


# Resting metabolic rate and lung function in fasted and fed rough-toothed dolphins, *Steno bredanensis*

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## Abstract

We measured resting metabolic rate (RMR), tidal volume ( $V_T$ ), breathing frequency ( $f_R$ ), respiratory flow, and end-expired gases in rough-toothed dolphins (*Steno bredanensis*) housed in managed care after an overnight fast and 1–2 hr following a meal. The measured average ( $\pm$  standard deviation)  $V_T$  ( $4.0 \pm 1.3$  L) and  $f_R$  ( $1.9 \pm 1.0$  breaths/min) were higher and lower, respectively, as compared with estimated values from both terrestrial and aquatic mammals, and the average  $V_T$  was 43% of the estimated total lung capacity. The end-expired gas levels suggested that this species keep alveolar  $O_2$  (10.6% or 80 mmHg) and  $CO_2$  (7.6% or 57 mmHg), and likely arterial gas tensions, low and high, respectively, to maximize efficiency of gas exchange. We show that following an overnight fast, the RMR ( $566 \pm 158$  ml  $O_2$ /min) was 1.8 times the estimated value predicted by Kleiber for terrestrial mammals of the same size. We also show that between 1 and 2 hr after ingestion of a meal, the metabolic rate increases an average of 29% ( $709 \pm 126$  ml  $O_2$ /min). Both body mass ( $M_b$ ) and  $f_R$  significantly altered the measured RMR and we propose that both these variables should be measured when estimating energy use in cetaceans.

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## KEYWORDS

diving physiology, energetics, field metabolic rate, lung mechanics, marine mammals, pulmonary function test, spirometry, total lung capacity

## 1 | INTRODUCTION

Knowing energy flow between species and trophic levels is important for understanding the ecology of populations. The field metabolic rate (FMR) is the sum of all energy used over a given duration for an individual (Nagy, 2005). For a nonpregnant, and not lactating, adult mammal in thermoneutrality it is generally made up of the basal metabolic rate (BMR), the locomotor cost (LC), and the cost of digestion (usually referred to as heat increment of feeding [HIF] or specific dynamic action [SDA]). Determination of a species FMR provides the basis for understanding the energy needs, and allows bioenergetic modeling and assessment of the metabolic consequences due to disturbance or the impact of climate change (Pirotta, 2022; Pirotta et al., 2015; Winship et al., 2002). For modeling population consequences of disturbance (PCOD), the energy flow within populations is one of the parameters that has the largest influence on the model output (McHuron et al., 2022; Pirotta et al., 2015). For most marine mammals neither BMR, HIF, nor LC are known, and therefore FMR is difficult to estimate.

BMR is a fundamental unit for understanding the essential energy expenditures to sustain the basic functions of an individual homeotherm. When measuring BMR, several criteria must be met; the animal has to be resting (inactive but not sleeping), postabsorptive, in a thermoneutral environment, and a nonpregnant adult. Meeting all these criteria for BMR is not always possible, and one alternative is to measure the resting metabolic rate (RMR) and define the conditions of the measurement (He et al., 2023). With an estimate of the BMR or RMR, the FMR can be estimated by assuming or measuring the additional costs for other variables such as movement (LC) and digestion (HIF) (Bejarano et al., 2017; Winship et al., 2002).

The BMR, or RMR, has been measured in a limited number of marine mammals under human care, in enclosures and open water environments (Allen et al., 2022; Hurley & Costa, 2001; Kastelein et al., 2000; Pedersen et al., 2020; Reed et al., 1994, 2000; Rosen & Trites, 2013; Sparling et al., 2007; Worthy et al., 2013; Yazdi et al., 1999; Yeates & Houser, 2008). Based on those data, it was shown that the BMR for small (<100 kg) marine mammals is greater than those predicted by Kleiber's allometric equation ( $\dot{V}_{O_2} = \text{BMR} = 0.00993 M_b^{0.75}$ , where  $\dot{V}_{O_2}$  is the rate of  $O_2$  consumption in liters of  $O_2$  per minute and  $M_b$  the body mass in kilograms) for terrestrial mammals (He et al., 2023; Kleiber, 1961). The higher metabolic demand in smaller marine mammals was suggested to represent a higher metabolic demand to support thermoregulation in an aquatic environment. The limited number of measurements on marine mammals would therefore provide additional information to test this hypothesis.

