specific behaviours for adult walrus.

To increase our understanding about the energetic expenditure in the walrus, the present study aimed to measure the metabolic rate during three different in-water behaviours using flow-through respirometry. Three adult female Pacific walrus were trained to perform the experimental procedures for measuring the O₂ consumption rate (\dot{V}_{O_2} , l O₂ min⁻¹): (1) while floating inactive at the water surface (surface); (2) during shallow stationary dives (stationary); and (3) during horizontal subsurface swimming (swim). We hypothesized that the \dot{V}_{O_2} would be lower for stationary dives and subsurface swimming compared with periods while floating at the surface as previously reported for other pinniped species (Castellini et al., 1992; Fahlman et al., 2013; Hurley and Costa, 2001; Reed et al., 1994; Sparling and Fedak, 2004). In addition, we also hypothesized that the \dot{V}_{O_2} would be higher during subsurface swimming than that measured during stationary dives.

MATERIALS AND METHODS**Study subjects and training methodology**

Three adult (not spayed) female Pacific walrus (*Odobenus rosmarus divergens* Illiger 1815) born in 2003 and housed at the Oceanogràfic (Valencia, Spain) participated in the present study. Prior to initiating data collection, the animals underwent 7 months of desensitization to the respirometry equipment and were trained to perform the different experiments using operant conditioning. This allowed for data collection in a relaxed physiological state, where the animals were free to decide their participation in each experimental trial and could withdraw at any point. The health of the walrus was assessed daily, and all experiments were approved by the Animal Care and Welfare Committee of Fundació Oceanogràfic de la Comunitat Valenciana (Animal Care number: OCE-1-18), and the Animal Care and Use Committee of the U.S. Geological Survey Alaska Science Centre (Review code 2020-01).

General procedures and experimental variables

Data collection took place between August 2018 and November 2019. No data were collected during the reproductive season (from around February to March in the study subjects) as during this time the animals showed little interest in participation. Body mass (M_b , kg) was measured before the first feeding in the morning the same week of the metabolic trial ($\pm 0-4$ days from data collection) and ranged from 682 to 1035 kg ($n=3$, mean \pm s.d.=842 \pm 116 kg) during the overall experimental period. Ambient pressure, temperature and humidity were measured before commencing each experimental trial (thermometer and hygrometer OH513 Oh Haus & Co), and averaged, respectively, 102.0 \pm 0.6 kPa (range=100.9–103.3 kPa), 19.1 \pm 2.8°C (range=13.0–25.0°C) and 69 \pm 7% (range=53–84%), during the data collection period. The animals were post-absorptive during metabolic measurements and had not had a meal for at least 15 h prior to initiating the experimental trials, but some food reinforcement was provided during the last minute of most respirometry trials to help reinforce the required experimental behaviour. The regular diet included a mixture of fish (capelin and herring) and molluscs (squid and mussels) supplemented with vitamins. The estimated energy intake (kJ_{est}, kJ) during each metabolic trial was calculated using the measured amount of consumed food (kg) and the measured energetic content for each type of food (kJ kg⁻¹). This energetic content was estimated in-house through bomb calorimetry of random samples of the food items that arrived at the aquarium.

All metabolic measurements were conducted in a 3 m deep seawater pool with a total water volume of 267 m³. The water temperature at the facility was measured daily and ranged from 12.9 to 18.6°C (mean \pm s.d.=15.9 \pm 1.0°C) during the experimental period. Data collection was performed using an open flow respirometry system described below in this section. The animals were trained to surface into a respirometry dome and keep breathing inside the respirometer while floating in a relaxed and inactive state. The walrus showed some corporal movement while maintaining the required position inside the respirometer. Consequently, the animals were not quiescent throughout the whole duration of the experimental trials. The measured changes in O₂ and CO₂ content of the air exiting the respirometry dome relative to atmospheric air were used to estimate the \dot{V}_{O_2} and the CO₂ production rate (\dot{V}_{CO_2} , l CO₂ min⁻¹) for each experimental trial. The estimated \dot{V}_{O_2} was used to define the metabolic rate for the three in-water behaviours: (1) while floating at the water surface [metabolic rate at the surface (MR_{Surface}, l O₂ min⁻¹)]; (2) during shallow stationary dives [diving metabolic rate during stationary dives (DMR_{Stationary}, l O₂ min⁻¹)]; or (3) during

subsurface swimming dives [diving metabolic rate while swimming (DMR_{Swim} , $l \text{ O}_2 \text{ min}^{-1}$)].

The $\text{MR}_{\text{Surface}}$ was estimated from at least 5 min of data collection while the walrus remained calmly floating inside the respirometer. For $\text{DMR}_{\text{Stationary}}$ measurements, the walrus was directed to submerge to a fixed point at the bottom of the pool and to remain stationary while holding its breath for at least 3 min. For the DMR_{Swim} estimation, the animal swam back and forth between two underwater target poles that were positioned approximately ~ 7 m apart, until reaching ~ 90 m of horizontal subsurface swimming. The walrus swam at a depth of ~ 1.5 m, and all trials were timed to calculate the swimming velocity. These methods are similar to the swimming trials conducted with juvenile walrus by Rosen (2020). To determine either $\text{DMR}_{\text{Stationary}}$ or DMR_{Swim} , the walrus was guided to surface inside the respirometry dome at completion of the dives to measure the gas exchange during the post-dive recovery period. The post-dive recovery period ended when the \dot{V}_{O_2} and \dot{V}_{CO_2} had returned to similar values recorded during the last portion of $\text{MR}_{\text{Surface}}$ measurements, and remained stable for at least 1 min. Exploratory trials prior to data collection showed that the \dot{V}_{O_2} and \dot{V}_{CO_2} returned to steady values within the range (mean \pm s.d.) of those measured during $\text{MR}_{\text{Surface}}$ trials between ~ 4 and ~ 6 min for the stationary dives and subsurface swimming, respectively (see an example in Fig. 1). Therefore, to ensure the inclusion of the entire

