Check for updates

Received: 15 June 2023 | Accepted: 18 August 2023

DOI: 10.1111/mms.13068

ARTICLE

Marine Mammal Science

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

Andreas Fahlman[1,2,3,4] | Kaylee Rhieu[5] | Brie Alessi[5] | Shelly Marquardt[5] | Michelle B. Schisa[6] | Guillermo J. Sanchez-Contreras[7] | Josefin Larsson[3]

[1]Global Diving Research SL, Valencia, Spain

[2]Fundación Oceanografic de la Comunidad Valenciana, Valencia, Spain

[3]Kolmården Wildlife Park, Kolmården, Sweden

[4]IFM, Linköping University, Linköping, Sweden

[5]Clearwater Marine Aquarium, Clearwater, Florida

[6]Gulf World, Panama City Beach, Florida

[7]The Dolphin Company, Cancún, Mexico

Correspondence
Andreas Fahlman, Global Diving Research SL, Cl Felix Pizcueta 5 Pt 9, 4600 Valencia, Spain.
Email: gdrsl16@gmail.com

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 (± standard deviation) V_T (4.0 ± 1.3 L) and f_R (1.9 ± 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 ± 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 ± 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.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2023 The Authors. *Marine Mammal Science* published by Wiley Periodicals LLC on behalf of Society for Marine Mammalogy.

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 jubutus*) 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 herring), 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

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

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 ± 20 kg, and mean age of 14 ± 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 (°C)	f_R (breaths/min)
Sb1	Male	85	2016	42	25.4 ± 0.2	1.4 ± 0.4
Sb2	Female	122.9	2007	41	25.0 ± 0.7	1.2 ± 0.2
Sb3	Female	112.2	1997	45	25.0 ± 0.7	1.1 ± 0.1
Sb4	Female	82.7	2015	39	25.0 ± 0.7	1.2 ± 0.2
Mean	—	101 ± 20	—	42 ± 2	25.2 ± 0.3	1.2 ± 0.1

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

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 (± standard deviation) air temperature, humidity, and ambient pressure during trials were 22°C ± 2°C (range 17°C–26°C), 69% ± 14% (41%–90%), and 101.3 ± 0.4 kPa (100.6–101.9 kPa). The mean water temperature during trials was 25.2°C ± 0.6°C (range: 23.8°C –25.7°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°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.

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

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 ≤ .05 were considered as significant and p-values ≤ .1 were considered potentially suggestive of a trend. Data are presented as the mean ± 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 ± 1.1 breaths/min) and fed (2.0 ± 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 ± 1.0 breaths/min) as compared with focal observations (1.2 ± 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 ± 0.4 breaths/min) and focal observations (1 df, $\chi^2 = 2.6$, $p = .1076$).

Figure 1 shows mean ± 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 ± 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 ± 3.5 L/s, range: 9.5–11.6 L/s) as compared with fasted (12.6 ± 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 ± 1.3 L and 4.0 ± 1.3 L, respectively (Figure 1c). The mean V_{Tinsp} was 43% ± 14% (range: 26%–58%) of the estimated total lung capacity (TLCest; Fahlman et al., 2017).

The end-expired O_2 varied with fasting state, log10-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):

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

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:

