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Validating the relationship between 3-dimensional body acceleration and oxygen consumption in trained Steller sea lions

Beth L. Volpov[1] · David A. S. Rosen[2] · Andrew W. Trites[2] · John P. Y. Arnould[1]

Abstract We tested the ability of overall dynamic body acceleration (ODBA) to predict the rate of oxygen consumption ($s\dot{V}_{O_2}$) in freely diving Steller sea lions (*Eumetopias jubatus*) while resting at the surface and diving. The trained sea lions executed three dive types—single dives, bouts of multiple long dives with 4–6 dives per bout, or bouts of multiple short dives with 10–12 dives per bout—to depths of 40 m, resulting in a range of activity and oxygen consumption levels. Average metabolic rate (AMR) over the dive cycle or dive bout calculated was calculated from $s\dot{V}_{O_2}$. We found that ODBA could statistically predict AMR when data from all dive types were combined, but that dive type was a significant model factor. However, there were no significant linear relationships between AMR and ODBA when data for each dive type were analyzed separately. The potential relationships between AMR and ODBA were not improved by including dive duration, food consumed, proportion of dive cycle spent submerged, or number of dives per bout. It is not clear whether the lack of predictive power within dive type was due to low statistical power, or whether it reflected a true absence of a relationship between ODBA and AMR. The average percent error for predicting AMR from ODBA was 7–11 %, and standard error of the estimated AMR was 5–32 %. Overall, the extensive range of dive behaviors and physiological conditions we tested indicated that ODBA was not suitable for estimating AMR in the field due to considerable error and the inconclusive effects of dive type.

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✉ Beth L. Volpov
byou@deakin.edu.au

1 School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia

2 Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, BC, Canada

Abbreviations

M_b	Body mass (kg)
ODBA	Overall dynamic body acceleration averaged over dive cycle or dive bout (g, 1 g = 9.81 m s^2)
V_{O_2}	Total oxygen consumption
$\dot{V}_{O_2}$	Whole animal rate of oxygen consumption rate (ml O$_2$ min^{-1})
$s\dot{V}_{O_2}$	Mass-corrected rate of oxygen consumption rate (ml O$_2$ min^{-1} kg$^{-0.75}$)
MRs	Surface metabolic rate ~2 min prior to diving (ml O$_2$ min^{-1} kg$^{-0.75}$)
AMR	Average metabolic rate over dive cycle or dive bout calculated from $s\dot{V}_{O_2}$ (ml O$_2$ min^{-1} kg$^{-0.75}$)
DLW	Doubly labeled water
cADL	Calculated aerobic dive limit
Dive cycle	Single dive + 1 surface interval until $s\dot{V}_{O_2}$ within 5 % of pre-dive MRs
Dive bout	Series of dives + surface intervals until final $s\dot{V}_{O_2}$ within 5 % of pre-dive MRs. Surface intervals within a dive bout do not return to within 5 % of MRs
Bout of short dives	10 or 12 dives per dive bout; goal of 1–2 min per dive
Bout of long dives	4–6 dives per dive bout; goal of 4–6 min per dive
Single dives	1 dive cycle with a dive duration goal of 4–6 min

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Introduction

Accurate measures of energy expenditure for marine mammals are vital for developing population-level and ecosystem-level bioenergetic models (e.g., Winship et al. 2002). The costs associated with foraging and diving behavior represent major components of marine mammal energy budgets (reviewed in Boyd et al. 2010). In addition, accurate estimates of the costs of diving (Castellini 1992; Costa and Gales 2000, 2003; Sparling and Fedak 2004; Trillmich and Kooyman 2001; Williams et al. 2004) permit energetic assessments of foraging strategies or patterns (e.g., Shepard et al. 2009; Staniland et al. 2007).

While accurate means have been developed for characterizing dive behavior in free-ranging pinnipeds (Boyd et al. 2010), methods to quantify the associated energetic expenditure are limited. Traditionally, field metabolic rates have been measured using the doubly labeled water (DLW) turnover technique, but this only yields a mean metabolic estimate over a limited time interval (Speakman 1997). Heart rate has also been used to estimate activity-specific energy expenditure in several marine mammals (McPhee et al. 2003; Williams et al. 1991; Young et al. 2010, 2011), but the technical constraints for applying this technique are considerable.