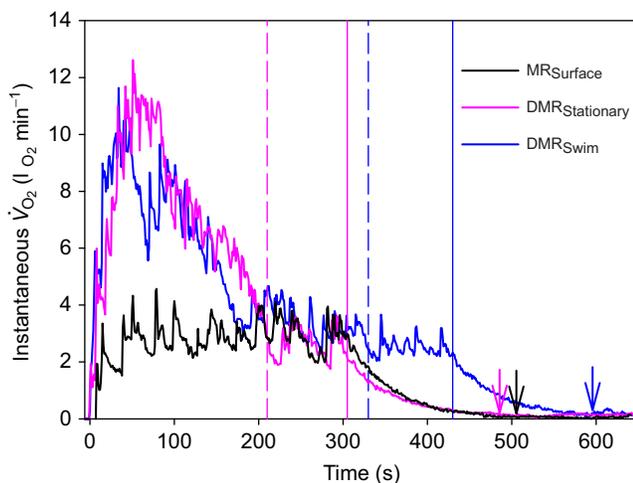


Fig. 1. An example representation of instantaneous \dot{V}_{O_2} measurements for one walrus during three in-water behaviours. Measured instantaneous O_2 consumption rate (\dot{V}_{O_2}) for one adult female Pacific walrus (*O. rosmarus divergens*, Animal ID=26005388) during \dot{V}_{O_2} measurements while floating at the water surface ($\text{MR}_{\text{Surface}}$), and during post-dive \dot{V}_{O_2} measurements for stationary dives ($\text{DMR}_{\text{Stationary}}$) and subsurface swimming (DMR_{Swim}). For the three experimental trials, the walrus entered the dome at time=0 s. For the post-dive recovery period of both underwater experiments, the dashed vertical lines represent the beginning of the period when the instantaneous \dot{V}_{O_2} was similar to that obtained during the last portion (~ 2 min) of $\text{MR}_{\text{Surface}}$ measurements, while the solid vertical lines indicate the time when the walrus left the respirometer ($\text{DMR}_{\text{Stationary}}$: pink lines; DMR_{Swim} : blue lines). The total volume of O_2 consumed for each trial was computed by integrating the instantaneous \dot{V}_{O_2} from when the walrus entered the dome until the O_2 returned to ambient values (instantaneous $\dot{V}_{\text{O}_2} \sim 0$) which is indicated by the arrows ($\text{MR}_{\text{Surface}}$: black; $\text{DMR}_{\text{Stationary}}$: pink; DMR_{Swim} : blue). For both underwater behaviours, the $\text{DMR}_{\text{Stationary}}$ and DMR_{Swim} were computed as the total volume of consumed O_2 divided by the entire dive cycle (dive duration+post-dive recovery duration). As an example, the represented $\text{DMR}_{\text{Stationary}}$ was estimated by integrating the \dot{V}_{O_2} until the position of the pink arrow and dividing the obtained O_2 volume by the dive duration (180 s) plus the duration of the measurement (304 s, i.e. when the walrus left the respirometer).

physiological recovery for all trials, the post-dive recovery period was extended, respectively, to 5 and 7 min for the stationary dives and subsurface swimming.

Respiratory gas exchange measurements

The open-flow respirometry system (Fig. 2) consisted of a vacuum pump (FlowKit Mass Flow Generator, FK-500-1, Sable Systems International, Las Vegas, NV, USA) pulling air through a floating transparent Plexiglas dome of 120 cm internal diameter (i.d.) via an 800 cm length and 4.5 cm i.d. plastic corrugated tube. The dome was made buoyant by attaching polyethylene foam to the base. A flow-through rate of 500 l min^{-1} of air assured that the O_2 and CO_2 were maintained $>19\%$ and $<2\%$, respectively. The O_2 and CO_2 content were measured using a fast-response gas analyser (Gemini Respiratory Gas Analyzer, part no. 14-1000, CWE Inc., Allentown, PA, USA), which pulled a subsample of the outlet air from the corrugated tube at a flow rate of 200 ml min^{-1} via a 310 cm length and 2 mm i.d. firm-walled, flexible tubing. This flexible tubing was attached to a hydrophobic filter (13 mm i.d.), followed by a 60 cm length and 1.5 mm i.d. Nafion[®] sample line connected to the gas analyser. The gas analyser was routinely calibrated using ambient air and a commercial gas mixture (5% O_2 , 5% CO_2 and 90% N_2 ; UN1956 Air Liquide, USA). Both, respiratory gas concentrations and air flow rates were captured at 400 Hz using a data acquisition system (Powerlab 8/35, ADInstruments, Colorado Springs, CO, USA), and displayed on a laptop computer running Labchart (v. 8.1, ADInstruments). A simultaneous CO_2 and N_2 dilution test was conducted to evaluate the system for possible leaks, and to assess the accuracy in measured O_2 and CO_2 concentrations (Fahlman et al., 2008; Fedak et al., 1981), which were within 6% of estimated values. The effective volume of the system was 465 l, which resulted in a time constant of 0.93 min (Bartholomew et al., 1981). The time required to reach a 95% fractional transformation to a new steady state was 167 s (2.79 min) or 3 times the time constant (Bartholomew et al., 1981; Fahlman et al., 2007).

Data processing and criteria for data inclusion

The gas analyser baseline drift during an experimental trial was corrected by measuring the ambient air concentrations at the end of the trial. The mass flow generator automatically corrected flow rates to standard temperature and pressure conditions (STP), and measured flow was corrected for humidity inside the respirometry dome to standard temperature and pressure dry (STPD; Quanjer et al., 1993). Corrected flow rates and measured gas concentrations were then multiplied to calculate the instantaneous \dot{V}_{O_2} and \dot{V}_{CO_2} , which were corrected for variation in the respiratory exchange ratio (Withers, 1977).

The following criteria were used to include a metabolic trial in the analysis. For all trials, the walrus had to remain calm with all breaths taken inside the respirometer. For experiments while floating at the surface, the walrus had to remain for at least 5 min inside the respirometer. For diving trials, the walrus had to: (1) complete the pre-determined dive duration of 3 min for the stationary dives or the horizontal swimming distance of ~ 90 m for the subsurface swimming, and (2) remain inside the respirometer during the post-dive recovery for at least 5 min for stationary dives or 7 min for subsurface swimming.

Metabolic rates calculations and conversions

To determine the total volume of O_2 consumed during each experimental trial, the instantaneous \dot{V}_{O_2} was integrated over the period from when the walrus surfaced into the respirometer, until the

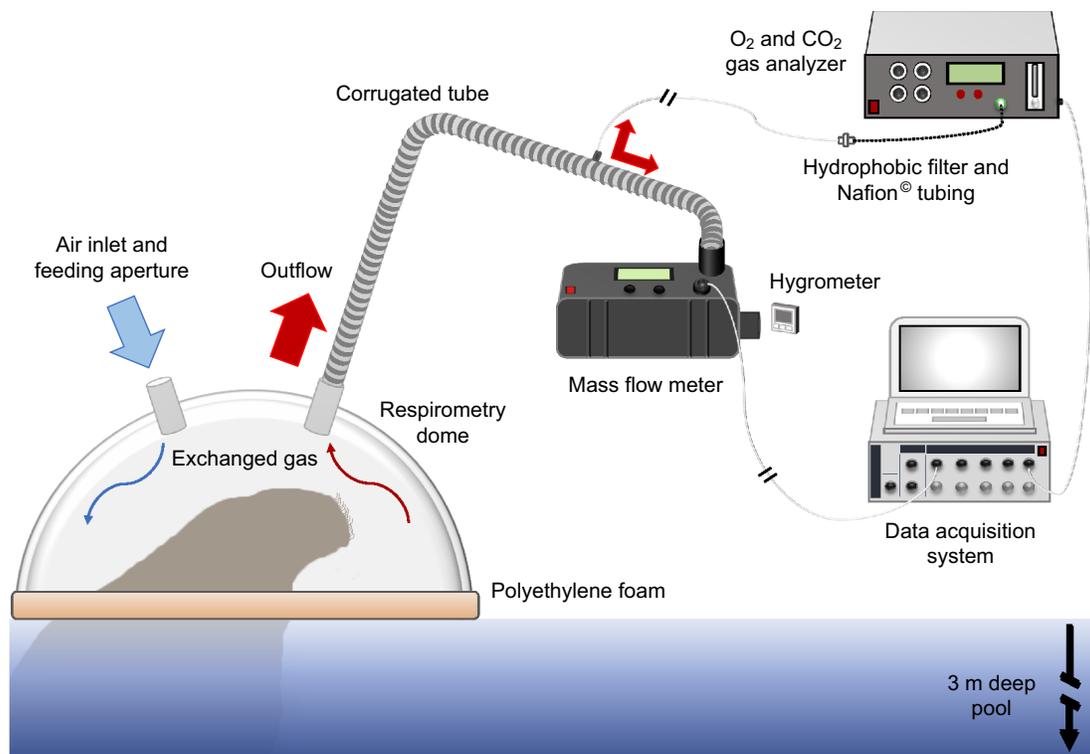


Fig. 2. Open-flow respirometry system used to measure metabolic rates of Pacific walrus. Schematic diagram (unscaled) of the open-flow respirometry system set up used in the present study while measuring O₂ consumption and CO₂ production rates in Pacific walrus. The arrows show the direction of the air through the system. The grey solid lines represent the sampling connections between the different components described in the Materials and Methods.

