Received: 6 September 2022 | Accepted: 12 March 2023
DOI: 10.1111/mms.13023

ARTICLE

Marine Mammal Science

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

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Abstract

High-resolution dive depth and acceleration recordings from nearshore (Sarasota Bay, dive depth < 30 m), and off-shore (Bermuda) bottlenose dolphins (*Tursiops* spp.) were used to estimate the diving metabolic rate (DMR) and the locomotor metabolic rate (LMR, L O_2/min) during three phases of diving (descent, bottom, and ascent). For shallow dives (depth ≤ 30 m), we found no differences between the two ecotypes in the LMR during diving, nor during the postdive shallow interval between dives. For intermediate (30 m < depth ≤ 100 m) and deep dives (depth > 100 m), the LMR was significantly higher during ascent than during descent and the bottom phase by 59% and 9%, respectively. In addition, the rate of change in depth during descent and ascent (meters/second) increased with maximal dive depth. The dynamic aerobic dive limit (dADL) was calculated from the estimated DMR and the estimated predive O_2 stores. For the Bermuda dolphins, the dADL decreased with dive depth, and was 18.7, 15.4, and 11.1 min for shallow, intermediate, and deep dives, respectively. These results provide

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Funding information
Funding received by Aarhus Institute of Advanced Studies through the FP7 program of the EU (Agreement No. 609033); Dolphin Quest; Office of Naval Research, Grant/Award Numbers: N000141410410, N000141410563, N000142112652

a useful approach to understand the complex nature of physiological interactions between aerobic metabolism, energy use, and diving capacity.

KEYWORDS
cetacean, diving physiology, field metabolic rate, locomotor cost, marine mammal, ODBA

1 | INTRODUCTION

Marine mammals divide their time between being underwater, where they search and capture prey, and at the surface, where they replenish the O_2 used for aerobic metabolism during their submergence. The total time spent on a single dive will influence both the type of prey they can access and the amount of prey that can be obtained. Thus, an individual's ability to maximize prey capture during diving is a function of the metabolic cost of a dive, or the O_2 consumed, and the total available O_2 stores that can be used to fuel aerobic metabolism. Although marine mammals have the capacity for anaerobic metabolism, most species perform most of their dives utilizing aerobic metabolism (Kooyman et al., 2020), and extended dives fueled by anaerobic metabolism eventually result in reduced foraging efficiency (Fedak & Thompson, 1993). Adaptations to enhance the aerobic dive duration in marine mammals include hydrodynamic shape to minimize drag to lower the metabolic cost of swimming and increased O_2 stores (Fish, 1994; Ponganis, 2015). In addition, theoretical work has suggested that the dive response helps regulate perfusion to optimize utilization of available O_2 so that the duration for aerobic metabolism is maximized (Davis & Kanatous, 1999).

The O_2 stores are in three compartments: the lungs, blood, and skeletal muscle (Davis, 2019; Ponganis, 2015). Species that perform long and deep dives generally have a greater volume of blood relative to body mass and a greater blood O_2 capacity (more O_2 per unit volume of blood). The blood O_2 capacity is enhanced by a higher proportion of red blood cells per volume of blood (the hematocrit) and by an elevated concentration of hemoglobin within the red blood cells. In addition, extreme divers generally also have a greater overall muscle mass, with large muscle fibers, low mitochondrial volume, and higher concentration of muscle myoglobin that also binds and stores oxygen (Kooyman & Ponganis, 1998; Noren & Williams, 2000; Pabst et al., 2016; Ponganis, 2015). Greater muscle and blood O_2 stores increase the available O_2, while increased muscle mass proportional to body mass lowers the overall metabolic rate as the metabolic rate of muscle is lower than most other tissues (Pabst et al., 2016). Lungs, on the other hand, have limited ability to enhance available O_2, especially in deep divers, as the alveoli compress during diving, which reduce or eliminate gas exchange (Bostrom et al., 2008; Kooyman, 1973; Scholander, 1940).

In cetaceans there is limited knowledge of the total O_2 stores (Arregui et al., 2021; Noren & Williams, 2000; Velten et al., 2013), and although studies have estimated the resting or swimming metabolic rate (Allen et al., 2022; Noren et al., 2013; Pedersen et al., 2020; Williams et al., 1993; Worthy et al., 2013, Yeates & Houser, 2008), the O_2 utilization during dives has not been determined. Methods to estimate field metabolic rate (FMR), such as the rate of O_2 consumption, using respirometry, energy intake, or stable isotopes, are logistically difficult in fully aquatic free-ranging marine mammals (Arranz et al., 2019; Noren, 2011; Rojano-Doñate et al., 2018). Even in the best-studied cetacean, the common bottlenose dolphin (*Tursiops truncatus*), few estimations of FMR exist (Allen, 2021; Bejarano et al., 2017; Rimbach et al., 2021). The basal metabolic rate (BMR) has been measured in trained bottlenose dolphins (Allen et al., 2022; Noren et al., 2013; Pedersen et al., 2020; van der Hoop et al., 2014; Williams et al., 1993; Yeates & Houser, 2008), and used as a proxy to estimate FMR by multiplying BMR by a factor of between 3 to 6 (Arranz et al., 2019; Bejarano et al., 2017; Noren, 2011).

While measuring FMR for wild, unrestrained animals is challenging, proxies such as activity have shown promise in estimating diving metabolic rate (DMR; Fahlman et al., 2008, 2013), and thus ultimately FMR. For trained bottlenose dolphins, physical activity proxies for metabolic rate have recently been validated against metabolic rate estimates based on O_2 consumption rate, stable isotopes, and energetic intake, and have been used to evaluate the energetic impact of disturbance for wild, unrestrained animals (Allen, 2021; Allen et al., 2022). In the current study we used time-series dive data to estimate *in situ* activity levels in two populations of bottlenose dolphins; one coastal ecotype that exhibits short and shallow dives (Wells et al., 2013), and one offshore ecotype that conducts long, deep foraging dives (Fahlman, Jensen, et al., 2018; Klatsky et al., 2007). We used the established relationship between activity and locomotor metabolic rate (LMR, L O_2/min; Allen et al., 2022), along with estimates of BMR and heat increment of feeding (HIF) to estimate variation in the metabolic rates at the surface and while diving, i.e., DMR, for the two ecotypes. We then used a previously developed gas dynamics model to determine the dynamic aerobic dive limit (dADL) from the estimated DMR and the O_2 stores before the dive. Thus, the dADL is similar to the calculated ADL (cADL), but varies between dives depending on the DMR and the estimated O_2 stores following the period of recovery at the surface. Finally, the energetic costs were compared for various activities of these two populations.