The LC has been estimated using different proxies. One method estimated the energetic cost for the stroking frequency, which has been used in some studies (Jeanniard-Du-Dot et al., 2016; Williams et al., 2004, 2017). Another approach has been to integrate the overall activity in 3-dimensions using the so-called Overall Dynamic Body Acceleration (Wilson et al., 2006, 2020), which has been used successfully to estimate the LC and diving metabolic cost in both cetaceans and pinnipeds (Allen et al., 2022; Fahlman et al., 2013; Jeanniard-Du-Dot et al., 2017). These proxies have been used in a few studies to estimate FMR (e.g., Fahlman et al., 2023; Noren, 2011; Williams et al., 2017).

It is well known that digestion increases metabolic cost, with an increase that is related to the meal size and the time after a meal (Rosen & Trites, 1997; Secor, 2009; Yeates & Houser, 2008). The metabolic cost of digestion, commonly called Heat Increment of Feeding (HIF) or Specific Dynamic Action (SDA), has been studied in the Steller sea lion (*Eumetopias jubatus*) and the common bottlenose dolphin (*Tursiops truncatus*; Rosen & Trites, 1997; Yeates & Houser, 2008). In the former, the metabolism peaked between 2.8–3.7 hr after food ingestion (2 kg or 4 kg of her-ring), with metabolism increasing 1.76–2.13 times, with a higher increase and longer delay to maximum for the larger meal size (Rosen & Trites, 1997). In the bottlenose dolphin, the metabolic rate 30–230 min after ingesting 1.4 kg of capelin was measured and compared against the RMR following an overnight fast. These data showed that the

metabolic rate peaked around 50 min following the meal, with a maximal increase of 57.1% higher than the resting value, at which time it decreased back to fasted values around 120 min after feeding (Yeates & Houser, 2008). Consequently, as digestion significantly alters the metabolic cost, and as few measurements have been made in marine mammals, and especially odontocetes, there is a need to better understand how food ingestion alters energy use.

The rough-toothed dolphin (*Steno bredanensis*) is a smaller dolphin species, that inhabits deep oceanic waters throughout tropical and warm temperate areas. It is a species listed as of least concern by IUCN, but little is known about their physiology, and we are not aware of any past study that has attempted to measure their bioenergetic needs or lung function. For this reason, we measured RMR, tidal volume ( $V_T$ ), breathing frequency ( $f_R$ ), respiratory flow, and end-expired gases in rough-toothed dolphins housed in managed care. Based on a past study that estimated BMR in aquatic and terrestrial mammals (He et al., 2023), we hypothesized that the RMR would be slightly higher in this small cetacean as compared with similar sized terrestrial mammals. We showed that following an overnight fast, the RMR was 1.8 times the estimated value predicted by Kleiber for terrestrial mammals. We also showed that between 1 and 2 hr after ingestion of a meal, the metabolic rate increases an average of 29%. The results showed that compared with other odontocete species, the  $f_R$  and  $V_T$  is lower and higher, respectively, in the rough-toothed dolphin. We propose that these data provide a valuable contribution for improved understanding of the bioenergetic needs for oceanic dolphins, which may help improve conservation efforts.

## 2 | MATERIALS AND METHODS

### 2.1 | Animals

All measurements were performed between April 24 and May 13, 2023, where three females and one male rough-toothed dolphins, with a mean body mass ( $M_b$ ) of  $101 \pm 20$  kg, and mean age of  $14 \pm 9$  years at the time of the measurements were studied (Table 1). The animals were originally stranded and rehabilitated but deemed nonreleasable.

For all respirometry trials, a custom-made breath-by-breath respirometry system, including custom-built pneumotachometer and fast-response  $O_2$  and  $CO_2$  analyzers allowed assessment of lung function and resting rates of  $O_2$  consumption ( $\dot{V}_{O_2}$ ) and  $CO_2$  production ( $\dot{V}_{CO_2}$ ). All respirometry trials (breath-by-breath lung function and end-expired  $O_2$  and  $CO_2$ ) were measured with the dolphin staying inactive while submerged in water and breathing voluntarily. Respirometry trials lasted a minimum of 10 min, with the dolphin being inactive 2–5 min before the trial started.

### 2.2 | Respiratory flows (lung function)

The procedures and equipment used were identical to those used in previous studies on similar species housed in human care, or during similar conditions on restrained wild dolphins (Fahlman et al. 2015, 2018), briefly summarized below. Respiratory flows were measured using a custom-made Fleisch type pneumotachometer (Mellow Design,

**TABLE 1** Animal identification, sex, body mass ( $M_b$ ), blood hematocrit concentration ([Hct], %), water temperature, and breathing frequency ( $f_R$ ) during focal observations.