O₂ had returned to ambient levels after leaving the respirometer (Fig. 1). The measured volume of O₂ consumed was then divided by the measurement period for the MR_{Surface} trials, and by the total dive cycle or the dive time plus the post-dive recovery time for the DMR_{Stationary} and DMR_{Swim} trials (see an example in Fig. 1).

The Kleiber ratio was calculated for each behaviour by dividing the measured \dot{V}_{O_2} by the predicted basal metabolic rate (BMR_{est} , $l\ O_2\ min^{-1}$) for a similarly sized terrestrial mammal ($BMR_{est}=0.0093M_b^{0.75}\ l\ O_2\ min^{-1}$; Kleiber, 1975). The \dot{V}_{CO_2} for each behaviour was computed as described for \dot{V}_{O_2} and used to determine the respiratory exchange ratio (RER, \dot{V}_{CO_2} divided by \dot{V}_{O_2}). The mass-specific metabolic rate was calculated for each experimental procedure (floating at the surface: sMR_{Surface}; stationary dives: sDMR_{Stationary}; subsurface swimming: sDMR_{Swim}; ml O₂ kg⁻¹ min⁻¹) by dividing the metabolic rate by M_b and assuming isometry. Measured metabolic rates and mass-specific conversions for the different experimental procedures were converted into daily energetic requirements as: metabolic rate (kJ day⁻¹)=(16.218+4.716×RER)× \dot{V}_{O_2} ×60×24. This formula is based on the assumptions that protein catabolism is negligible, while carbohydrates and lipids use 20.93 and 19.55 kJ per 1 litre of consumed O₂, respectively (see table 17 in Jungas et al., 1992). The respiratory frequency (f_R , breaths min⁻¹) was computed for each behaviour as the number of observed breaths divided by the total time of the measurement period. The calculated aerobic dive limit (cADL, min) was estimated by dividing the estimated total body O₂ stores by the obtained DMR_{Swim} (Butler, 2006). The calculations to yield the total accessible body O₂ stores during diving are detailed in the supplementary Materials and Methods and were performed by summing the O₂ capacity of different tissues (blood, muscle and lungs), and by estimating the level of O₂ utilization from each tissue during the dive (Kooyman, 1989).

Statistical analysis

We initially analysed the relationship between measured MR_{Surface}, DMR_{Stationary}, DMR_{Swim} and the experimental covariates (M_b , and water temperature as continuous variables) using linear models (lm function in R; <https://www.r-project.org/>). We used a backward stepping procedure implemented by the R-function ‘step’ to identify whether M_b and water temperature were important in affecting metabolic rates, based on the combination of variables that had the lowest Akaike information criterion (AIC). The importance of the covariates in the final models were verified by performing the log-likelihood ratio test to confirm that the full model was better than a model containing just the intercept. Measured MR_{Surface}, DMR_{Stationary} and DMR_{Swim} were then compared using an ANCOVA F -test that included the experiment as a fixed factor, and the covariates identified from the backward stepping procedure as independent variables. The animal identification (ID) was initially included as a random effect to account for the correlation between repeated measurements on the same individual (Littell et al., 1998), but was removed from the models due to its strong correlation with M_b . A Tukey HSD *post hoc* test was used to determine whether DMR_{Stationary} and DMR_{Swim} were different from MR_{Surface}. For all analyses M_b and \dot{V}_{O_2} were transformed using the base 10 logarithm. Homoscedasticity and normality were assessed through evaluation of residual plots. In the present study, P -values ≤ 0.05 were considered significant, and data are presented as means±s.d.

RESULTS

Total and selected trials, and experimental variables

The three female Pacific walrus participated in a total of 108 respirometry experimental trials including training and sampling sessions (2018: $n=20$ trials, 2019: $n=88$ trials). From the total experimental trials, 5 trials for each animal and behaviour ($n=45$ for

Table 1. Body mass and estimated energy intake for each female walrus

Animal ID	M_b (kg)	kJ_{est} (kJ)	% kJ_{tot}
26005388	705±9 (688–721)	1236±2108 (100–6238) ¹⁵	1.2±1.9 (0.1–5.5)
26005389	975±25 (950–1030)	1586±2445 (96–6238) ¹⁴	1.4±2.1 (0.1–5.5)
26005390	825±7 (813–834)	207±74 (100–339) ¹⁵	0.2±0.1 (0.1–0.3)

For trials included in the analysis ($n=45$), data are shown for animal identification (ID) and average (\pm s.d.) and ranges of body mass (M_b), estimated energy intake during the experimental procedure (kJ_{est}), and percentage of energy intake in relation to the total daily intake for the days of the experiments (% kJ_{tot}). Superscripts in the kJ_{est} column indicate the number of trials where the animals were provided with food during the last minute of the procedure.

all animals and behaviours) passed the selection criteria to be included in the analysis. For selected trials, the measured M_b ranged from 688 to 1030 kg (835±112 kg; Table 1) and the kJ_{est} ranged from 96 to 6238 kJ ($n=44$) which represented 0.1–5.5% of the established total daily energy intake of the animals for the dates of data collection (Table 1). For trials included in the analysis, the measured humidity outside and inside the dome was 71±7% (54–82%) and 69±7% (53–81%), respectively, while the ambient pressure and air temperature at the facility housing the animals were 101.8±0.4 kPa (100.9–102.6 kPa) and 19.2±2.1°C (15.4–23.1°C), respectively. The water temperature for selected trials averaged 15.4±1.0°C (Table 2). The backward stepping procedure showed that the elimination of the covariate ‘water temperature’ from the model increased the AIC for $MR_{Surface}$ trials ($\Delta AIC=0.313$) and decreased AIC for both underwater behaviours by less than 2 units ($DMR_{Stationary}$: $\Delta AIC=1.28$; DMR_{Swim} : $\Delta AIC=1.74$). For all experiments, the coefficient for water temperature was not significant (Wald’s t -test, P -value: $MR_{Surface}=0.18$; $DMR_{Stationary}=0.45$; $DMR_{Swim}=0.65$). Because water temperature either did not improve model fit or had only a minor, non-significant effect on metabolic rate, we did not include it in models comparing metabolic rates between behaviours. Alternatively, the log-likelihood ratio test showed that inclusion of M_b improved the fit of the model compared with the intercept-only model ($P<0.05$ for all experiments; Table 3). Therefore, we included only M_b in the ANCOVA F -test comparing metabolic rates between behaviours. For each studied behaviour, measured M_b , \dot{V}_{CO_2} , f_R and RER are reported in Table S1, while measured \dot{V}_{O_2} for each participating walrus and behaviour is reported in terms of daily energetic requirements in Table S2.