2 | MATERIAL AND METHODS

2.1 | Abbreviations

ADL: aerobic dive limit, the dive duration until the blood lactate begins to increase, usually assumed an estimate of the time when aerobic metabolism is used to support the dive.
bADL: behavioral aerobic dive limit, an estimate of the ADL based on the cumulative dive frequency, usually assumed to be the dive duration that 97.5% of all dives are within.
cADL: calculated aerobic dive limit, an estimate of the available oxygen stores divided by the oxygen consumption rate.
dADL: dynamic aerobic dive limit, an estimate of the available oxygen stores before a dive divided by the diving metabolic rate.
BMR: basal metabolic rate, the metabolic rate used to support life in an inactive, postabsorptive adult mammal in a thermoneutral environment.
DMR: diving metabolic rate, the energetic cost for an individual dive.
FMR: field metabolic rate, the daily metabolic rate of an animal in the field.
HIF: heat increment of feeding, the additional metabolic cost due to digestion. Also called specific dynamic action (SDA).
LMR: locomotor metabolic rate, expressed as a metabolic rate in L O_2/min.
MR: metabolic rate, in this study, the total metabolic rate estimated as the sum of BMR + HIF + LMR.
ODBA: Overall dynamic body acceleration, the acceleration due to movement of a body often used as a proxy of metabolic rate.
RMR: Resting metabolic rate, the metabolic rate of an inactive animal that may not comply with the strict definition of BMR.

2.2 | Animals and habitats

We used previously collected and published high resolution time-depth recordings and physiological data from six bottlenose dolphins (*Tursiops* spp.; Table 1) studied in Sarasota Bay, Florida (coastal/nearshore, shallow diving ecotype) and off the coast of Bermuda (offshore, deep diving ecotype; Fahlman, Jensen, et al., 2018). The animals residing in and around Sarasota Bay are smaller and shallow-diving, with average dive depths around 1 m, and dive durations around 40 s (Fahlman, Jensen, et al., 2018; Wells & Scott, 2018). The dolphins residing in Bermuda are of a

TABLE 1 Animal identification (Dtag ID), Platform Transmitting Terminal id (PTT id) and given name, sex (M-male, F-female), year of birth (YOB), body mass (M_b), straight length (SL), maximum girth (G), hours of high resolution Dtag data, and maximum dive depth (Max DD, m) recorded from satellite tag published previously (Fahlman et al., 2023).

Animal ID	PTT id/Name	Sex	YOB (year)	M_b (kg)	SL (cm)	G (cm)	Hours of tag data	Maximum DD (m)
Sarasota								
tt15_131a	F123 (Eve)	F	1998	166	241	135	20.6	—
tt15_134a	F199 (WAN2)	F	2002	142	236	125	16.4	—
tt16_128a	FB33 (Saida Beth)	F	1982	195	258	142	24.1	—
Mean (± *SD*)				168 ± 27	245 ± 12			
Bermuda								
tt16_243a	110606/Devonshire	M	—	294	256	142	4.7	872
tt16_244a	110610/Paget	F	—	173	238	144	21.7	840
tt16_244b	110608/Pembroke	M	—	282	251	144	17.2	808
Mean (± *SD*)				258 ± 57	252 ± 10	143 ± 1		

larger pelagic ecotype which commonly perform dives beyond 200 m and a maximum recorded dive depth of 1,000 m (Fahlman, Jensen, et al., 2018; Fahlman et al., 2023; Klatsky et al., 2007). The shallow-diving ecotype has lower hematocrit and smaller body size, indicating lower body O_2 stores (Fahlman, Jensen, et al., 2018; Schwacke et al., 2009), but the resting metabolic rate and respiratory tidal volumes do not differ (Fahlman, Brodsky, et al., 2018; Fahlman, McHugh, et al., 2018).

Three (two male and one female) dolphins were studied off Bermuda in August 2016 (Fahlman, Jensen, et al., 2018; Fahlman et al., 2023). The animals were captured by a break-away hoop netting technique (Asper, 1975), and briefly restrained for a health assessment, tagging, and sampling. Once in the net, swimmers managed the animal and moved it onto a buoyant foam mat. The animal was moved onto a sling and then brought onto the sampling boat. Once on the boat, the dolphin was weighed (±0.2 kg;, Ohaus 3000 Series industrial floor scale) and underwent a basic health examination (e.g., Fahlman, McHugh, et al., 2018; Wells et al., 2004).

In Sarasota Bay, Florida, three female, long-term resident bottlenose dolphins (27°22′40.31″N, 82°35′9.40″W) were sampled during May 12–20, 2015, and May 6–11, 2016. These animals were measured during temporary catch-and-release health assessments by the Sarasota Dolphin Research Program (SDRP), and were briefly captured with a seine net, examined, and sampled before being released on site (Fahlman, Brodsky, et al., 2018; Wells et al., 2004).

At the end of the health examination, dolphins from both the Bermuda and Sarasota populations were instrumented with a sound and movement-recording archival DTAG (Johnson & Tyack, 2003) prior to release. Tags were attached using four small suction cups approximately half-way between the dorsal fin and the blowhole and programmed to detach within 24 hr, after which they were retrieved using VHF tracking.

2.3 | Tag data collection

All tags were version 3 DTAGs (Johnson et al., 2009; Johnson & Tyack, 2003) sampling stereo sound (240 kHz) as well as depth, accelerometry and magnetometry (200 Hz). All tag data were processed initially using custom-made DTAG tools (https://www.soundtags.org) in Matlab R2020 (Mathworks, Natick, MA). All sensor data were corrected for tag-specific calibrations before down-sampling data to a sample rate of 25 Hz. The exact release time of each animal as well as the time of tag detachment were identified manually using the acoustic data. Data were then inspected for possible sliding of the tag along the dolphin's body using estimated angle-of-arrival from focal echolocation clicks extracted using a supervised click detector (Jensen et al., 2020). For one Bermuda animal, a tag slide was identified immediately prior to dusk. All data were then cropped to the time period from release until either first tag slide or tag detachment, whichever came first.