Animal ID	Sex	$M_b$ (kg)	Year of birth	[Hct] (%)	Water temperature ( $^{\circ}C$ )	$f_R$ (breaths/min)
Sb1	Male	85	2016	42	$25.4 \pm 0.2$	$1.4 \pm 0.4$
Sb2	Female	122.9	2007	41	$25.0 \pm 0.7$	$1.2 \pm 0.2$
Sb3	Female	112.2	1997	45	$25.0 \pm 0.7$	$1.1 \pm 0.1$
Sb4	Female	82.7	2015	39	$25.0 \pm 0.7$	$1.2 \pm 0.2$
Mean	—	$101 \pm 20$	—	$42 \pm 2$	$25.2 \pm 0.3$	$1.2 \pm 0.1$

Valencia, Spain), which housed a low-resistance laminar flow matrix (Item # Z9A887-2; Merriam Process Technologies, Cleveland, OH). A differential pressure transducer (Spirometer Pod, ML 311; ADInstruments, Colorado Springs, CO) was connected to the pneumotachometer with two 310-cm lengths of 2-mm I.D., firm walled, flexible tubing. The differential pressure transducer was connected to a data acquisition system (Powerlab 8/35; ADInstruments, Colorado Springs, CO), and the data were captured at 400 Hz and displayed on a computer running LabChart (v. 8.1; ADInstruments, Colorado Springs, CO). The differential pressure was used to determine flow and was calibrated using a 7.0-L calibration syringe (Series 4900; Hans-Rudolph Inc, Shawnee, KS). The signal was integrated, and the flow determined as detailed previously (Fahlman et al. 2015, 2018).

### 2.3 | Respiratory gas composition

The concentrations of expired  $O_2$  and  $CO_2$  were subsampled via a port in the pneumotachometer and passed through a 310-cm length of 2 mm I.D., firm walled, flexible tubing and a 30-cm length of 1.5 mm I.D. Nafion tubing, to a fast-response  $O_2$  and  $CO_2$  analyzer (ML206  $O_2/CO_2$  fast response gas analyzer; ADI Instruments) at a flow rate of 200 ml/min. The gas analyzer was connected to the data acquisition system and sampled at 400 Hz. The gas analyzer was calibrated before and after the experiment using a commercial mixture of 5%  $O_2$ , 5%  $CO_2$ , and 90%  $N_2$  (Product No. 17 L-340; GASCO, Oldsmar, FL). Ambient air and pure  $O_2$  were used to check the calibration before and after each experimental trial. Mean ( $\pm$  standard deviation) air temperature, humidity, and ambient pressure during trials were  $22^\circ C \pm 2^\circ C$  (range  $17^\circ C$ – $26^\circ C$ ),  $69\% \pm 14\%$  (41%–90%), and  $101.3 \pm 0.4$  kPa (100.6–101.9 kPa). The mean water temperature during trials was  $25.2^\circ C \pm 0.6^\circ C$  (range:  $23.8^\circ C$ – $25.7^\circ C$ ).

### 2.4 | Metabolic rates (respirometry)

The metabolic rates were estimated as detailed previously (Allen et al., 2022; Fahlman et al., 2015, 2018) and summarized here. The respiratory gas signals were phase-corrected for  $CO_2$  and  $O_2$ , to match the respirations, and the expiratory flow-rate and expired  $O_2$  and  $CO_2$  content were multiplied to calculate the instantaneous  $O_2$  consumption rate ( $\dot{V}_{O_2}$ ) and  $CO_2$  production rate ( $\dot{V}_{CO_2}$ ) after correction using equation 4b in Withers (Withers 1977). The instantaneous  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  were integrated over each breath to yield the total volume of  $O_2$  and  $CO_2$  exchanged during each breath. The volumes were summed for each trial period and divided by the duration of the trial to provide an estimate of the oxygen consumption and carbon dioxide production rates for that period. The response time of the gas analyzer was corrected using the method outlined by Allen et al. (2022).

The spirometry trials consisted of a total of 56 fasted ( $n = 28$ ) and fed ( $n = 28$ ) measurements. Following the fasted trials, the dolphins were fed between 1,133 kcal and 1,411 kcal, followed by a second metabolic measurement. For eight of these the duration between the fasted and fed measurements was 1 hr, and for the remaining 20 fed trials the duration was 2 hr. In addition, we performed focal observations on separate days in the morning before feeding to assure that the respirometry trials did not affect the  $f_R$ .

The Kleiber ratio was calculated as the measure  $\dot{V}_{O_2}$  divided by the estimated BMR from Kleiber's equation for BMR for terrestrial mammals (Kleiber 1961).