Metabolic rate while floating at the water surface

The average duration for $MR_{Surface}$ trials was 5.7±0.6 min (Table 2). The average $MR_{Surface}$ (4.64±1.04 l O_2 min⁻¹; Table 4) was higher than the predicted BMR_{est} for a similarly sized terrestrial mammal (1.55±0.17 l O_2 min⁻¹; Fig. 3), and the Kleiber ratio was >1 for all animals (3.0±0.5; range: 2.3–3.9). The $MR_{Surface}$ increased with M_b with a mass-exponent close to 1 (Table 3 and Fig. 3).

Metabolic rates during stationary dives and subsurface swimming

The average breath-hold duration for stationary dives and subsurface swimming was 3.2±0.1 and 1.6±0.2 min, respectively

(Table 2), with an average swimming velocity of 1.0±0.1 m s⁻¹ (range: 0.9–1.3 m s⁻¹) during the subsurface swimming. The average post-dive recovery duration for $DMR_{Stationary}$ trials was 5.2±0.1 min, and 7.2±0.1 min for DMR_{Swim} trials (Table 2). The $MR_{Surface}$ differed from those measured during the underwater behaviours (one-way ANCOVA F -test, $F_{2,41}=16.48$, $P<0.05$; Fig. 3), where the $DMR_{Stationary}$ (3.82±0.56 l O_2 min⁻¹; Table 4) was significantly lower as compared with $MR_{Surface}$ (Tukey HSD test, mean difference=-0.071, 95% CI [-0.117, -0.026], $P<0.05$), while DMR_{Swim} (4.91±0.77 l O_2 min⁻¹, Table 4) and $MR_{Surface}$ did not differ (Tukey HSD test, mean difference=0.034, 95% CI [-0.011, 0.080], $P<0.05$). The Kleiber ratio was higher than 1 for all animals and underwater behaviours (Fig. 3) and averaged 2.5±0.3 (range=1.9–2.8) for stationary dives, and 3.2±0.3 (range=2.6–3.5) for subsurface swimming. For an 835 kg adult female walrus the cADL was 7.7 min.

DISCUSSION

In this study, we report the first metabolic rate estimates from adult individuals of the largest pinniped species yet studied while floating at the water surface and during stationary dives and subsurface swimming in a controlled environment. Our results from the three adult female Pacific walruses are similar to those previously reported for post-absorptive adult pinnipeds, where measured resting metabolic rate (RMR) was 2–3 times greater as compared with BMR_{est} (Dassis et al., 2012; Fahlman et al., 2008, 2013; Hurley and Costa, 2001; Sparling and Fedak, 2004). The range for $sMR_{Surface}$ for the adult female walruses in our study overlapped and exceeded the upper end of $sMR_{Surface}$ measured for juvenile walruses (Rosen, 2020). We hypothesized that the $DMR_{Stationary}$ and DMR_{Swim} would be lower than the $MR_{Surface}$, and that subsurface swimming would be more energetically costly than stationary dives. However, the results indicated that $DMR_{Stationary}$ was lower than $MR_{Surface}$ and DMR_{Swim} , while DMR_{Swim} was similar to $MR_{Surface}$. These results agree with previous studies in pinnipeds that showed a lower diving metabolic rate (DMR) for inactive dives compared with RMR at the surface (Castellini et al., 1992; Hurley and Costa, 2001), and other studies reporting a DMR_{Swim} lower or similar to RMR (Castellini et al., 1992; Fahlman et al., 2008, 2013; Sparling and Fedak, 2004). Our results suggest that both stationary diving and subsurface swimming are not energetically costly for walruses. The value obtained for $sDMR_{Swim}$ in the present study was lower than that measured in juvenile walruses

Table 2. Trial information and water temperature for each experimental behaviour

Experiment	Dive duration (min)	Data collection (min)	Water temperature (°C)
Floating at the water surface	–	5.1–7.0	12.9–17.0
Stationary dive	3.0–3.3	5.0–5.6	14.3–17.1
Subsurface swimming	1.2–1.8	7.0–7.5	14.1–16.9

For trials included in the analysis ($n=15$ for each metabolic experiment), ranges of dive duration for underwater behaviours, duration of data collection, and water temperature are given for metabolic trials with three participating adult female Pacific walruses while floating at the water surface, and after performing stationary dives and subsurface swimming.

Table 3. Results for linear models evaluating the relationship between metabolic rate and body mass for each in water behaviour

Experiment	χ^2	P-value	β_0	$\log_{10}(M_b)$	R^2
$\log_{10}(\text{MR}_{\text{Surface}})$	13.73	<0.05	-2.91 ± 0.81	1.22 ± 0.28	0.60
$\log_{10}(\text{DMR}_{\text{Stationary}})$	7.96	<0.05	-1.55 ± 0.71	0.73 ± 0.24	0.41
$\log_{10}(\text{DMR}_{\text{Swim}})$	27.60	<0.05	-2.61 ± 0.40	1.13 ± 0.14	0.84

For each metabolic behaviour measured in three adult female Pacific walrus ($n=15$ per each metabolic experiment), linear models included \log_{10} -transformed (\log_{10}) metabolic rate measured in $\text{l O}_2 \text{ min}^{-1}$ (floating at the water surface: $\text{MR}_{\text{Surface}}$; stationary dives: $\text{DMR}_{\text{Stationary}}$; subsurface swimming: DMR_{Swim}) as the dependent variables, and \log_{10} body mass (M_b , measured in kg) as the covariate. The results show the χ^2 for the log-likelihood ratio test and the obtained P-value when comparing the model including M_b with the model including only the intercept. The intercept (β_0), the coefficient for $\log_{10}(M_b)$ together with the standard error, and the R^2 resulting from the final models including M_b are additionally reported.

performing similar subsurface swimming trials (Rosen, 2020) and also lower than the mass-specific FMR for free-ranging adult male walrus (Acquarone et al., 2006). The estimated cADL was within the range of dive durations observed in free-ranging walrus (Acquarone et al., 2006; Born et al., 2005; Gjertz et al., 2001; Wiig et al., 1993).

Metabolic rates while floating at the water surface

Measured $\text{MR}_{\text{Surface}}$ in the present study was similar to results from previous studies reporting basal metabolic rate (BMR) or RMR from post-absorptive and desensitized adult pinnipeds, where measured metabolic rates were 2–3 times greater than that predicted by Kleiber's equation for terrestrial mammals (Dassis et al., 2012; Fahlman and Madigan, 2016; Fahlman et al., 2020, 2008, 2013; Hurley and Costa, 2001; Rosen, 2020; Sparling and Fedak, 2004). While the reasons for the higher measured BMR or RMR in marine mammals as compared with the predictions from Kleiber's remain unclear, it has been suggested that different methodologies and physiological states of the animals during metabolic measurements may be possible reasons for these differences (Lavigne et al., 1986). Kleiber (1975) defined the standard conditions that a study subject should accomplish to obtain comparable metabolic measurements under basal conditions or BMR: (1) reproductively mature individuals, under (2) post-absorptive state of digestion, (3) thermoneutral conditions, and (4) minimal activity level while awake. In the present study, the procedures fulfilled most of these established criteria. The three female walrus were adults, and the experimental procedures took place following an overnight fast. Although a small amount of food was given during the last minute of the trial, this is unlikely to have significantly altered measured metabolic rates considering that it takes approximately 30 min to detect a metabolic increase after food ingestion (Rosen and Trites, 1997). The thermoneutral zone for

walrus in water is still unknown, and the water temperatures in their natural environment at the Chukchi Sea (temperature range at the surface: from 0 to 10°C, and at 30 m depth: from -1 to 6°C; Luchin and Panteleev, 2014) are lower than those measured during selected trials in the present study (12.9–17.1°C). However, measured metabolic rates were not related to the range of water temperatures during the metabolic trials in the current study. Therefore, owing to the lack of information about the thermoneutral range in this species, we do not propose that the measured $\text{MR}_{\text{Surface}}$ in the current study are estimates of BMR for the walrus.