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

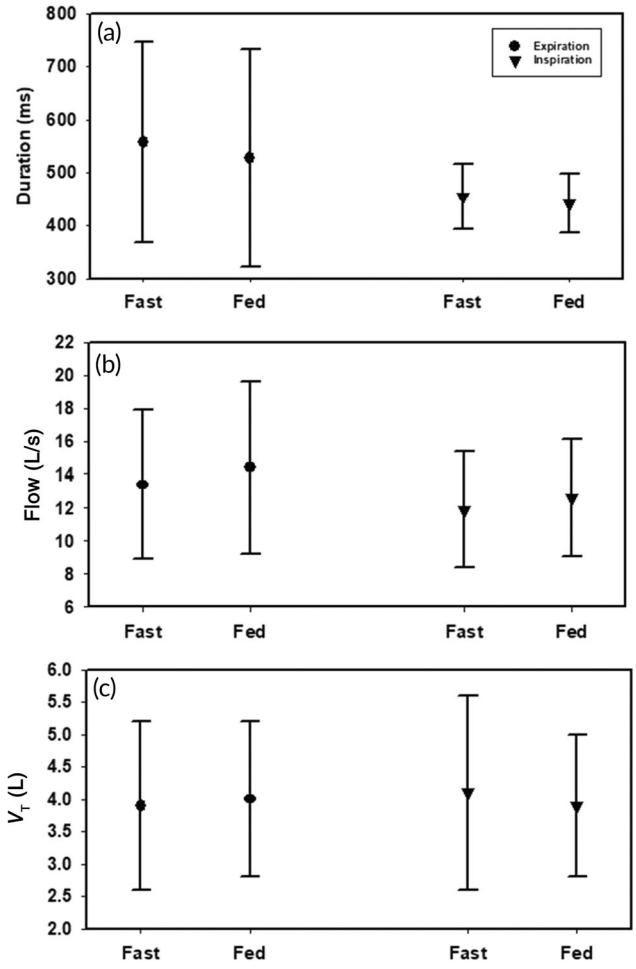

FIGURE 1 Data on lung function in four rough-toothed dolphins. Panels show mean (± standard deviation) expiratory and inspiratory (a) breath durations, (b) respiratory flows, and (c) tidal volumes (V_T).

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

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

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

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 · kg)] in inactive dolphins were 566 ± 158 ml O_2/min (range: 388 ml O_2/min to 747 ml O_2/min), and 5.6 ± 0.9 ml O_2/(min · kg), [range: 4.6 ml

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

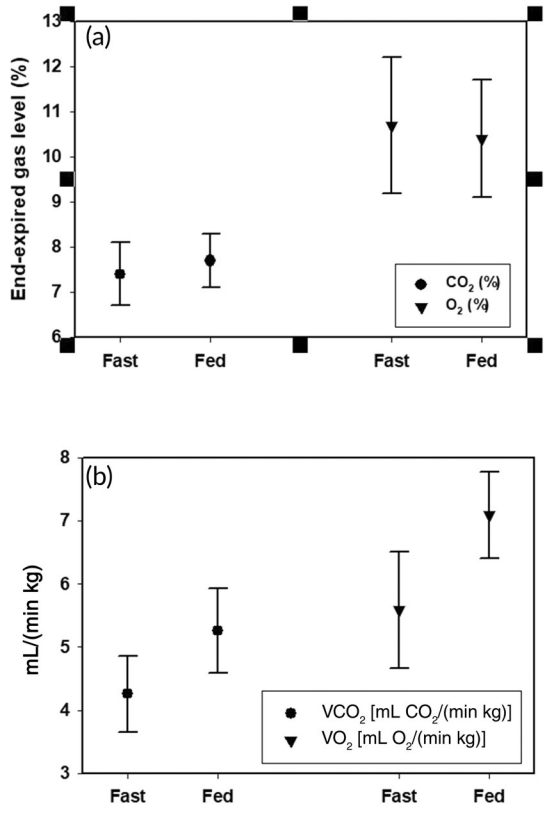

FIGURE 2 Mean (± standard deviation) of (a) end-expired O_2 and CO_2 and (b) mass-specific rate of O_2 consumption ($\dot{V}_{O_2}$) and CO_2 production ($\dot{V}_{CO_2}$) in fasted and fed rough-toothed dolphins.

O_2/(min · kg) to 6.7 ml O_2/(min · kg)], respectively. The mean respiratory quotient (RQ, $\dot{V}_{CO_2}/\dot{V}_{O_2}$) was 0.76 ± 0.04 for fasted dolphins, and 0.74 ± 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, $\chi^2 = 8.77$, $p = .0031$).

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

The mean Kleiber ratio for fasted and fed dolphins were, respectively, 1.8 ± 0.3 (range: 1.4–2.2) and 2.3 ± 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, $\chi^2 = 12.2$, $p < .001$):

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

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

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

metabolic rate increases on average 29% ± 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 ml O_2/(min · kg)] as compared with the other individuals [range: 4.56–5.97 ml O_2/(min · 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

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

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 (Boutilier 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.