### 2.5 | Data processing and statistical analysis

All gas volumes were converted to standard temperature pressure dry (STPD; Quanjer et al., 1993). Exhaled air was assumed saturated at  $37^\circ C$ , inhaled air volume was corrected for ambient temperature and relative humidity. Metabolic data are reported as the average  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  for an entire trial.

A general linear mixed-effects (GLM) model, with nested random effects of animal, to account for the correlation between repeated measurements on the same individual (Littell et al., 1998) was used to assess how fasting (fed or fasted), amount of food ingested before a trial (kilocalories),  $M_b$ , and age (independent fixed covariates) affected metabolic rate ( $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$ ), pulmonary gas concentration (end-expired  $O_2$  and  $CO_2$ ), and lung function ( $f_R$ ,  $V_T$ , breath duration and respiratory flow). We transformed  $\dot{V}_{O_2}$ ,  $\dot{V}_{CO_2}$ ,  $M_b$ ,  $f_R$ , and  $V_T$  using the 10-base logarithm ( $\log_{10}$ ). Models were fitted in the R statistical computing software (Posit Team, 2023; R Core Team, 2021) using the *nlme* package (Pinheiro et al., 2021). Initially, a univariate analysis on each independent variable was performed, and only those variables with  $p < .20$  (Wald's tests) were considered in the multivariate analysis. Stepwise techniques were used to search for the best model. We used the likelihood ratio test to determine significance of parameters between nested models, i.e., models with added parameters.

In this study  $p$ -values  $\leq .05$  were considered as significant and  $p$ -values  $\leq .1$  were considered potentially suggestive of a trend. Data are presented as the mean  $\pm$  standard deviation, unless otherwise stated.

### 3 | RESULTS

Data for lung function, expired gas concentration, and metabolic rates for each individual dolphin are available in Tables S1 and S2.

#### 3.1 | Respiratory function and gas exchange

The average  $f_R$  during fasted ( $1.8 \pm 1.1$  breaths/min) and fed ( $2.0 \pm 0.9$  breaths/min) respirometry trials were not found to be different (1 df,  $\chi^2 = 1.5$ ,  $p > .2$ ). However,  $f_R$  was 58% higher during respirometry trials ( $1.9 \pm 1.0$  breaths/min) as compared with focal observations ( $1.2 \pm 0.3$ , 1 df,  $\chi^2 = 9.5$ ,  $p = .002$ ). The increased  $f_R$  during respirometry trials was mainly due to one dolphin (Sb3), and when this individual was removed, no differences were apparent in  $f_R$  between respirometry trials ( $1.4 \pm 0.4$  breaths/min) and focal observations (1 df,  $\chi^2 = 2.6$ ,  $p = .1076$ ).

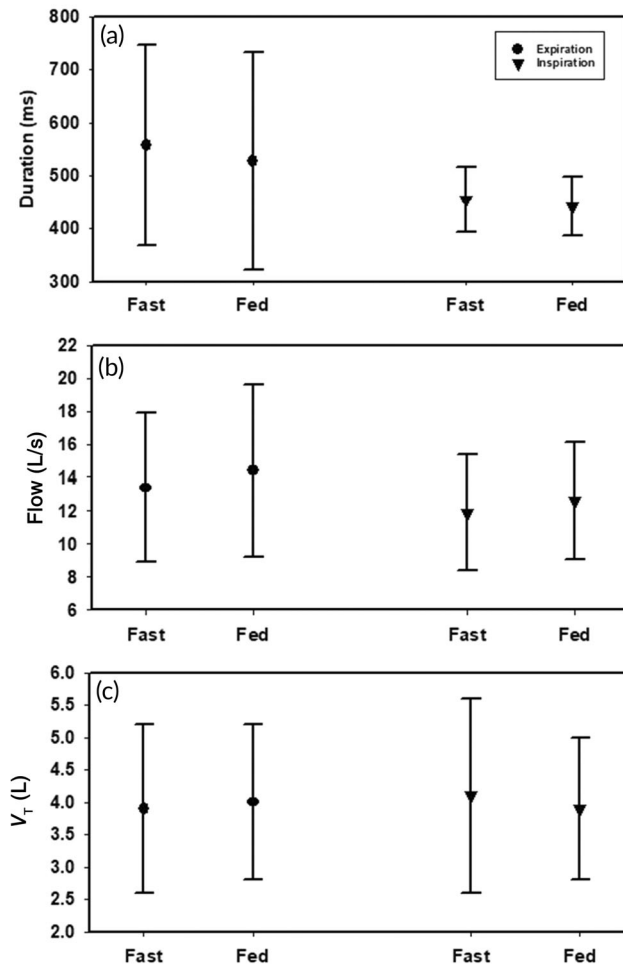
Figure 1 shows mean  $\pm$  standard deviation (a) breath durations, (b) respiratory flow, and (c)  $V_T$ 's for fed and fasted dolphins, separated by expiration and inspiration. For breath durations, neither fasting state, nor  $M_b$  were important predictors, but the inspiratory duration decreased by 6 ms with each year of age (1 df,  $\chi^2 = 8.35$ ,  $p = .0039$ ). A similar trend was also seen for expiratory duration (1 df,  $\chi^2 = 3.30$ ,  $p = .069$ ), and total breath duration (1 df,  $\chi^2 = 3.57$ ,  $p = .059$ ), with a 15 ms and 20 ms decrease in duration per year.