In addition, the animals were trained to maintain a relaxed and inactive state during metabolic measurements to allow for measuring RMR, which is defined as the metabolic rate measured at rest when other conditions for BMR are not met. However, it is worth mentioning that the measured $\text{MR}_{\text{Surface}}$ may have been higher than actual RMR because the walrus had to move to maintain their upright position inside the respirometry dome. In fact, juvenile walrus that remained motionless while in a respirometry dome (Rosen, 2020) had slightly lower $\text{sMR}_{\text{Surface}}$ (73.1–166.1 $\text{kJ kg}^{-1} \text{ day}^{-1}$) than the adult females in our study (126.3–203.9 $\text{kJ kg}^{-1} \text{ day}^{-1}$; Table S2), despite higher $\text{sMR}_{\text{Surface}}$ being expected for juvenile individuals because of their higher mass-specific metabolic rates and investment in growth and development (Costa, 1993). Other studies have similarly noted difficulty maintaining the animals motionless when in water (Dassis et al., 2012; Fahlman et al., 2008). For example, in Patagonia sea lions (*Otaria flavescens*), measured RMR on land was 1.4 times lower compared with $\text{MR}_{\text{Surface}}$, which was attributed to movement inside the respirometry dome (Dassis et al., 2012). Still, the movement shown by the participating walrus at the water surface in this investigation may be consistent with the actual behaviour in their natural environment, where it could be difficult to maintain a motionless position at sea surface conditions. Therefore, although the obtained Kleiber ratio for measured $\text{MR}_{\text{Surface}}$ in the present study was similar to BMR or RMR previously reported for pinnipeds, we suggest that measured $\text{MR}_{\text{Surface}}$ in the current study may be elevated as compared with RMR because of observed movement while in the respirometer, but may represent a more appropriate approximation of the actual $\text{MR}_{\text{Surface}}$ for those animals in the wild. In addition, metabolic rates have been reported to scale exponentially with M_b with a mass-exponent of 0.75 (Kleiber, 1975). While in the present study obtained $\text{MR}_{\text{Surface}}$ closely followed a linear relationship with M_b (see Table 3 and Fig. 3), the limited M_b range may not allow an appropriate analysis to determine whether the relationship is linear or exponential.

Metabolic rates during stationary dives and subsurface swimming

On average, $\text{DMR}_{\text{Stationary}}$ of the adult female walrus was lower as compared with $\text{MR}_{\text{Surface}}$ and DMR_{Swim} , which is consistent with

Table 4. Summary of metabolic measurements

Animal ID	$\text{MR}_{\text{Surface}}$ ($\text{l O}_2 \text{ min}^{-1}$)	$\text{sMR}_{\text{Surface}}$ ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$)	$\text{DMR}_{\text{Stationary}}$ ($\text{l O}_2 \text{ min}^{-1}$)	$\text{sDMR}_{\text{Stationary}}$ ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$)	DMR_{Swim} ($\text{l O}_2 \text{ min}^{-1}$)	$\text{sDMR}_{\text{Swim}}$ ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$)
26005388	3.62 ± 0.42	5.09 ± 0.57	3.55 ± 0.32	5.04 ± 0.41	3.92 ± 0.28	5.57 ± 0.34
26005389	5.57 ± 0.70	5.61 ± 0.86	4.41 ± 0.27	4.60 ± 0.26	5.57 ± 0.23	5.76 ± 0.22
26005390	4.74 ± 0.85	5.74 ± 0.98	3.48 ± 0.50	4.25 ± 0.61	5.24 ± 0.14	6.31 ± 0.16
Overall range	3.22–6.57	4.29–6.92	2.90–4.69	3.53–5.40	3.50–5.80	5.08–6.52

For each participating female Pacific walrus (animal ID) and behaviour, mean \pm s.d. measured metabolic rate (floating at the water surface: $\text{MR}_{\text{Surface}}$; stationary dives: $\text{DMR}_{\text{Stationary}}$; subsurface swimming: DMR_{Swim}) and mass-specific metabolic rate (floating at the water surface: $\text{sMR}_{\text{Surface}}$; stationary dives: $\text{sDMR}_{\text{Stationary}}$; subsurface swimming: $\text{sDMR}_{\text{Swim}}$) are shown. $N=5$ for all experiments with each individual. Overall ranges for each behaviour are also reported.

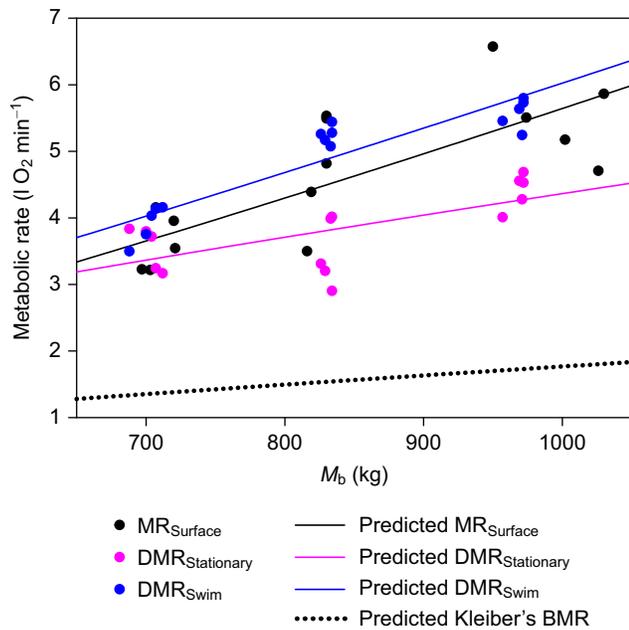


Fig. 3. Measured metabolic rates in relation to body mass for each behaviour and participating walrus. Relationship between measured metabolic rates and body mass (M_b) from three adult female Pacific walrus participating in experimental trials ($n=5$ per each animal and experimental procedure) while floating at the water surface (MR_{Surface}), and during stationary dives ($DMR_{\text{Stationary}}$) and subsurface swimming (DMR_{Swim}). The solid lines represent the predicted metabolic rates ($l\ O_2\ \text{min}^{-1}$) obtained from the results of the linear models reported in Table 3 ($MR_{\text{Surface}}=0.00123M_b^{1.22}$; $DMR_{\text{Stationary}}=0.0282M_b^{0.73}$; $DMR_{\text{Swim}}=0.00245M_b^{1.13}$). The dotted line represents the predicted Kleiber's basal metabolic rate ($BMR_{\text{est}}=0.00993M_b^{0.75}\ l\ O_2\ \text{min}^{-1}$; Kleiber, 1975).

previous studies investigating stationary or inactive dives in pinnipeds (Castellini et al., 1992; Hurley and Costa, 2001). For example, in trained California sea lions (*Zalophus californianus*), Hurley and Costa (2001) reported lower $DMR_{\text{Stationary}}$ than MR_{Surface} for shallow dives (see fig. 3 in Hurley and Costa, 2001). In freely diving Weddell seals (*Leptonychotes weddellii*), Castellini et al. (1992) reported metabolic rates during short sleep or inactive apneas (<14 min) below MR_{Surface} (see fig. 3 in Castellini et al., 1992). The same authors also reported that the overall DMR_{Swim} during free diving was 1.5 times greater than that observed for sleep apneas of similar duration (Castellini et al., 1992), which is similar to the results from our study in which DMR_{Swim} was 1.3 times greater than $DMR_{\text{Stationary}}$.