ACKNOWLEDGMENTS

A special thanks to the many volunteers and staff at Clearwater Marine Aquarium and Gulf World for making these measurements possible. A special thanks to Ellen Leonard, Mel Mason, Beth Schumacher, Hailee Crocket, Rhegan Shields, and Kodi Underwood at Gulf World, and Camelle Zodrow and Brooke Bowersox at Clearwater Marine

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Aquarium. We also would like to thank the referees whose constructive comments helped improve this manuscript. All procedures in this study were approved by the Clearwater Marine Aquarium Animal Care and Use Committee (Protocol #2022-06), the veterinary and research department of the Dolphin Company (2023-01), and the Animal Care Committee of Fundacion Oceanografic (Oce-23-1). All procedures were supervised by the attending veterinarian at both facilities.

AUTHOR CONTRIBUTIONS

Andreas Fahlman: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – original draft. **Kaylee Rhieu:** 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.

ORCID

Andreas Fahlman https://orcid.org/0000-0002-8675-6479

REFERENCES

Allen, A. S. (2021). *Estimating the cost of locomotion in common bottlenose dolphins: calibration, validation, and application to study the impacts of disturbance* [Doctoral dissertation]. Duke University.

Allen, A. S., Read, A. J., Shorter, K. A., Gabaldon, J., Blawas, A. M., Rocho-Levine, J., & Fahlman, A. (2022). Dynamic body acceleration as a proxy to predict the cost of locomotion in bottlenose dolphins. *Journal of Experimental Biology*, *225*(4), Article jeb243121. https://doi.org/10.1242/jeb.243121

Bejarano, A. C., Wells, R. S., & Costa, D. P. (2017). Development of a bioenergetic model for estimating energy requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. *Ecological Modelling*, *356*(6), 162–172. https://doi.org/10.1016/j.ecolmodel.2017.05.001

Boutilier, R. G., Reed, J. Z., & Fedak, M. A. (2001). Unsteady-state gas exchange and storage in diving marine mammals: the harbor porpoise and gray seal. *American Journal of Physiology*, *281*(2), R490–R494. https://doi.org/10.1152/ajpregu.2001.281.2.R490

Dolphin, W. F. (1987). Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. *Canadian Journal of Zoology*, *65*(1), 83–90. https://doi.org/10.1139/z87-013

Fahlman, A., Allen, A. S., Blawas, A., Sweeney, J., Stone, R., Trainor, R., Jensen, F. H., McHugh, K., Allen, J. B., Barleycorn, A. A., & Wells, R. S. (2023). Surface and diving metabolic rates, and dynamic aerobic dive limits (dADL) in near- and off-shore bottlenose dolphins, *Tursiops* spp., indicate that deep diving is energetically cheap. *Marine Mammal Science*, *39*(3), 976–993. https://doi.org/10.1111/mms.13023

Fahlman, A., Borque-Espinosa, A., Facchin, F., Ferrero Fernandez, D., Muñoz Caballero, P., Haulena, M., & Rocho-Levine, J. (2020). Comparative respiratory physiology in cetaceans. *Frontiers Physiology*, *11*. https://doi.org/10.3389/fphys.2020.00142

Fahlman, A., Brodsky, M., Wells, R., McHugh, K., Allen, J., Barleycorn, A., Sweeney, J. C., Fauquier, D., & Moore, M. (2018). Field energetics and lung function in wild bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay Florida. *Royal Society Open Science*, *5*, Article 171280. https://doi.org/10.1098/rsos.171280

Fahlman, A., Loring, S. H., Levine, G., Rocho-Levine, J., Austin, T., & Brodsky, M. (2015). Lung mechanics and pulmonary function testing in cetaceans. *Journal of Experimental Biology*, *218*(13), 2030–2038. https://doi.org/10.1242/jeb.119149

Fahlman, A., Moore, M. J., & Garcia-Parraga, D. (2017). Respiratory function and mechanics in pinnipeds and cetaceans. *Journal of Experimental Biology*, *220*(10), 1761–1763. https://doi.org/10.1242/jeb.126870