The mean maximum spontaneous expiratory flow ( $\dot{V}_{exp}$ ) was  $13.9 \pm 4.8$  L/s (range: 10.4–20.8 L/s), and did not vary with age,  $M_b$  or fasting state ( $p > .1$  for all; Figure 1b). Similarly, the maximum spontaneous inspiratory flow ( $\dot{V}_{insp}$ ) was not found to differ with age or  $M_b$  ( $p > .1$ ), but was 6% higher in fed ( $11.9 \pm 3.5$  L/s, range: 9.5–11.6 L/s) as compared with fasted ( $12.6 \pm 3.5$  L/s, range: 9.3–17.3 L/s, 1 df,  $\chi^2 = 4.54$ ,  $p = .033$ ) animals. Neither fasting state,  $M_b$  or age were important to explain  $V_{Tinsp}$ , and the mean  $V_{Texp}$  and  $V_{Tinsp}$  were  $3.9 \pm 1.3$  L and  $4.0 \pm 1.3$  L, respectively (Figure 1c). The mean  $V_{Tinsp}$  was  $43\% \pm 14\%$  (range: 26%–58%) of the estimated total lung capacity (TLCest; Fahlgren et al., 2017).

The end-expired  $O_2$  varied with fasting state,  $\log_{10}$ -transformed  $f_R$  ( $\log_{10}[f_R]$ ) and  $M_b$  ( $\log_{10}[M_b]$ ), as (Equation 1, 1 df,  $\chi^2 = 5.35$ ,  $p = .0207$ ; Figure 2a):

$$ETO_2 = -5.07 (5.10) - 0.48 (0.25) \times fed + \log_{10}[f_R] \times 3.43 (0.83) + \log_{10}[M_b] \times 7.61 (2.58) \quad (1)$$

This, and similar prediction equations, are based on the best fit regression model with parameter estimates and their associated standard error in parenthesis. Factors, such as feeding state is either 1 or 0. For Equation 1,  $ETO_2$  for a 100 kg, fed dolphin with a breathing frequency of 2 breaths/min would be:



**FIGURE 1** Data on lung function in four rough-toothed dolphins. Panels show mean ( $\pm$  standard deviation) expiratory and inspiratory (a) breath durations, (b) respiratory flows, and (c) tidal volumes ( $V_T$ ).

$$ETO_2 = -5.07 - 0.48 \times 1 + \log_{10}[2] \times 3.43 + \log_{10}[100] \times 7.61$$

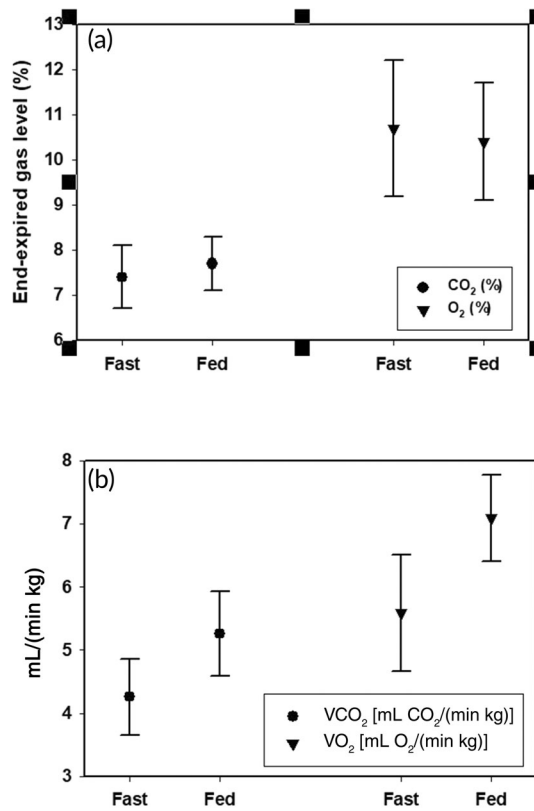
End-expired  $CO_2$  varied with fasting state, and  $\log_{10}[f_R]$  as (Equation 2, 1 df,  $\chi^2 = 21.7$ ,  $p < .001$ ):

$$ETCO_2 = 7.84 (0.15) + 0.36 (0.12) \times fed - \log_{10}[f_R] \times 2.43 (0.40) \quad (2)$$