Alternatively, DMR_{Swim} did not differ from MR_{Surface} which agrees with previous studies in pinnipeds that reported a DMR_{Swim} close to or below RMR in freely diving animals (Castellini et al., 1992; Sparling and Fedak, 2004) or in subjects trained to swim vertically (Fahlman et al., 2008, 2013). In addition, these studies also reported a decreased DMR_{Swim} with increased dive duration, suggesting that pinnipeds can decrease their energetic investment depending on the dive requirements. This extended diving hypometabolism was first described by Scholander (1940), and was suggested to be an ability to reduce metabolism by decreasing the activity of different metabolic processes (e.g. digestion, liver and kidney function, etc.), that would increase the dive duration. Although changes in DMR with increased dive duration were not assessed in the present study, our results suggest an efficient O_2 use during underwater behaviours in the walrus. This physiological capacity could explain the reduced $DMR_{\text{Stationary}}$ and how measured

DMR_{Swim} was similar to MR_{Surface} despite the additional energetic investment during subsurface swimming.

Despite the similarity of the procedures during subsurface swimming trials in two juvenile walrus trained to swim horizontally for 110 m, at a depth of ~ 1.2 m, and at constant velocities (male: $1.6\pm 0.1\ \text{m}\ \text{s}^{-1}$; female: $2.1\pm 0.1\ \text{m}\ \text{s}^{-1}$), the obtained average $sDMR_{\text{Swim}}$ (male: $242.9\pm 60.0\ \text{J}\ \text{kg}^{-1}\ \text{min}^{-1}$; female: $336.6\pm 84.4\ \text{J}\ \text{kg}^{-1}\ \text{min}^{-1}$; Rosen, 2020) were up to 2.8 times greater than that measured in the present study ($121.3\pm 7.0\ \text{J}\ \text{kg}^{-1}\ \text{min}^{-1}$). However, Rosen (2020) noticed that the estimated cost of transport during subsurface swimming in these juvenile walrus was elevated over to that predicted for a similarly sized marine mammal, which was suggested to be related with non-optimal swimming speed and with the higher underlying maintenance costs of young individuals (Rosen, 2020). Thus, the decreased $sDMR_{\text{Swim}}$ reported in the adult female walrus may be partly related with the lower swim speeds ($1.0\pm 0.1\ \text{m}\ \text{s}^{-1}$) and distance (90 m) for subsurface swimming trials in the present study, but also to the decrease in mass-specific metabolic rates with age (Kleiber, 1975). In addition, obtained RER ranges for all experimental behaviours (0.81–1.06; see Table S1) were within expected values. While the RER immediately following a dive tends to change dynamically as the blood and tissues are recovering (Fahlman et al., 2008; Reed et al., 1994), the average for RER during trials at the water surface (0.97 ± 0.05) were similar to those obtained during the post-dive recovery period for both underwater experiments (stationary dives: 0.94 ± 0.07 ; subsurface swimming: 0.94 ± 0.06), and agreed with data reported for resting periods at the surface and for conditioned dives in Steller sea lions (see table 1 in Fahlman et al., 2008).

When translating the results obtained in this study to free-ranging walrus, we found similar characteristics of subsurface swimming behaviour with those previously reported in free-ranging animals that were associated with travelling or exploratory behaviours (Gjertz et al., 2001; Jay et al., 2001). These dives are reported to be shallow (<4 m), with most of them lasting <3 min, and occurring most frequently at the beginning and ending of foraging trips (Gjertz et al., 2001; Jay et al., 2001). The associated ascent and descent swimming velocity reported for these short dives is $\sim 0.5\ \text{m}\ \text{s}^{-1}$, but exceeds $1\ \text{m}\ \text{s}^{-1}$ for longer and deeper dives (Gjertz et al., 2001; Jay et al., 2001). Thus, considering that the animals in the present study performed the subsurface swimming trials at their individual comfort, and the similarities with described underwater behaviour of wild walrus, we suggest that measured DMR_{Swim} could be considered as a suitable approximation of the energetic swimming requirements for walrus when travelling to and from foraging areas or over long-distance migrations. However, the experimental procedures at facilities housing animals are not usually representative of the wild, and differences in underwater behaviours (e.g. social interactions, exploratory behaviours, etc.), or environmental conditions (e.g. water current, water temperature, etc.) experienced by free-ranging walrus could result in different energetic requirements during diving and swimming. This could explain why the observed $sDMR_{\text{Swim}}$ in the present study (see Table S2) is ~ 2 – 3 times lower than the mass-specific FMR measured in two male adult Atlantic walrus, as that approximation accounted for behaviours in the wild (Acquarone et al., 2006). Despite this inherent limitation, these novel metabolic measurements on adult female walrus in water, could help improve energetic requirements estimations during these travelling subsurface dives, while helping interpret measurements of FMR associated with behavioural information.

Aerobic limitation estimated in the present study

The estimated cADL in the present study (7.7 min) was longer than the dive duration for both underwater behaviours (stationary dives: 3.2 ± 0.1 min; subsurface swimming: 1.6 ± 0.2 min) and the duration of travelling and foraging dives observed in free-ranging male Pacific walrus (median dive duration = 7.2 min; Jay et al., 2001) that were suggested to occur within the aerobic dive limit (ADL). Therefore, the dives by females in our study were well within the estimated cADL and likely supported by aerobic metabolism. In addition, the cADL of the walrus in this study was also longer than the average durations for most frequent dives (5–6 min) observed in adult male walrus foraging over continental shelf habitats at depths from 10 to 70 m (Acquarone et al., 2006; Gjertz et al., 2001; Wiig et al., 1993). However, walrus also take deeper and longer dives, exceeding 100 m depth (Acquarone et al., 2006) with a maximum reported dive depth of 234 m (Born et al., 2005) and a dive duration of 24 min (Gjertz et al., 2001). While, reported cADL in the present study could be overestimated as a result of lower energetic demands derived in laboratory conditions, if hypometabolism is related to dive duration in the walrus as in other pinnipeds, cADL may in fact longer during extended dives. Thus, further investigations of the metabolic requirements for dives of different duration in this species would help clarify whether these animals are able to achieve the reported prolonged dive durations (>10 min; Acquarone et al., 2006; Gjertz et al., 2001; Wiig et al., 1993) while avoiding the blood lactate accumulation.