Body acceleration metrics (measures of physical activity) such as 3-dimensional movement (overall dynamic body acceleration, ODBA; Wilson et al. 2006) or partial dynamic body acceleration (e.g., PDBA; Dalton et al. 2014) have emerged as potential tools for studying the foraging behavior and energetics of marine mammals (see Boyd et al. 2010; Halsey et al. 2011c). Data are obtained from biologging tags that measure accelerometry via instantaneous changes in speed in three axes: sway (side-to-side movement), surge (forward and backward movement), and heave (vertical up and down movement). In theory, there should be a positive relationship between this measure of fine-scale body movement and energy expenditure that is activity specific (Gleiss et al. 2011).

Several studies have used body-mounted accelerometers to calculate ODBA and the estimate field metabolic rate in a range of vertebrates (Green et al. 2009; Halsey et al. 2008, 2011a; Payne et al. 2011; Wilson et al. 2006). However, there is a growing evidence that the (potential) relationship between ODBA and energy expenditure could be influenced by several factors including body mass, the environment (water vs. air vs. land), drag, buoyancy, locomotion type, and behavior (Gleiss et al. 2011; Halsey et al. 2011a, c; King et al. 2004). It is also unclear if the predictive power of ODBA (a physical measurement) is diminished by concurrent physiological processes that can affect metabolism but are not associated with body movement, such as digestion, thermoregulation, or diurnal changes

in resting metabolism (e.g., Dalton et al. 2014; Rosen and Trites 1997, 2003).

The potential effect of physical and physiological processes on using body acceleration as a proxy for energy expenditure requires calibration studies to determine the strength and specific nature of the relationship between body movement and rates of oxygen consumption ($\dot{V}_{O_2}$, a recognized measure of energy expenditure) under specific conditions. The relationship between ODBA and $\dot{V}_{O_2}$ has been reported to be linear in submerged swimming sea turtles, *Chelonia mydas* or *Caretta caretta* (Enstipp et al. 2011; Halsey et al. 2011b) and diving Steller sea lions, *Eumetopias jubatus* (Fahlman et al. 2013, 2008b). In contrast, other studies of cormorants, *Phalacrocorax auritus*, and northern fur seals, *Callorhinus ursinus* have failed to find linear relationships between acceleration and $\dot{V}_{O_2}$ (Dalton et al. 2014; Halsey et al. 2011a), and questions have been raised regarding the strength of some of the previously reported relationships (Halsey et al. 2011a, b, c).

There are particular concerns that ODBA may not be able to predict $\dot{V}_{O_2}$ in air-breathing divers given the temporal disconnect between activity and gas exchange, and the inherent physiological changes associated with diving (Halsey et al. 2011a, b). Many of the previous calibration studies of air-breathing diving vertebrates have been limited by tank depth or dive duration, or have not included realistic foraging bouts (Fahlman et al. 2008b; Halsey et al. 2011a, b). To be appropriately applied to field studies, calibrations of the relationship between ODBA and $\dot{V}_{O_2}$ should encompass behaviors that are similar to wild animals of that species, which include foraging with comparable depths, dive patterns, and dive durations for marine mammals. In the wild, 92–98 % of the dives by adult female Steller sea lions are <4.0 min, and most dives are to depths of 21–53 m (Gerlinsky et al. 2013; Merrick and Loughlin 1997). While past calibration studies with captive Steller sea lions have used animals trained to dive in the open ocean (Fahlman et al. 2008b, 2013), these studies did not incorporate realistic dive bouts or durations, likely incorporated minimal movement at depth, all of which potentially limited the range of physiological responses.

Testing under a range of realistic behaviors is particularly important given the hypothesis that physiological changes that occur in diving mammals can affect the relationship between $\dot{V}_{O_2}$ and ODBA. For example, while single dives and bouts of multiple dives may appear superficially similar to each other in terms of behavior, bouts of long dives are known to incur cumulative physiological effects—most notably progressive oxygen depletion (Fahlman et al. 2008a; Gerlinsky et al. 2013; Kooyman et al. 1973; Ponganis et al. 1993). The oxygen consumed while diving is partially replenished during surface intervals

Table 1 Age and body mass at start of trials, mass deviation over the course of the trials (±s.d.), and number of repetitions of each trial type per Steller sea lion ($n = 122$ trials)

Animal ID	Age (year)	Mass		Trial type			
		(kg)	(±s.d.)	Surface	Single dive	Bout of short dives	Bout of long dives
F97SI	14	168.0	(13.9)	16	6	4	8
F97HA	14	164.0	(4.2)	12	7	4	5
F00BO	11	143.0	(6.0)	14	7	5	9
F97YA	11	201.5	(22.5)	10	6	2	7
Total				52	26	15	29