Thus, increasing  $f_R$  resulted in higher and lower  $ETO_2$  and  $ETCO_2$ , respectively, while feeding, on the other hand, decreased and increased  $ETO_2$  and  $ETCO_2$ , respectively.

### 3.2 | Metabolic rates

The mean resting  $\dot{V}_{O_2}$  (ml  $O_2$ /min; Figure 2b), and mass-specific  $\dot{V}_{O_2}$  [ $s\dot{V}_{O_2}$ , ml  $O_2$ /(min  $\cdot$  kg)] in inactive dolphins were  $566 \pm 158$  ml  $O_2$ /min (range: 388 ml  $O_2$ /min to 747 ml  $O_2$ /min), and  $5.6 \pm 0.9$  ml  $O_2$ /(min  $\cdot$  kg), [range: 4.6 ml



**FIGURE 2** Mean ( $\pm$  standard deviation) of (a) end-expired O<sub>2</sub> and CO<sub>2</sub> and (b) mass-specific rate of O<sub>2</sub> consumption ( $\dot{V}_{O_2}$ ) and CO<sub>2</sub> production ( $\dot{V}_{CO_2}$ ) in fasted and fed rough-toothed dolphins.

O<sub>2</sub>/(min · kg) to 6.7 ml O<sub>2</sub>/(min · kg)], respectively. The mean respiratory quotient (RQ,  $\dot{V}_{CO_2}/\dot{V}_{O_2}$ ) was  $0.76 \pm 0.04$  for fasted dolphins, and  $0.74 \pm 0.07$  after feeding. The log-10 transformed  $\dot{V}_{O_2}$  ( $\log_{10}[\dot{V}_{O_2}]$ ) was affected by fasting state (fed or fasted), and both  $\log_{10}[f_R]$  and  $\log_{10}[M_b]$  (Equation 3, 1 df,  $\chi^2 = 8.77$ ,  $p = .0031$ ).

$$\log_{10}(\dot{V}_{O_2}) = -1.69 (0.28) + 0.09 (0.02) \times \text{fed} + \log_{10}[f_R] \times 0.35 (0.05) + \log_{10}[M_b] \times 0.67 (0.14) \quad (3)$$

The mean Kleiber ratio for fasted and fed dolphins were, respectively,  $1.8 \pm 0.3$  (range: 1.4–2.2) and  $2.3 \pm 0.2$  (range: 2.1–2.5).

For  $\log_{10}$ -transformed  $\dot{V}_{CO_2}$  [ $\log_{10}(\dot{V}_{CO_2})$ ], the most parsimonious model also contained fasting state,  $\log_{10}[f_R]$  and  $\log_{10}[M_b]$ , as (Equation 4, 1 df,  $\chi^2 = 12.2$ ,  $p < .001$ ):

$$\log_{10}(\dot{V}_{CO_2}) = -2.25 (0.26) + 0.08 (0.02) \times \text{fed} + \log_{10}[f_R] \times 0.31 (0.05) + \log_{10}[M_b] \times 0.90 (0.13) \quad (4)$$

## 4 | DISCUSSION

In the current study, we measured the resting metabolism in rough-toothed dolphins housed in managed care after an overnight fast and 1–2 hr following ingestion of a meal. We show that the  $\dot{V}_{O_2}$  is 1.8 times Kleiber, and that the

metabolic rate increases on average  $29\% \pm 18\%$  following a meal. While the thermoneutral zone is not known for this species, individuals were maintained in water similar to their natural habitat in the Gulf of Mexico and we propose that these values represent the basal levels of metabolism for this species. Furthermore, we also present data on their respiratory capacity, which show that in this small odontocete,  $f_R$  and  $V_T$ , are, respectively, lower and higher as compared with measurements on other small and medium sized odontocete species.