Fahlman, A., Svärd, C., Rosen, D. A. S., Jones, D. R., & Trites, A. W. (2008). Metabolic costs of foraging and the management of O_2 and CO_2 stores in Steller sea lions. *Journal of Experimental Biology*, *211*, 3573–3580. https://doi.org/10.1242/jeb.023655

Fahlman, A., Svärd, C., Rosen, D. A. S., Wilson, R. S., & 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. *Aquatic Biology 18*(2), 175–184. https://doi.org/10.3354/ab00500

Fahlman, A., van der Hoop, J., Moore, M., Levine, G., Rocho-Levine, J., & Brodsky, M. (2016). Estimating energetics in cetaceans from respiratory frequency: why we need to understand physiology. *Biology Open*, *5*(4), 436–442. https://doi.org/10.1242/bio.017251

Folkow, L. P., & Blix, A. S. (1992). Metabolic rates of minke whales (*Balaenoptera acutorostrata*) in cold water. *Acta Physiologica Scandinavica*, *146*(1), 141–150. https://doi.org/10.1111/j.1748-1716.1992.tb09402.x

Folkow, L. P., & Blix, A. S. (2017). On the importance of understanding physiology when estimating energetics in cetaceans. *Biology Open*, *6*(2), 306–308. https://doi.org/10.1242/bio.023929

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hampton, I. F. G., & Whittow, G. C. (1976). Body temperature and heat exchange in the Hawaiian spinner dolphin, *Stenella longirostris*. *Comparative Biochemistry and Physiology Part A: Physiology*, *55*(2), 195–197. https://doi.org/10.1016/0300-9629(76)90092-X

Hampton, I. F. G., Whittow, G. C., Szekerczes, J., & Rutherford, S. (1971). Heat transfer and body temperature in the Atlantic bottlenose dolphin, *Tursiops truncatus*. *International Journal of Biometeorology*, *15*, 247–253. https://doi.org/10.1007/BF01803907

He, R. S., De Ruiter, S., Westover, T., Somarelli, J. A., Blawas, A., Dayanidhi, D. L., Singh, A., Steves, B., Driesinga, S., Halsey, L. G., & Fahlman, A. (2023). Allometric scaling of metabolic rate and cardiorespiratory variables in aquatic and terrestrial mammals. *Physiological Reports*, *11*(11), Article e15698. https://doi.org/10.14814/phy2.15698

Hurley, J. A., & Costa, D. P. (2001). Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). *Journal of Experimental Biology*, *204*(19), 3273–3281. https://doi.org/10.1242/jeb.204.19.3273

Jeanniard-du-Dot, T., Guinet, C., Arnould, J. P. Y., Speakman, J. R., & Trites, A. W. (2017). Accelerometers can measure total and activity-specific energy expenditures in free-ranging marine mammals only if linked to time-activity budgets. *Functional Ecology*, *31*(2), 377–386. https://doi.org/10.1111/1365-2435.12729

Jeanniard-du-Dot, T., Trites, A. W., Arnould, J. P. Y., Speakman, J. R., & Guinet, C. (2016). Flipper strokes can predict energy expenditure and locomotion costs in free-ranging northern and Antarctic fur seals. *Scientific Reports*, *6*, Article 33912. https://doi.org/10.1038/srep33912

Kastelein, R. A., Mosterd, J., Schooneman, N. M., & Wiepkema, P. R. (2000). Food consumption, growth, body dimensions, and respiration rates of captive false killer whales (*Pseudorca crassidens*). *Aquatic Mammals*, *26*(1), 33–44.

Kleiber, M. (1961). *The fire of life: An introduction to animal energetics*. Wiley.