Trial types included resting at the surface prior to diving, single dives, bouts of short dives (10–12 dives per bout), and bouts of long dives (4–6 dives per bout)

within a dive bout, but is often not fully replaced until the animal completes an extended surface time typically seen at the end of a dive bout (Enstipp et al. 2011; Fahlman et al. 2008a; Kooyman et al. 1973; Ponganis et al. 1993). Similarly, complete off-loading of metabolic byproducts such as CO_2 and lactate may only occur during this extended post-dive surface interval. Consequently, the dive bout represents a distinct physiological unit that should not be separated into individual dives (Fedak et al. 1988; Kooyman and Ponganis 1998). ODBA is a physical measure that may not be able to account for such physiological changes that occur during prolonged diving in bouts.

We investigated the ability of ODBA to predict rates of oxygen consumption across a range of behavioral and physiological conditions. We investigated the relationship across a broad range of natural foraging behaviors by having trained Steller sea lions swim between two feeding stations at depth for longer dive durations and more dives per bout than previous studies that have been undertaken on this species (Fahlman et al. 2008b, 2013). Our specific objectives were to determine the relationship between ODBA and rates of oxygen consumption in diving sea lions, and to investigate whether this relationship differed between single dives and dive bouts. We also examined the effects of dive duration—and the resulting level of oxygen depletion—on the relationship between ODBA and oxygen consumption.

Materials and methods

Data were collected between October and May in 2011–2013 on four trained female Steller sea lions housed at the University of British Columbia's Open Water Research Station (Port Moody, BC, Canada, Table 1). The animals were previously trained to dive freely in the open ocean and were familiar with all experimental procedures (Hastie et al. 2006). All animal work was conducted voluntarily under trainer control and authorized under UBC Animal Care Permit #A11-0397.

Body movement was measured by a 3-dimensional accelerometer that sampled surge, heave, and sway at 20 Hz ($±6$ g, 1 g $= 9.81$ m s^2, $7 × 3 × 2$ cm, 12-bit resolution, USB-Accelerometer 3-axis Self Recording Accelerometer X6-2mini, Gulf Coast Data Concepts, Waveland, MS, USA). We also measured dive behavior (dive and surface durations and depth) and water temperature via a time–depth recorder ($2.5 × 3.3 × 4.4$ cm, TDR, SU-05272, ReefNet Inc., Mississauga, ON, Canada, sampling frequency 1 Hz,). Both instruments were mounted between the shoulders, on a tight-fitting, custom-made harness worn by the sea lions.

Open-circuit gas respirometry was used to measure the rates of oxygen consumption and carbon dioxide production in a 100 l respirometry dome floating at the water surface (for details see Hastie et al. 2006; Young et al. 2011). Air was drawn through the respirometry dome at a constant rate of 475 l min^{-1}. A dried subsample of the excurrent airstream was analyzed for oxygen and carbon dioxide concentrations (Sable FC-1B and CA-1B analyzers, Sable Systems, Las Vegas, NV, USA) and average concentrations were recorded every 0.5 s on a laptop computer. Oxygen consumption rates were calculated from changes in O_2 and CO_2 concentrations from ambient baselines (Eq. 3b in Withers 1977) using Warthog Systems Lab Analyst (M. Chappell, U.C. Riverside, CA, USA). Unfortunately, there is no consensus on whether metabolic rate scales intra-specifically with body mass, and no consensus about which specific exponent to employ (Brown and West 2005; Packard and Boardman 1999; Savage et al. 2007; Schmidt-Nielsen 1975; White and Seymour 2005). Given the range of body masses among and within animals (Table 1), coupled with the long duration of the study (3 years), we chose to calculate a mass-corrected rate of oxygen consumption using a 0.75 exponent ($s\dot{V}_{O_2}$).

Dive trial protocol

The sea lions and metabolic measurement equipment were transported to the dive site in separate boats. The sea lions were previously trained to dive between the respirometry

dome floating at the surface and two feeding tubes placed at 40-m depth, ~9 m apart. Gas concentrations in the dome were continuously monitored throughout the trials, whether or not the sea lion was at the surface. Mean water temperature measured on the TDR was 7.7 ± 1.3 s.d. and ranged from 2.4 to 20.5 °C during dive trials (70 % of the trial days had water temperatures >6 °C). Pre-dive rates of $s\dot{V}_{O_2}$ were measured for 8–15 min as the animal rested calmly at the surface.