Metabolic measurements in marine mammals are commonly done using flow-through respirometry (e.g., van der Hoop et al., 2014; Yazdi et al., 1999; Yeates & Houser, 2008), and while breath-by-breath respirometry is common in humans and other terrestrial mammals it has not been used extensively in marine mammals until recently (Allen, 2021; Pedersen et al., 2020). Although these respirometry methods both estimate energy use by measuring the  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$ , their differences could potentially be a reason why some studies report different results in the same species (e.g., Allen et al., 2022; Williams et al., 2004). However, measured  $\dot{V}_{O_2}$ s in the same individual dolphins following an overnight fast have confirmed that these two methods provide equivalent results (Allen, 2021; van der Hoop et al., 2014). Consequently, differences in measured metabolic rates between studies using either conventional flow-through or breath-by-breath respirometry are therefore likely not due to methodological reasons. The results presented in the current study suggest that differences in  $f_R$  may be one possible reason for variation in results between studies. We show that  $f_R$  alters pulmonary gas levels, and thereby the partial pressure gradient for gas exchange with the pulmonary capillaries. These results indicate that without accounting for  $f_R$ , the estimated  $\dot{V}_{O_2}$  would be different. One example in the current study was the almost double  $f_R$  in dolphin (Sb3), which also had the highest  $\dot{V}_{O_2}$  [ $6.66 \text{ ml O}_2/(\text{min} \cdot \text{kg})$ ] as compared with the other individuals [range:  $4.56\text{--}5.97 \text{ ml O}_2/(\text{min} \cdot \text{kg})$ ]. When this animal was removed, there were no longer differences in  $f_R$  during respirometry measurements and focal observations. Variation in  $f_R$  may be one possible reason why there has been large discrepancies in measured  $\dot{V}_{O_2}$  in marine mammals in different studies, and measuring and reporting  $f_R$  would be useful in future studies attempting to measure metabolic costs.

The most parsimonious model included  $M_b$  and  $f_R$ , and showed that the metabolism increased after feeding. Interestingly, despite a small data set of only four animals with limited body mass range, the allometric mass-exponents for both  $M_b$  and  $f_R$  agree with results from studies including several species (He et al., 2023; Mortola & Limoges, 2006). The metabolic rates from the fasted animals were, on average, 1.8 higher than those from similar sized terrestrial mammals (Kleiber, 1961). The higher metabolic rate in marine mammals is common in smaller species, and may be associated with higher thermal heat loss (He et al., 2023). These results provide further evidence that these data are physiologically relevant and that the measured fasted metabolic rates can be considered basal levels for this species.

That feeding alters metabolic rate is well known and both the caloric intake and time affect the temporal response (Secor, 2009). We are only aware of one past measurement in a cetacean, where a 220-kg bottlenose dolphin provided the time course of  $\dot{V}_{O_2}$  following ingestion of 1,800 kcal (assuming an energy equivalent of 1,295 kcal/kg capelin; Yeates & Houser, 2008). The data reported in the past study suggested that the 25 min following the meal, the metabolic rate increased by 20%, and with a maximal increase of about 40% between 60 and 100 min after feeding (Yeates & Houser, 2008). Repeating several metabolic measurements without providing food was not possible in the current study. For this reason, we did the initial measurement fasted, then provided food and performed a single repeated measurements 1 or 2 hr afterwards without additional food in between. Although this only provides two points on the curve describing the temporal response, we were not able to show a difference between 1 and 2 hr after the meal. The results presented in the current study suggest that the elevated metabolic rate is on average 29% higher at 1 hr following feeding and remain elevated for at least 2 hr. We suggest that digestion of food is the most likely explanation for these results. However, we acknowledge that we did not perform any controlled experiment with animals not being fed between the first and second measurement.

The measured  $\dot{V}_{O_2}$  compares well with measurements in other cetacean species (Allen et al., 2022; Hampton & Whittow, 1976; Hampton et al., 1971; Pedersen et al., 2020; Rechsteiner et al., 2013; Reed et al., 2000; Rosen & Trites, 2013; Worthy et al., 2013; Yazdi et al., 1999; Yeates & Houser, 2008), and further support the recent study



that proposed that small cetaceans have higher mass-specific metabolic rate as compared with land mammals (He et al., 2023).