Littell, R. C., Henry, P. R., & Ammerman, C. B. (1998). Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science*, *76*(4), 1216–1231. https://doi.org/10.2527/1998.7641216x

McHuron, E. A., Adamczak, S., Arnould, J. P. Y., Ashe, E., Booth, C., Bowen, W. D., Christiansen, F., Chudzinska, M., Costa, D. P., Fahlman, A., Farmer, N. A., Fortune, S. M. E., Gallagher, C. A., Keen, K. A., Madsen, P. T., McMahon, C. R., Nabe-Nielsen, J., Noren, D. P., Noren, S. R., … Williams, R. (2022). Key questions in marine mammal bioenergetics. *Conservation Physiology*, *10*(1), Article coac055. https://doi.org/10.1093%2Fconphys%2Fcoac055

McKnight, J. C., Bennett, K. A., Bronkhorst, M., Russell, D. J. F., Balfour, S., Milne, R., Bivins, M., Moss, S. E. W., Colier, W., Hall, A. J., & Thompson, D. (2019). Shining new light on mammalian diving physiology using wearable near-infrared spectroscopy. *PLoS Biology*, *17*(6), Article e3000306. https://doi.org/10.1371/journal.pbio.3000306

Milsom, W. K. (1991). Intermittent breathing in vertebrates. *Annual Review of Physiology*, *53*, 87–105. https://doi.org/10.1146/annurev.ph.53.030191.000511

Mortola, J. P., & Limoges, M.-J. (2006). Resting breathing frequency in aquatic mammals: A comparative analysis with terrestrial species. *Respiratory Physiology and Neurobiology*, *154*(3), 500–514. https://doi.org/10.1016/j.resp.2005.12.005

Nagy, K. A. (2005). Field metabolic rate and body size. *Journal of Experimental Biology*, *208*(9), 1621–1625. https://doi.org/10.1242/jeb.01553

Noren, D. P. (2011). Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science*, *27*(1), 60–77. https://doi.org/10.1111/j.1748-7692.2010.00386.x

Olsen, C. R., Hale, F. C., & Elsner, R. (1969). Mechanics of ventilation in the pilot whale. *Respiration Physiology*, *7*(2), 137–149. https://doi.org/10.1016/0034-5687(69)90001-2

Pedersen, M. B., Fahlman, A., Borque-Espinosa, A., Madsen, P. T., & Jensen, F. H. (2020). Whistling is metabolically cheap for communicating bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology*, *223*(1), Article jeb212498. https://doi.org/10.1242/jeb.212498

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2021). *nlme: Linear and nonlinear mixed effects models* (R package version 3) [Computer software]. R Core Team.

Pirotta, E. (2022). A review of bioenergetic modelling for marine mammal populations. *Conservation Physiology*, *10*(1), Article coac036. https://doi.org/10.1093/conphys/coac036

Pirotta, E., Harwood, J., Thompson, P. M., New, L., Cheney, B., Arso, M., Hammond, P. S., Donovan, C., & Lusseau, D. (2015). Predicting the effects of human developments on individual dolphins to understand potential long-term population consequences. *Proceedings of the Royal Society B: Biological Sciences*, *282*, Article 20152109. https://doi.org/10.1098/rspb.2015.2109

Posit Team. (2023). *RStudio: Integrated development environment for R* [Computer software]. Posit Software. http://www.posit.co/.

Quanjer, P. H., Tammeling, G. J., Cotes, J. E., Pedersen, O. F., Peslin, R., & Yernault, J.-C. (1993). Lung volumes and forced ventilatory flows. *European Respiratory Journal*, *6*(Suppl 16), 5–40. https://doi.org/10.1183/09041950.005s1693

R Core Team. (2021). *R: A language and environment for statistical computing* (Version 4.2.2) [Computer software]. R Foundation for Statistical Computing.

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rechsteiner, E. U., Rosen, D. A. S., & Trites, A. W. (2013). Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model. *Journal of Mammalogy*, *94*(4), 820–832.https://doi.org/10.1644/12-MAMM-A-206.1

Reed, J. Z., Chambers, C., Fedak, M. A., & Butler, P. J. (1994). Gas exchange of captive freely diving grey seals (*Halichoerus grypus*). *Journal of Experimental Biology*, *191*(1), 1–18. https://doi.org/10.1242/jeb.191.1.1

Reed, J. Z., Chambers, C., Hunter, C. J., Lockyer, C., Kastelein, R., Fedak, M. A., & Boutilier, R. G. (2000). Gas exchange and heart rate in the harbour porpoise, *Phocoena phocoena*. *Journal of Comparative Physiology B*, *170*(1), 1–10. https://doi.org/10.1007/s003600050001

Rosen, D. A. S., & Trites, A. W. (1997). Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. *Comparative Biochemistry and Physiology Part A: Physiology*, *118*(3), 877–881. https://doi.org/10.1016/s0300-9629(97)00039-x

Rosen, D. A. S., & Trites, A. W. (2013). Resting metabolic rate of a mature male beluga whale (*Delphinapterus leucas*). *Aquatic Mammals*, *39*, 85–88.