Conclusions

Walrus are currently facing changes to their environment that have altered the availability of their sea ice habitat, which have resulted in changes in their travelling and foraging behaviour, and geographical distribution (Jay et al., 2012; Udevitz et al., 2017). This has led to an increased concern about the future of the walrus populations, raising interest in studies aimed to obtain information about basal, reproductive, or diving and swimming energetic demands (Noren et al., 2012, 2014; Rosen, 2020; Udevitz et al., 2017). Studies measuring the energetic costs for different behaviours and life stages will help improve the accuracy of previous energetic models to predict the potential impacts of environmental change (Udevitz et al., 2017). In the present study, we report the first direct measurements of metabolic rates in female adult Pacific walrus while floating in water and during short and shallow stationary dives and subsurface swimming. The results are consistent with previous work reporting a low energetic cost of diving in marine mammals and confirms that the walrus are able to reduce their metabolic rates during both stationary dives and subsurface swimming. These metabolic estimates would help quantify energetic consequences of reported increased in-water behaviours in the walrus (Jay et al., 2012). In addition, as a benthic feeding marine mammal, walrus spend 70–93% of their time in water, of which much of this time is spent diving to the ocean floor to feed on benthic invertebrates (Jay et al., 2017; Udevitz et al., 2009). Therefore, while the data reported in this study would help improve bioenergetic models, further investigations measuring the metabolic rate for different types of dives (e.g. longer durations or higher swimming requirements), and/or environmental parameters (e.g. water temperature or wind and water current), will help quantify the effect of these parameters on metabolic rates and further improve these models. Similarly, measurements of the metabolic demands while resting on land would add relevant information that will also improve theoretical models aimed at forecasting the conservation scenario of this species.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.B.-E., K.D.R., A. Fahlman; Methodology: A.B.-E., D.F.-F., A. Fahlman; Software: A. Fahlman; Validation: A.B.-E., A. Fahlman; Formal analysis: A.B.-E., A. Forte, A. Fahlman; Investigation: A.B.-E., D.F.-F., A. Fahlman; Resources: A. Fahlman; Data curation: A.B.-E., A. Fahlman; Writing - original draft: A.B.-E.; Writing - review & editing: K.D.R., D.F.-F., A. Forte, R.C.-A., A. Fahlman; Visualization: A.B.-E., A. Fahlman; Supervision: R.C.-A., A. Fahlman; Project administration: A. Fahlman; Funding acquisition: A. Fahlman.

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Data availability

Data used in this study are available from the United States Geological Survey (USGS): <https://doi.org/10.5066/P9UQVFSW>.

References

- Acquarone, M., Born, E. W. and Speakman, J. R. (2006). Field metabolic rates of walrus (*Odobenus rosmarus*) measured by the doubly labeled water method. *Aquat. Mamm.* **32**, 363–369. doi:10.1578/AM.32.3.2006.363
- Bartholomew, G. A., Vleck, D. and Vleck, C. M. (1981). Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. *J. Exp. Biol.* **90**, 17–32. doi:10.1242/jeb.90.1.17
- Born, E. W., Acquarone, M., Knutsen, L. Ø. and Toudal, L. (2005). Homing behaviour in an Atlantic walrus (*Odobenus rosmarus rosmarus*). *Aquat. Mamm.* **31**, 23. doi:10.1578/AM.31.1.2005.23
- Butler, P. J. (2006). Aerobic dive limit. What is it and is it always used appropriately? *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **145**, 1–6. doi:10.1016/j.cbpa.2006.06.006
- Castellini, M. A., Kooyman, G. L. and Ponganis, P. J. (1992). Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J. Exp. Biol.* **165**, 181–194. doi:10.1242/jeb.165.1.181
- Costa, D. P. (1993). Reproductive and foraging energetics of pinnipeds: implications for life history patterns. In *The Behaviour of Pinnipeds* (ed. D. Renouf), pp. 300–344. Dordrecht: Springer Netherlands.
- Dassis, M., Rodríguez, D. H., Ieno, E. N. and Davis, R. W. (2012). Submerged swimming and resting metabolic rates in southern sea lions. *J. Exp. Mar. Biol. Ecol.* **432–433**, 106–112. doi:10.1016/j.jembe.2012.07.001
- Fahlman, A. and Madigan, J. (2016). Respiratory function in voluntary participating Patagonia sea lions (*Otaria flavescens*) in sternal recumbency. *Front. Physiol.* **7**, 528. doi:10.3389/fphys.2016.00528
- Fahlman, A., Schmidt, A., Jones, D. R., Bostrom, B. L. and Handrich, Y. (2007). To what extent might N₂ limit dive performance in king penguins? *J. Exp. Biol.* **210**, 3344–3355. doi:10.1242/jeb.008730
- Fahlman, A., Svärd, C., Rosen, D. A. S., Jones, D. R. and Trites, A. W. (2008). Metabolic costs of foraging and the management of O₂ and CO₂ stores in Steller sea lions. *J. Exp. Biol.* **211**, 3573–3580. doi:10.1242/jeb.023655
- Fahlman, A., Loring, S. H., Ferrigno, M., Moore, C., Early, G., Niemeyer, M., Lentell, B., Wenzel, F., Joy, R. and Moore, M. J. (2011). Static inflation and deflation pressure-volume curves from excised lungs of marine mammals. *J. Exp. Biol.* **214**, 3822–3828. doi:10.1242/jeb.056366
- Fahlman, A., Svärd, C., Rosen, D. A. S., Wilson, R. S. and Trites, A. W. (2013). Activity as a proxy to estimate metabolic rate and to partition the metabolic cost of diving vs. breathing in pre- and post-fasted Steller sea lions. *Aquat. Biol.* **18**, 175–184. doi:10.3354/ab00500