There was a clear change in the measured  $\dot{V}_{O_2}$  with  $f_R$ , and in a 100-kg fasted rough-toothed dolphin, the predicted  $\dot{V}_{O_2}$  (Equation 3) increased by 28% with a doubling in  $f_R$  from 1 breath/min to 2 breaths/min (from 447 ml  $O_2$ /min to 569 ml  $O_2$ /min). Similar results have also been reported in the Hawaiian spinner dolphin (*Stenella longirostris*) and common bottlenose dolphin, where the authors reported similar changes in  $\dot{V}_{O_2}$  with  $f_R$  (Hampton & Whittow, 1976; Hampton et al., 1971). These data provide an interesting alternative method to estimate resting  $\dot{V}_{O_2}$  in these species from  $f_R$  alone. A number of studies have attempted to use  $f_R$  to estimate changes in  $\dot{V}_{O_2}$  in freely swimming cetaceans (Dolphin, 1987; Folkow & Blix, 1992), but the validity of this method has been discussed (Fahlman et al., 2016; Folkow & Blix, 2017). However, the data presented here provide support for this method when properly calibrated, and the data presented in the present and past studies of dolphins have been on inactive animals (Hampton & Whittow, 1976; Hampton et al., 1971). As changes in  $f_R$ ,  $V_T$ , and  $O_2$  extraction may affect the  $\dot{V}_{O_2}$ , appropriate validation studies would have to be performed to assure that a similar relationship also holds for active animals (e.g., Fahlman et al., 2016).

The respiratory pattern in the rough-toothed dolphins differs from the allometric predictions from the larger bottlenose dolphin, beluga whale (*Delphinapterus leucas*), pilot whale (*Globicephala macrorhynchus*), and false killer whale (*Pseudorca crassidens*), and also the smaller harbor porpoise (*Phocoena phocoena*), with lower  $f_R$ 's (except dolphin Sb3), and higher  $V_T$ 's, but with a minute and alveolar ventilation that was only 55% and 57%, respectively, of predicted values (Fahlman et al., 2020; He et al., 2023; Olsen et al., 1969; Reed et al., 2000). This lower ventilation resulted in a lower end expired  $PO_2$  and higher  $PCO_2$  (Table S2) as compared with the bottlenose dolphin and harbor porpoise (Fahlman et al., 2015; Reed et al., 2000). The aquatic (intermittent) breathing pattern with a low  $f_R$  and high  $V_T$  may be a way to reduce the work of breathing, similar to what is seen in some terrestrial mammals (Milsom, 1991). During repeated breath-hold dives in both pinnipeds and cetaceans, it has been shown that replenishment of the  $O_2$  stores is incomplete and the duration of the surface interval determined by removal of  $CO_2$  (Boutillier et al., 2001; Fahlman et al., 2008; Reed et al., 1994, 2000). In the Steller sea lion, the resulting  $O_2$  debt, by incomplete recovery of the  $O_2$  stores, helps improve gas exchange as delivery of  $O_2$  is more efficient on the steep portion of the  $O_2$  dissociation curve (Fahlman et al., 2008). This strategy of retaining an  $O_2$  debt is particularly important during repeated foraging dives, where time at the surface should be minimized and the aerobic dive duration maximized. The data presented in the current study suggest that rough-toothed dolphins also employ this strategy to support basal needs, where an unusually low  $f_R$  for their size helps maintain the end-expired, and likely arterial,  $PO_2$  low. This creates a favorable partial pressure gradient for gas diffusion and  $O_2$  uptake. This proposed strategy could be tested using near-infrared spectroscopy in addition to breath-by-breath respirometry, where both alveolar and arterial gas content could be measured (McKnight et al., 2019; Ruesch et al., 2022).

In the current study we report data on resting, postprandial, metabolic rates in a small cetacean species, which we propose are representative of basal values. We show that these estimates of BMR in the rough-toothed dolphins are on average 1.8 times higher than those predicted by the allometric equation for terrestrial mammals published by Kleiber (Kleiber, 1961), and agree with the proposal that small aquatic mammals have higher basal requirements than terrestrial mammals. We further show that between 1 and 2 hr after ingestion of a meal, the metabolic rate increases by an average of 29%. Our results also suggest that both  $M_b$  and  $f_R$  affect the metabolic rate, and without accounting for this variation in  $f_R$  may complicate comparisons between and within individuals, species, trials, and studies. In three out of four dolphins, the  $f_R$  and  $V_T$  were, respectively, lower, and higher as compared with other cetaceans when accounting for  $M_b$ . This may be a strategy to keep the arterial  $PO_2$  reduced, which enhances  $O_2$  uptake for each breath and may help minimize the cost of breathing.

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## AUTHOR CONTRIBUTIONS

**Andreas Fahlman:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – original draft. **Kaylee Rhiue:** Investigation; resources. **Brie Alessi:** Investigation; resources; supervision. **Shelly Marquardt:** Investigation; resources; supervision. **Michelle Schisa:** Investigation; resources; supervision. **Guillermo Sánchez Contreras:** Investigation; resources; supervision. **Josefin Larsson:** Data curation; formal analysis; investigation; writing – review and editing.

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