A dive was defined as a submergence deeper than 1.5 m (1.15 ATA) and longer than 10 s, and the period between dives termed postdive shallow interval. Thus, for nearshore dolphins, who frequently spend time in areas where the water depth is <1.5 m, the available depth may be shallower than this threshold. The start and end of each dive was calculated as the first and last point of the dive that exceeded 0.1 m depth, and the surface interval was defined as the time from current dive to previous dive (Fahlman, Jensen, et al., 2018).

As a proxy for activity, accelerometer data were used to estimate the overall dynamic body acceleration (ODBA) by filtering each accelerometer channel with a 0.5 Hz high-pass filter (analogous to a 2 s window length for separating static from dynamic acceleration), and then summing the total dynamic acceleration across channels (Wilson et al., 2006). Mean ODBA was then calculated in 10 s sliding windows with a 90% overlap. To estimate the metabolic rate of locomotion, mean ODBA was converted to LMR using a correlation established with trained bottlenose dolphins (Allen et al., 2022).

2.4 | Estimating locomotor cost and total field metabolic rate

The overall metabolic rate (MR) during a surface interval and while diving was assumed to consist of basal metabolic rate (BMR), heat increment of feeding (HIF), and the LMR, e.g., MR = BMR + HIF + LMR. The BMR was estimated from previous measurements of bottlenose dolphins and scaled for the body mass of the animals in the current study (Allen et al., 2022; Pedersen et al., 2020; van der Hoop et al., 2014; Yeates & Houser, 2008). It was assumed that the effect of digestion was constant during the surface period and during diving, and equal to 28% of BMR (Allen, 2021). To estimate changes in LMR at the surface and while diving, we used the calibrated relationship between the O_2 consumption rate ($\dot{V}_{O_2}$) and the overall dynamic body acceleration (ODBA), established using trained bottlenose dolphins (Allen et al., 2022) with tags attached in the same location to ensure that acceleration measurements from body movement were recorded consistently by accelerometers. The estimated instantaneous LMR was averaged for each dive and surface interval and added to the BMR and HIF estimations to obtain an estimate of the total DMR and surface MR.

2.5 | Activity during descent and ascent

To assess the metabolic costs of different phases of the dive for Bermuda dolphins, we divided each dive into descent, bottom, and ascent phases. The descent phase was defined as beginning at the start of the dive until the dolphin reached a depth that was ≥85% of the maximum depth for that dive. The ascent phase began from the last time the dolphin ascended above a depth that was 85% of the maximum depth until the end of that dive (Hooker & Baird, 2001; Stimpert et al., 2014). The bottom phase was then defined as the time from the end of the descent until the beginning of the ascent. The mean and maximum ODBA, and mean LMR were calculated for each dive phase. These data were then divided into shallow (≤ 30 m), intermediate (>30 m and ≤ 100 m), and deep dives (>100 m). Descent and ascent rates were calculated as the change in depth per second.

2.6 | Gas dynamics model

We used a previously published model to estimate blood and tissue O_2, CO_2, and N_2 in the bottlenose dolphin (Fahlman et al. 2009; Fahlman, Jensen, et al., 2018). The model was revised to allow movement (acceleration), a proxy for metabolic rate (O_2 consumption and CO_2 production rates, see below) (Allen et al., 2022; Fahlman et al., 2013), and its corresponding changes in perfusion (Fahlman, Brodsky, et al., 2019; Fahlman, Miedler, 2019;

Miedler et al., 2015), to vary between dives and surface intervals. The details of the model and its previous revisions have been explained in detail elsewhere (Fahlman et al. 2006, 2009; Fahlman, Jensen, et al., 2018; Hooker et al., 2009; Kvadsheim et al., 2012), and we only detail the changes made to the version used in this study.

The gas dynamics model was used to confirm that the available O_2 would support the estimated DMR to allow aerobic metabolism for each dive. Within the gas dynamics model, the MR for each tissue was distributed as previously defined (Fahlman, Jensen, et al., 2018). The effect of HIF was assumed to increase the metabolic rate of the digestive tract, while the changes in LMR were assumed to alter the metabolic rate of the muscle compartment (Table 2; Fahlman, Jensen, et al., 2018).

The cardiac output was based on empirical measurements in bottlenose dolphins before, and after exercise and also before, during, and following static breath-holds (Fahlman, Miedler, et al., 2019; Miedler et al., 2015). The blood flow distribution was varied, assuming that diving caused peripheral vasoconstriction and most perfusion was to central organs. If a tissue ran out of O_2 during a dive, the cardiac output and blood flow distribution were changed to support aerobic metabolism. Thus, the tissue specific and total metabolic cost, cardiac output, and blood flow distribution were assumed constant throughout each dive and surface interval.

2.7 | Estimating dynamic aerobic dive limit (dADL)

The dADL was estimated from the estimated DMR and the O_2 stores before each dive for each individual dolphin. The DMRs for all dives within a depth phase were averaged for each individual and used to estimate the dADL. The O_2 stores were taken from a previous theoretical study looking at tissue and blood O_2, CO_2, and N_2 tensions in the Bermuda dolphins (Fahlman, Jensen, et al., 2018).

2.8 | Data processing and statistical analysis

Comparisons between population means were done using an independent *t*-test, or *z*-test. For three or more comparisons, we used the linear mixed model (*lme*; Pinheiro et al., 2015) in R, using animal as a random effect, with a post hoc test (*emmeans*; Lenth et al., 2022) to compare differences. In this study *p*-values ≤.05 or ≤ .01 were considered

TABLE 2 Table showing the estimated postdive shallow interval cardiac output (CO); compartment (central circulation, muscle, brain, and adipose/bone) specific resting metabolic rate (RMR, including heat increment of feeding); and tissue, lung, and blood O_2 stores; and dynamic aerobic dive limit (dADL) for shallow (S, depth ≤ 30 m), intermediate (I, 30 m < depth ≤ 100 m), and deep (D, depth > 100 m) dives.