- Fahlman, A., Meegan, J., Borque-Espinosa, A. and Jensen, E. D.** (2020). Pulmonary function and resting metabolic rates in California sea lions (*Zalophus californianus*) on land and in water. *Aquat. Mamm.* **46**, 67-79. doi:10.1578/AM.46.1.2020.67
- Fay, F. H.** (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *N. Am. Fauna* **74** 1-279. doi:10.3996/nafa.74.0001
- Fedak, M. A., Rome, L. and Seeherman, H. J.** (1981). One-step N₂-dilution technique for calibrating open-circuit VO₂ measuring systems. *J. Appl. Physiol.* **51**, 772-776. doi:10.1152/jappl.1981.51.3.772
- Fischbach, A. and Jay, C. V.** (2016). A strategy for recovering continuous behavioral telemetry data from Pacific walruses. *Wildl. Soc. Bull.* **40**, 599-604. doi:10.1002/wsb.685
- Gjertz, I., Griffiths, D., Krafft, B. A., Lydersen, C. and Wiig, Ø.** (2001). Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biol.* **24**, 314-319. doi:10.1007/s003000000211
- Hurley, J. A. and Costa, D. P.** (2001). Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). *J. Exp. Biol.* **204**, 3273-3281. doi:10.1242/jeb.204.19.3273
- Jay, C. V., Farley, S. D. and Garner, G. W.** (2001). Summer diving behavior of male walruses in Bristol Bay, Alaska. *Mar. Mamm. Sci.* **17**, 617-631. doi:10.1111/j.1748-7692.2001.tb01008.x
- Jay, C. V., Heide-Jørgensen, M. P., Fischbach, A. S., Jensen, M. V., Tessler, D. F. and Jensen, A. V.** (2006). Comparison of remotely deployed satellite radio transmitters on walruses. *Mar. Mamm. Sci.* **22**, 226-236. doi:10.1111/j.1748-7692.2006.00018.x
- Jay, C. V., Fischbach, A. S. and Kochnev, A. A.** (2012). Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Mar. Ecol. Prog. Ser.* **468**, 1-13. doi:10.3354/meps10057
- Jay, C. V., Taylor, R. L., Fischbach, A. S., Udevitz, M. S. and Beatty, W. S.** (2017). Walrus haul-out and in water activity levels relative to sea ice availability in the Chukchi Sea. *J. Mammal.* **98**, 386-396. doi:10.1093/jmammal/gyw195
- Jungas, R. L., Halperin, M. L. and Brosnan, J. T.** (1992). Quantitative analysis of amino acid oxidation and related gluconeogenesis in humans. *Physiol. Rev.* **72**, 419-448. doi:10.1152/physrev.1992.72.2.419
- Kanatous, S. B., DiMichele, L. V., Cowan, D. F. and Davis, R. W.** (1999). High aerobic capacities in the skeletal muscles of pinnipeds: adaptations to diving hypoxia. *J. Appl. Physiol.* **86**, 1247-1256. doi:10.1152/jappl.1999.86.4.1247
- Kleiber, M.** (1975). *The Fire of Life: An Introduction to Animal Energetics*, New York: Krieger Publishing.
- Knutsen, L. Ø. and Born, E. W.** (1994). Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. *J. Zool.* **234**, 371-385. doi:10.1111/j.1469-7998.1994.tb04854.x
- Kooyman, G. L.** (1973). Respiratory adaptations in marine mammals. *Am. Zool.* **13**, 457-468. doi:10.1093/icb/13.2.457
- Kooyman, G. L.** (1989). *Diverse Divers: Physiology and Behavior*, Berlin: Springer-Verlag.
- Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., Ferguson, S. H., Wiig, Ø., Boveng, P., Angliss, R. P. et al.** (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv. Biol.* **29**, 724-737. doi:10.1111/cobi.12474
- Lavigne, D. M., Innes, S., Worthy, G. A. J. and Kovacs, K. M.** (1986). Metabolic rate—body size relations in marine mammals. *J. Theor. Biol.* **122**, 123-124. doi:10.1016/S0022-5193(86)80228-4
- Lenfant, C., Johansen, K. and Torrance, J. D.** (1970). Gas transport and oxygen storage capacity in some pinnipeds and the sea otter. *Respir. Physiol.* **9**, 277-286. doi:10.1016/0034-5687(70)90076-9
- Littell, R. C., Henry, P. R. and Ammerman, C. B.** (1998). Statistical analysis of repeated measures data using SAS procedures. *J. Anim. Sci.* **76**, 1216-1231. doi:10.2527/1998.7641216x
- Luchin, V. and Panteleev, G.** (2014). Thermal regimes in the Chukchi Sea from 1941 to 2008. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **109**, 14-26. doi:10.1016/j.dsr2.2014.05.007
- MacCracken, J. G.** (2012). Pacific walrus and climate change: observations and predictions. *Ecol. Evol.* **2**, 2072-2090. doi:10.1002/ece3.317
- Markus, T., Stroeve, J. C. and Miller, J.** (2009). Recent changes in Arctic sea ice melt onset, freezeup, and melt season length. *J. Geophys. Res. Oceans.* **114**, 1-14. doi:10.1029/2009JC005436
- Noren, S. R., Udevitz, M. S. and Jay, C. V.** (2012). Bioenergetics model for estimating food requirements of female Pacific walruses *Odobenus rosmarus divergens*. *Mar. Ecol. Prog. Ser.* **460**, 261-275. doi:10.3354/meps09706
- Noren, S. R., Udevitz, M. S. and Jay, C. V.** (2014). Energy demands for maintenance, growth, pregnancy, and lactation of female Pacific walruses (*Odobenus rosmarus divergens*). *Physiol. Biochem. Zool.* **87**, 837-854. doi:10.1086/678237
- Noren, S. R., Jay, C. V., Burns, J. M. and Fischbach, A. S.** (2015). Rapid maturation of the muscle biochemistry that supports diving in Pacific walruses (*Odobenus rosmarus divergens*). *J. Exp. Biol.* **218**, 3319-3329. doi:10.1242/jeb.125757
- Ponganis, P. J.** (2011). Diving mammals. *Compr. Physiol.* **1**, 447-465. doi:10.1002/cphy.c091003
- Quanjer, P. H., Tammeling, G. J., Cotes, J. E., Pedersen, O. F., Peslin, R. and Yernault, J.-C.** (1993). Lung volumes and forced ventilatory flows. *Eur. Respir. J.* **6**, 5-40. doi:10.1183/09041950.005s1693
- Reed, J. Z., Chambers, C., Fedak, M. A. and Butler, P. J.** (1994). Gas exchange of captive freely diving grey seals (*Halichoerus grypus*). *J. Exp. Biol.* **191**, 1-18. doi:10.1242/jeb.191.1.1
- Rosen, D. A. S.** (2020). Resting and swimming metabolic rates in juvenile walruses (*Odobenus rosmarus*). *Mar. Mamm. Sci.* **1**, 1-11. doi:10.1111/mms.12743
- Rosen, D. A. S. and Trites, A. W.** (1997). Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. *Comp. Biochem. Physiol. A Physiol.* **118**, 877-881. doi:10.1016/S0300-9629(97)00039-X
- Scholander, P. F.** (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrådetes Skrifter.* **22**, 1-131.
- Sparling, C. E. and Fedak, M. A.** (2004). Metabolic rates of captive grey seals during voluntary diving. *J. Exp. Biol.* **207**, 1615-1624. doi:10.1242/jeb.00952
- Udevitz, M. S., Jay, C. V., Fischbach, A. S. and Garlich-Miller, J. L.** (2009). Modeling haul-out behavior of walruses in Bering Sea ice. *Can. J. Zool.* **87**, 1111-1128. doi:10.1139/Z09-098
- Udevitz, M. S., Taylor, R. L., Garlich-Miller, J. L., Quakenbush, L. T. and Snyder, J. A.** (2013). Potential population-level effects of increased haul-out-related mortality of Pacific walrus calves. *Polar Biol.* **36**, 291-298. doi:10.1007/s00300-012-1259-3
- Udevitz, M. S., Jay, C. V., Taylor, R. L., Fischbach, A. S., Beatty, W. S. and Noren, S. R.** (2017). Forecasting consequences of changing sea ice availability for Pacific walruses. *Ecosphere* **8**, e02014. doi:10.1002/eecs2.2014
- Wiig, Ø., Gjertz, I., Griffiths, D. and Lydersen, C.** (1993). Diving patterns of an Atlantic walrus *Odobenus rosmarus rosmarus* near Svalbard. *Polar Biol.* **13**, 71-72. doi:10.1007/BF00236586
- Withers, P. C.** (1977). Measurement of VO₂, VCO₂, and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* **42**, 120-123. doi:10.1152/jappl.1977.42.1.120
- Wolk, E. and Kosygin, G. M.** (1979). A hematological study of the walrus, *Odobenus rosmarus*. *Acta Theriol. Sin.* **24**, 99-107. doi:10.4098/AT.arch.79-12