Ruesch, A., McKnight, J. C., Fahlman, A., Shinn-Cunningham, B. G., & Kainerstorfer, J. M. (2022). Near-infrared spectroscopy as a tool for marine mammal research and care. *Frontiers in Physiology*, *12*. https://doi.org/10.3389/fphys.2021.816701

Secor, S. M. (2009). Specific dynamic action: a review of the postprandial metabolic response. *Journal of Comparative Physiology B*, *179*(1), 1–56. https://doi.org/10.1007/s00360-008-0283-7

Sparling, C. E., Fedak, M. A., & Thompson, D. (2007). Eat now, pay later? Evidence of deferred food-processing costs in diving seals. *Biology Letters*, *3*(1), 94–98. https://doi.org/10.1098/rsbl.2006.0566

van der Hoop, J. M., Fahlman, A., Hurst, T., Rocho-Levine, J., Shorter, A. K., Petrov, V., & Moore, M. J. (2014). Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment. *Journal of Experimental Biology*, *217*(23), 4229–4236. https://doi.org/10.1242/jeb.108225

Williams, T. M., Fuiman, L. A., Horning, M., & Davis, R. W. (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *Journal of Experimental Biology*, *207*(6), 973–982. https://doi.org/10.1242/jeb.00822

Williams, T. M., Kendall, T. L., Richter, B. P., Ribeiro-French, C. R., John, J. S., Odell, K. L., Losch, B. A., Feuerbach, D. A., & Stamper, M. A. (2017). Swimming and diving energetics in dolphins: a stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes. *Journal of Experimental Biology*, *220*(6), 1135–1145. https://doi.org/10.1242/jeb.154245

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P. M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Geraldi, N. R., Duarte, C. M., Scott, R., Strano, M. S., Robotka, H., Eizaguirre, C., Fahlman, A., & Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172. https://doi.org/10.1111/1365-2656.13040

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090. https://doi.org/10.1111/j.1365-2656.2006.01127.x

Winship, A. J., Trites, A. W., & Rosen, D. A. S. (2002). A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Marine Ecology Progress Series*, *229*, 291–312. https://doi.org/10.3354/MEPS229291

Withers, P. C. (1977). Measurements of $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, and evaporative water loss with a flow-through mask. *Journal of Applied Physiology*, *42*(1), 120–123. https://doi.org/10.1152/jappl.1977.42.1.120

Worthy, G. A. J., Worthy, T. A. M., Yochem, P. K., & Dold, C. (2013). Basal metabolism of an adult male killer whale (*Orcinus orca*). *Marine Mammal Science*, *30*(3), 1229–1237. https://doi.org/10.1111/mms.12091

Yazdi, P., Kilian, A., & Culik, B. M. (1999). Energy expenditure of swimming bottlenose dolphins (*Tursiops truncatus*). *Marine Biology*, *134*(4), 601–607. https://doi.org/10.1007/s002270050575

Yeates, L. C., & Houser, D. S. (2008). Thermal tolerance in bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology*, *211*(20), 3249–3257. https://doi.org/10.1242/jeb.020610

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fahlman, A., Rhieu, K., Alessi, B., Marquardt, S., Schisa, M. B., Sanchez-Contreras, G. J., & Larsson, J. (2023). Resting metabolic rate and lung function in fasted and fed rough-toothed dolphins, *Steno bredanensis*. *Marine Mammal Science*, 1–12. https://doi.org/10.1111/mms.13068

17487692, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mms.13068, Wiley Online Library on [21/09/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License