Animal ID	CO (L/s) Postdive shallow interval	RMR L O_2/min				O_2 stores (L)			dADL (min)		
		CC	Muscle	Brain	Fat	Tissue	Lung	Blood	S	I	D
Sarasota											
tt15_131a	0.87	0.28	0.24	0.03	0.03	2.8	1.2	2.2	6.0	—	—
tt15_134a	0.78	0.25	0.21	0.03	0.03	2.4	1.1	1.9	3.9	—	—
tt16_128a	0.99	0.31	0.27	0.03	0.04	3.3	1.4	2.5	5.8	—	—
Bermuda											
tt16_243a	0.94	0.34	0.33	0.01	0.03	14.7	2.1	10.8	22.5	16.5	—
tt16_244a	0.63	0.23	0.22	0.01	0.02	8.7	1.3	6.4	15.0	12.3	10.8
tt16_244b	0.91	0.33	0.32	0.01	0.03	14.1	2.0	10.4	18.6	17.5	11.4

TABLE 3 Animal identification (ID), postdive shallow interval, dive duration, and mean (the mean depth during the dive) and maximum (the mean of the maximum depths) dive depths for shallow (S, maximum depth ≤ 30 m), intermediate (I, maximum depth > 30 m and ≤ 100 m), or deep dives (D, maximum depth > 100 m). Averages (Av) in the table are the average across individuals. All values reported as average (± *SD*).

Animal ID	Postdive shallow interval (s)			Dive duration (s)			Mean dive depth (m)			Maximum dive depth (m)		
Depth range	S	I	D	S	I	D	S	I	D	S	I	D
Sarasota												
tt15_131a	20 ± 82	—	—	27 ± 19	—	—	1.4 ± 0.5	—	—	1.7 ± 0.5	—	—
tt15_134a	41 ± 127	—	—	21 ± 16	—	—	1.5 ± 0.5	—	—	1.9 ± 0.7	—	—
tt16_128a	186 ± 775	—	—	28 ± 26	—	—	1.3 ± 0.6	—	—	1.6 ± 0.7	—	—
Av ± *SD*	82 ± 90	—	—	25 ± 4	—	—	1.4 ± 0.1	—	—	1.7 ± 0.2	—	—
Bermuda												
tt16_243	10 ± 11	14 ± 18		63 ± 78	188 ± 61		3.5 ± 3.2	25.8 ± 5.6	—	4.9 ± 4.7	48.8 ± 12.6	
tt16_244a	20.0 ± 75	48 ± 56	134 ± 92	32 ± 48	151 ± 41	415 ± 100	2.5 ± 2.6	20.8 ± 7.7	167.7 ± 66.6	3.5 ± 4.1	43.2 ± 15.1	275.6 ± 110.0
tt16_244b	12 ± 17	12 ± 13	26 ± 22	30 ± 47	185 ± 74	310 ± 76	2.7 ± 3.3	33.7 ± 12.8	107.5 ± 70.1	3.8 ± 4.9	60.0 ± 12.8	191.4 ± 70.8
Av ± *SD*	14 ± 5	25 ± 20	80 ± 76	42 ± 18	175 ± 21	362 ± 74	2.9 ± 0.5	26.8 ± 6.6	50.7 ± 8.6	4.1 ± 0.7	137.6 ± 42.6	233.5 ± 56.6

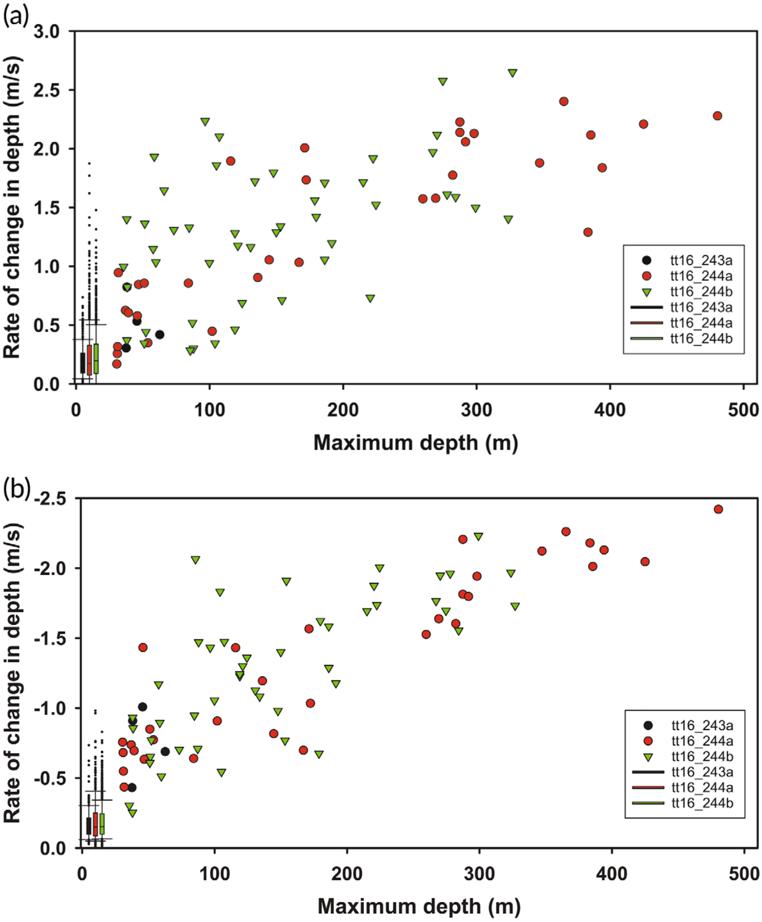

FIGURE 1 Rate of change in depth (m/s) against maximum dive depth (m) during (a) descent or (b) ascent. Dives with a dive depth less than 30 m are shown as box plots. Each data point shows the average rate of change in depth for a given dive against the maximum dive depth for that dive.

as significant and highly significant, respectively, and $p \leq .1$ was considered a trend. Data are presented as the mean ± standard deviation (*SD*), unless otherwise stated.

3 | RESULTS

3.1 | Dive behavior

Sarasota dolphins only performed shallow dives due to water depth constraints. Bermuda dolphins performed dives spanning all depth ranges, but a tag slide on one animal before sunset meant that only data in the first two depth regions were used here (Table 3). For shallow dives, the dive duration was significantly shorter (linear mixed effects model [*lme*], $df = 1$, $\chi^2 = 3.95$, $p < .05$) and the postdive shallow interval longer ($df = 1$, $\chi^2 = 4.07$, $p < .05$) in the Sarasota dolphins (Table 3). Similarly, both the mean ($df = 1$, $\chi^2 = 11.9$, $p < .001$) and maximum ($df = 1$, $\chi^2 = 12.1$, $p < .001$) dive depths for shallow dives were deeper in the Bermuda dolphins (Table 3).

TABLE 4 Animal identification, resting metabolic rate (RMR, including basal metabolic rate and the heat increment of feeding), calculated aerobic dive limit (cADL), average (± *SD*) locomotor metabolic rate (LMR) during postdive shallow intervals and during dives, and number (No.) of dives for shallow (S, depth ≤ 30 m), intermediate (I, 30 m < depth ≤ 100 m) and deep (D, depth > 100 m) dives. The cADL was estimated from the RMR and the maximal estimated O_2 stores. Thus, the true cADL during diving should also include the LMR, i.e., dynamic ADL (dADL, see Table 2).

			Postdive shallow intervals LMR (ml O_2/min)			Dive LMR (ml O_2/min)			No. dives		
Animal ID	**RMR (ml O_2/min)**	**cADL (min)**	**S**	**I**	**D**	**S**	**I**	**D**	**S**	**I**	**D**
Sarasota											
tt15_131a	579	10.7	513 ± 192	—	—	445 ± 189	—	—	1,576	—	—
tt15_134a	515	10.3	852 ± 430	—	—	843 ± 508	—	—	951	—	—
tt16_128a	653	11.2	693 ± 240	—	—	614 ± 216	—	—	406	—	—
Average	582 ± 69	10.7 ± 0.4	686 ± 170	—	—	634 ± 200	—	—	978 ± 585	—	—
Bermuda											
tt16_243a	716	38.5	612 ± 293	734 ± 248	—	513 ± 246	954 ± 331	—	226	3	0
tt16_244a	481	33.9	653 ± 269	868 ± 379	1,097 ± 248	608 ± 269	842 ± 180	900 ± 106	1,244	13	21
tt16_244b	693	38.2	748 ± 340	1,032 ± 338	1,269 ± 281	734 ± 340	823 ± 194	941 ± 169	1,133	19	31
Average	630 ± 130	36.9 ± 2.6	671 ± 70	878 ± 149	1,183 ± 122	618 ± 111	873 ± 71	920 ± 29	868 ± 558	12 ± 8	17 ± 16

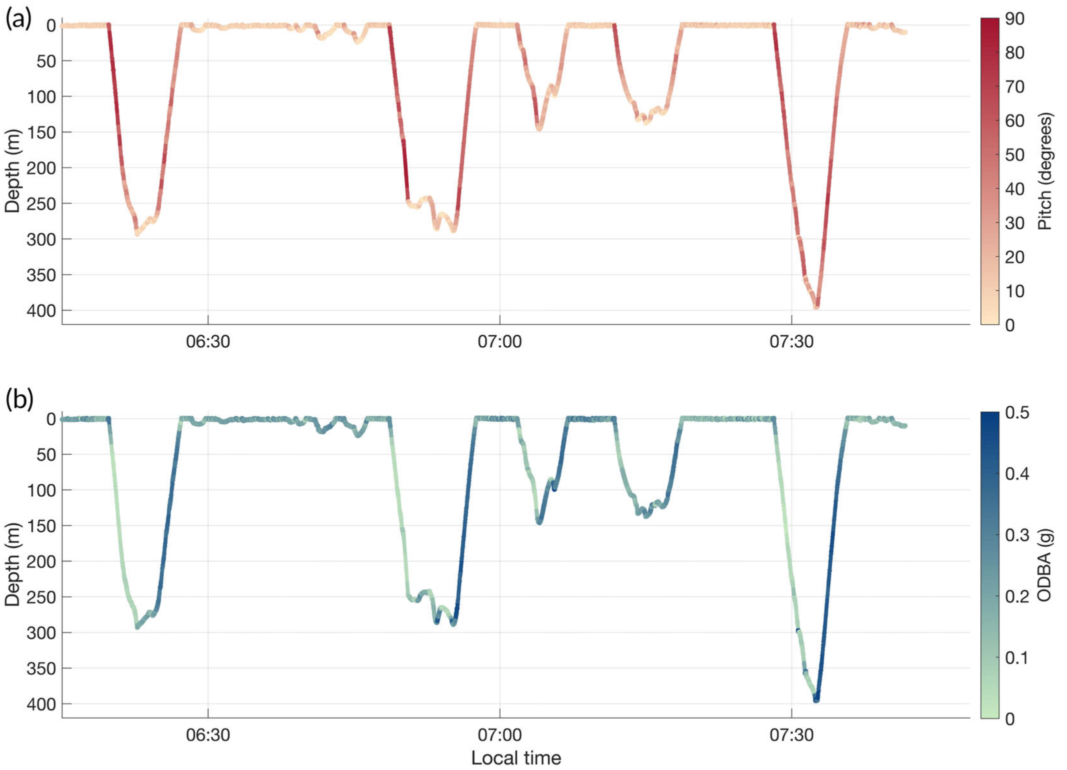

FIGURE 2 Dive depth (m), and (a) absolute value of pitch (°), and (b) overall dynamic body acceleration (ODBA, g) for dolphin tt16_244a with time in hours:minutes.

For change in depth during descent and ascent, the following equation was the most parsimonious and showed that (linear mixed effects model [*lme*], $df = 1$, $\chi^2 = 78.0$, $p < .001$; Figure 1):

$$\text{absolute change in depth (m/s)} = 0.21\,(\pm 0.01) + 0.0060\,(\pm 0.0007) \times \text{maxdepth (m)} - 0.0465\,(\pm 0.0052) \times \text{ascent} \tag{1}$$

where absolute change in depth is positive for either ascent or descent, maxdepth is the maximum depth reached during the dive, and ascent is a factor for ascent (1 if ascent and 0 otherwise). Thus, the change in depth during ascent was significantly slower as compared with descent. In addition, the rate of change in depth increased with maximal dive depth, meaning dolphins descended or ascended more quickly on deeper dives.

3.2 | Field metabolic rates

BMR was estimated from postprandial male bottlenose dolphins that were inactive and in their thermoneutral zone (Allen et al., 2022), and ranged from 480 to 716 ml O_2/min (Table 4). The average LMR during postdive shallow intervals following a dive did not differ between populations (unpaired *t*-test, $df = 4$, $t = 0.14$, $p > .8$) and ranged from 513 to 954 ml O_2/min and 445 to 843 ml O_2/min for Sarasota and Bermuda dolphins, respectively (Table 4). Similarly, the LMR during shallow dives for Bermuda and Sarasota dolphins (618 ± 111 ml O_2/min

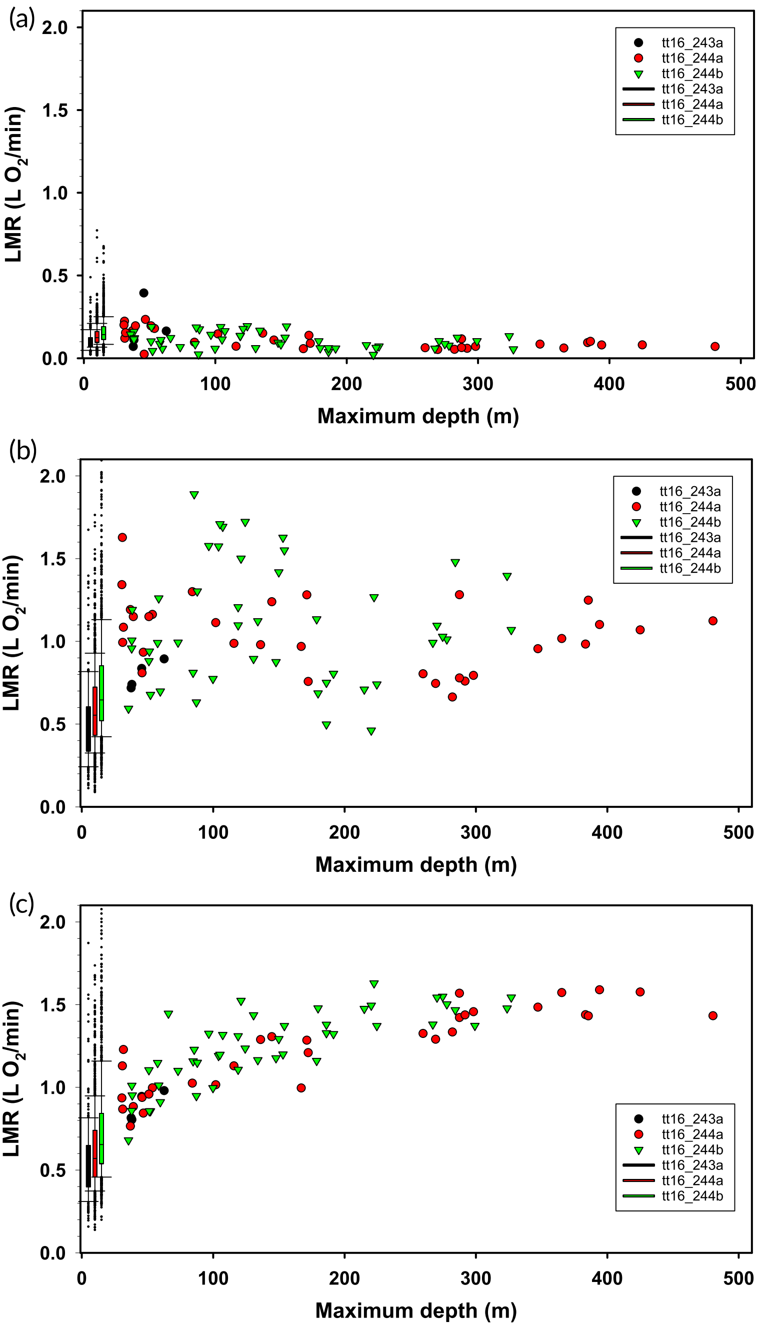

FIGURE 3 Locomotor metabolic rate (LMR, L O_2/min) against maximum dive depth (m) for three bottlenose dolphins during (a) descent, (b) at the bottom, or (c) during ascent. Dives with a dive depth less than 30 m are shown as box plots. Each data point shows the average LMR for each phase for a given dive, i.e., the average from the start until the end of descent for that dive and the maximum dive depth for that dive.

versus 634 ± 200 ml O_2/min, respectively; Table 4) did not differ (*df* = 4, *t* = 0.12, *p* > .9). When analyzed together, the LMR was 8% higher at the surface: 678.5 ml O_2/min) compared with during shallow dives (shallow dives: 626.2 ml O_2/min; *df* = 5, paired *t*-test, *t* = 3.55, *p* < .05).

3.3 | Activity and LMR during descent and ascent

When comparing the mean LMR for different dive phases (ascent, descent, bottom) against maximum dive depth for all dives (LMR_{all}), the most parsimonious model included dive phase and maximum depth as ([*lme*], $df = 1$, $\chi^2 = 83.6$, $p < .01$, [*lme*] followed by Tukey post hoc test [*emmeans*]; Figures 2 and 3):

$$LMR_{all}\,(ml\,O_2/min) = 648\,(\pm 52) - 25.9\,(\pm 8.9) \times phase_{bottom} - 55.5\,(\pm 8.9) \times phase_{descent} + 1.21\,(\pm 0.11) \times maxdepth \quad (2a)$$

where phase describes the dive phase (1 for the specific phase and 0 otherwise), and maxdepth (meters) is the maximal depth for that dive. As most dives (97%) were shallower than 30 m, we also analyzed the LMR for different dive phases for dives with a maximum depth > 30 m (LMR_{30}). The most parsimonious equation only included dive phase as a predictor ($df = 2$, $\chi^2 = 369$, $p < .001$):

$$LMR_{30}\,(ml\,O_2/min) = 1{,}220\,(\pm 26) - 112\,(\pm 51) \times phase_{bottom} - 716\,(\pm 51) \times phase_{descent} \quad (2b)$$

The post hoc testing showed that there were significant differences in LMR between ascent/descent ($df = 247$, $t = 11.9$, $p < .001$), and bottom/descent ($df = 247$, $t = 14.1$, $p < .001$), but not between ascent and bottom ($df = 247$, $t = 2.2$, $p < .1$).

3.4 | Estimating dynamic aerobic dive limit (dADL)

The O_2 stores for each individual dolphin were estimated as described in a previous study estimating blood and tissue gas tensions (Table 2 in Fahlman, Jensen, et al., 2018), and ranged from 6.2 to 27.6 L O_2 for the individual dolphins in the current study (Table 2). The cADL estimated from the resting metabolic rate (RMR) is reported in Table 4 and ranged from 10.3 to 38.5 min. The average (± *SD*) dADL when estimated from DMR was 5.2 ± 1.1 min (range: 3.9–6.1 min) for Sarasota dolphins during shallow dives, and 15.1 ± 3.8 min (range: 10.8–22.5 min) for Bermuda dolphins (Table 2). In the Bermuda dolphins, the dADL decreased with dive depth as the metabolic effort increased with depth, with averages (± *SD*) 18.7 ± 3.4 min, 15.4 ± 2.7 min, and 11.1 ± 0.4 min for shallow, intermediate, and deep dives, respectively ($df = 2$, $\chi^2 = 9.6$, $p < .01$).

4 | DISCUSSION

A number of estimates of FMR exist for cetaceans, but most only provide an overall cost and cannot provide estimates for specific activities (Allen, 2021; Arranz et al., 2019; Bejarano et al., 2017; Noren, 2011; Rimbach et al., 2021; Rojano-Doñate et al., 2018). Instead, researchers have established relationships between movement and energy use, which can be calibrated with dolphins in human care, and applied to movement data from wild dolphins to estimate their energetic needs (Allen et al., 2022; Fahlman et al., 2013; Williams & Noren, 2009; Williams et al., 1993, 2017). In the current study, we used an established relationship between activity, as evaluated using ODBA, and oxygen consumption in the bottlenose dolphin (Allen et al., 2022), combined with a gas dynamic model to evaluate differences in the diving capacities and metabolic requirements of dolphins in Sarasota and Bermuda. The results demonstrate that Bermuda dolphins dive deeper and longer than the dolphins in Sarasota, and that the dADL of Bermuda dolphins is up to three times longer than that of Sarasota dolphins, mainly due to greater overall O_2 stores. For shallow dives, we found no difference between the two ecotypes in the LMR during diving, nor during the postdive shallow intervals following dives (Table 4). For intermediate and deep dives, which were only performed by the Bermuda dolphins, the average LMR did not change with maximum dive depth, but the LMR was significantly higher during ascent as compared with descent or the bottom phase (Equation 2b). Although the LMR was higher during ascent and did not change with depth, the rate of change in depth was higher during descent as compared with ascent in Bermuda dolphins (Equation 1), suggesting either higher pitch (Figure 2) or higher swim speed due to changes in buoyancy-related locomotory efficiencies. The dADL in the current study was 11.1 min in the Bermuda dolphins during deep dives (>100 m), which is close to the 9.6–10.4 min estimated from behavior (bADL; Fahlman et al., 2023).

The ADL is a useful index to estimate the duration that a dive can be fueled by aerobic metabolism. Most breath-hold diving vertebrates seem to be performing most dives within their ADL, but also appear to have the capacity to dive beyond this duration as they switch to anaerobic metabolism (Kooyman et al., 1980). Diving beyond the ADL results in lactate build-up and changes in the acid base balance, which results in extended postdive shallow intervals as the lactate is processed aerobically. The ADL is defined as the duration when the lactate begins to increase, but it is difficult to measure in freely diving animals, and there are few species where it has been measured (Kooyman et al., 1980, 2020).

The dADL, on the other hand, relates the available O_2 stores to the rate of its use, i.e., rate of O_2 consumption (Butler, 2006). The maximal O_2 stores can be measured in deceased animals by summing the stores from the muscle, blood, and lungs. For example, the muscle myoglobin concentration total and muscle mass can be determined during dissection. Although this may be straightforward, the heterogeneity of myoglobin in different muscle groups (Arregui et al., 2021), the complexity of measuring blood volume, and the fact that the diving lung volumes can vary (Fahlman et al., 2020; Hooker et al., 2021; McDonald & Ponganis, 2012), makes this complicated. Similarly, the rate of O_2 consumption is not a static value but varies depending on effort. Thus, as the diving metabolic rate varies between species and throughout a dive (Williams et al., 2017) in relation to the activity (Fahlman et al., 2013), the dADL will vary depending on effort. The RMR or BMR is often used for the postdive shallow interval, and then a scaling factor used to estimate the cost while underwater (Bejarano et al., 2017; Fahlman, Jensen, et al., 2018). Thus, using the estimated relationship between ODBA and LMR in wild animals to calculate the dADL offers a more realistic estimate of the actual ADL as the estimated metabolic rate is allowed to change with activity level.

The significantly greater dADL in the Bermuda dolphins in the current study was due to the higher estimated O_2 stores for this larger offshore dolphin ecotype. Although the relative size of different body compartments has been published for nearshore dolphins (Mallette et al., 2016), little is known about the body composition of the offshore ecotype. It is therefore possible that the compartment sizes, their relative metabolic rates, and the true O_2 stores are somewhere in between the nearshore ecotype (the Sarasota dolphin) and the deep diving cetaceans (Pabst et al., 2016; Velten et al., 2013). With variation in the relative muscle mass of the deep diving ecotype, it is also possible that the relationship between activity and energy cost is different compared with that developed for dolphins during shallow surface swims (Allen et al., 2022). Still, the estimated dADL of 11.1 min for deep dives was reasonably close to the estimated bADL of 9.6–10.4 min in the same dolphins (Fahlman et al., 2023), suggesting that the dynamic gas model used in the current study provides reasonable results also for deep diving dolphins. However, better information of body composition of pelagic dolphins would help improve future modeling studies. Thus, the maximal dADL in the current study is likely overestimated, and the true ADL somewhere between 10 min and 11.1 min. In addition, this study provides a new index, the dADL, that allow a more realistic estimate of the aerobic capacity during diving and that is allowed to vary between individuals, and the metabolic costs of different activities and their relative duration during the dive.

The Bermuda dolphins appear to reduce activity and LMR by as much as 55% and 59% during descent compared with movement at the bottom phase or during ascent (Equation 2b, Figures 2 and 3). This behavioral control to reduce locomotory cost can be seen in Figures 1 and 3 as a plateau. Similar results in other species have been reported and proposed as a strategy to save energy during diving (Fahlman et al., 2008; Williams, 2001). Although past studies have examined activity throughout the different dive phases in diving mammals (e.g., see Figure 3 in Fahlman et al., 2008), we are not aware of any other study that has attempted to estimate the metabolic costs for the various phases from a species-specific calibrated relationship between ODBA and LMR. In the current study, we show that periods of gliding during descent may explain the lower LMR. This metabolic saving was possible despite a slightly higher rate of change in depth during descent as compared with ascent (Equation 1). The faster change in depth was in part due to the steeper pitch angle during descent as compared with ascent (Figure 2), and it is also possible that buoyancy changes with dive depth also contribute to a faster rate of change in depth. The deep diving swim behavior in the bottlenose dolphins appears to have similarities to that recently reported in Risso's dolphins (*Grampus griseus*). In the Risso's dolphin, during deep (>400 m) and long (>9 min) foraging dives, this species employed a spinning behavior with high activity and speed as they began the dive, followed by sinking as they became negatively buoyant (Visser et al., 2021). In the Bermuda dolphins, the rate of change in depth during descent and ascent increased with dive depth (Equation 1, Figures 1 and 2), and both the rate of change in dive depth during descent and ascent for deep dives was similar to those reported in the larger Risso's dolphin (Visser et al., 2021). This suggests that dolphins exhibit a cost-effective swim strategy to reach deep prey patches faster with minimal metabolic cost, where an initial burst of activity close to the surface and a steeper pitch angle help increase the rate of descent. However, unlike the Risso's dolphins, the deep diving Bermuda bottlenose dolphins do not appear to perform high activity spins during descent as the activity level was low and there were only brief bursts of activity close to the surface (Figure 2).

To illustrate how these differences affect the metabolic cost of different dives, we estimated the LMR for the different phases of a dive to 50 m versus 500 m. For this, we used the changes in descent and ascent rates (Equation 1) to estimate the duration and LMR of the descent, ascent, and the total time at the bottom. We used a dive duration of 225 s and 550 s for the dive to 50 m and 500 m, respectively, which are representative dive durations to these depths for these individuals (Fahlman et al., 2023). In this case, the dives to 50 m and 500 m would result in transit times of 206 s and 314 s, respectively. In this hypothetical case, the total time in the bottom phase would be 19 s for a dive to 50 m, while the dive to 500 m would have a bottom time of 236 s. Thus, both the absolute time and the relative time at the bottom were longer, being 43% for a deep dive as compared with only 8% for a shallow dive. To estimate the overall difference in metabolic cost of descending and ascending, the estimated LMR in Equation 2b for the various phases of the dive was used. The estimated metabolic rate for the combined descent and ascent (not including the bottom phase) for a 50 m dive would be 0.88 L O_2/min. For the dive to 500 m the overall metabolic rate would be 0.86 L O_2/min. Consequently, the higher LMR during the ascent in deeper dives is offset by the lower LMR during descent, resulting in a LMR that is similar during the two dives. The estimated LMR for the entire dive, on the other hand, would be 8% higher during the deeper dive ($LMR_{shallow} = 0.90$ L O_2/min versus $LMR_{deep} = 0.97$ L O_2/min), due to the higher LMR during ascent and longer time at the bottom. Thus, the reduced metabolic cost during descent agrees with the suggestion that the intermittent swimming strategy in breath-hold diving marine mammals helps reduce the overall metabolic cost of diving and extends the dADL (Williams, 2001).

In the current study, we estimated the DMR in two populations of bottlenose dolphins during different phases of diving and during postdive shallow intervals between dives. The data suggest that the ascent phase is energetically more expensive and that during deeper dives the dolphins spend more energy at depth compared with shallower dives. We propose that this deep diving behavior, which occurs mainly at night, allows these deep diving dolphins to access high energy prey, encounter prey at a higher rate, or encounter prey that is more easily captured similarly to other deep diving marine mammals. We also show that the dADL is a value that varies between individuals, and with the overall activity and swimming strategy used during the dive.

ACKNOWLEDGMENTS

A special thanks to the many volunteers and staff at Dolphin Quest. A special thanks to Nigel Pollard, the Bermuda Government, the Bermuda Aquarium, Museum & Zoo (BAMZ), and NOAA. We thank Andres Jabois and Teresa Lorenzo from the Oceanografic, Sunnie Brenneman of the Sarasota Dolphin Research Program, Guy Bedford and the

DQ team for their assistance in the field. None of the authors have competing interests and all authors gave final approval for publication. The editors and reviewer provided useful comments, which improved the paper.

Funding for this project was provided by the Office of Naval Research (ONR YIP Award # N000141410563 and #N000142112652), and Dolphin Quest, Inc. FHJ was supported by the Office of Naval Research (Award # N00014-1410410) and an AIAS-COFUND fellowship from Aarhus Institute of Advanced Studies under the FP7 program of the EU (Agreement No. 609033).

All work was approved by the IACUC at Texas A&M University Corpus Christi (TAMUCC-IACUC AUP#04-11), a research permit issued by the National Marine Fisheries Service (Scientific Research Permit No. 15543), and by a research permit issued by the Bermuda Government, Department of Environment and Natural Resources (Research permit number SP160401r). The Sarasota Bay research was approved annually by the Mote Marine Laboratory IACUC.

AUTHOR CONTRIBUTIONS

Andreas Fahlman: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; supervision; validation; visualization; writing – original draft. **Austin S Allen:** Conceptualization; formal analysis; methodology; visualization; writing – review and editing. **Ashley M Blawas:** Conceptualization; methodology; writing – review and editing. **Jay Sweeney:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **Rae Stone:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **Robyn Faulkner Trainor:** Investigation; project administration; writing – review and editing. **Frants H Jensen:** Investigation; writing – review and editing. **Katherine A McHugh:** Investigation; writing – review and editing. **Jason B Allen:** Investigation; methodology; writing – review and editing. **Aaron A Barleycorn:** Investigation; methodology; writing – review and editing. **Randall Wells:** Conceptualization; investigation; project administration; resources; supervision; writing – review and editing.

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How to cite this article: Fahlman, A., Allen, A. S., Blawas, A., Sweeney, J., Stone, R., Trainor, R. F., 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