Metabolic rate at the surface (MRs) was calculated as the average $s\dot{V}_{O_2}$ during the last 2.0–2.5 min before the animal was instructed to commence diving. If the animals were not calm, we extended the pre-dive sampling time for MRs until steady $s\dot{V}_{O_2}$ was achieved. A cage hanging below the respiratory dome (~1.5 × 1.5 × 2.6 m) with a trapdoor at the bottom ensured that the sea lion did not surface outside the dome prematurely during measurements of MRs, but the trapdoor was not closed during dive bouts. After a single dive cycle or dive bout (see below), post-dive oxygen consumption rate was measured until $s\dot{V}_{O_2}$ returned to within 5 % of the pre-dive levels (MRs).

Animals were fasted overnight before each trial. The feeding tubes delivered 20 g pieces of Pacific herring (*Culpea pallasii*) at depth, at a rate sufficient to ensure required dive times. The sea lions were also given pieces of herring inside the respirometry dome through a sealed PVC pipe delivery system to reinforce their behavior. The length of the Y-joint feeding tube (approximately 3 feet with 2 inch diameter) coupled with the negative pressure created by the high flow rate of 475 l min^{-1} most likely prevented expired gas from escaping. This was verified during calibrations prior to data collection. Animals were fed <0.5 kg herring during transport to the dive site, which took 15–20 min. In total, the sea lions consumed 6.1–14.5 kg of herring from loading onto the boat until the end of the dive trial (45–60 min total trial duration, mean = 10.6 ± 3.2 kg s.d.), which represents approximately twice their average daily food intake.

Rates of oxygen consumption and ODBA (detailed below) were measured concurrently during three trial types: single dives, bouts of long duration dives, or bouts of short duration dives ("long" or "short" refers to durations of individual dives within a bout). Each sea lion completed multiple trials of each trial type on separate days (Table 1). For bouts of long dives, animals executed 4–6 dives in a series with a goal of 4–6 min duration per dive. For bouts of short dives, animals executed 10 or 12 dives in a bout with a goal of 1–2 min duration per dive. Single dives had a dive duration goal of 4–6 min (similar to each dive within the long duration dive bouts). Unlike with dive bouts trials, 1–4 trials of single dives were completed in the same session. However, complete recovery of $s\dot{V}_{O_2}$ to MRs plus an additional 5 min buffer was ensured between individual trials.

The trial types were designed so that the bouts of short durations and bouts of long durations had similar cumulative dive durations (15–25 min cumulative dive durations per bout) with differing number of ascents and descents. The bout of long duration dives was designed to incur greater levels of oxygen depletion by encouraging animals to dive past their calculated aerobic dive limit (cADL) of 3.0 min (Gerlinsky et al. 2013). Specific dive durations were controlled by varying the feeding rate at depth and using a light cue at depth to signal a return to the surface.

Surface intervals between dives within a bout were controlled by the trainer and determined by visual examination of the raw O_2 and CO_2 data as it was collected. Our goal was to have the animals remain at the surface within a dive bout for only as long as they needed to replenish sufficient O_2 to reliably dive again (without surfacing outside the dome), but not long enough to return fully to pre-dive $s\dot{V}_{O_2}$ (MRs, i.e., animals had not fully recovered $s\dot{V}_{O_2}$ to pre-dive levels). In practice, we instructed the sea lion to dive a few minutes before the raw O_2 and CO_2 approached MRs. It took at least a minute for trainers to feed the sea lion a final piece of fish in the dome and for the sea lion to exit the dome. After each trial, we examined the raw O_2 and CO_2 data to confirm that $s\dot{V}_{O_2}$ during the surface intervals within a dive bout did not return to within 5 % of MRs.

Our dive trials were designed to keep the dives per bout, dive durations, and cumulative dive time per bout as consistent as logistically possible. However, variation in animal behavior resulted in controlled changes in the number of dives per bout, in order to maintain consistent cumulative dive duration. As a result, bouts of short dives all comprised 12 dives except for 1 trial of 10 dives. The bouts of long dives all consisted of 4 dives, except for 5 instances of 5 dives in a bout and 1 trial with 6 dives. Preliminary data analysis showed that removing the 10-dive trial from the dataset of bouts of short dives or removing the trials with more than 4 dives from the bouts of long dives dataset did not change the results. Therefore, all of the trials were included to increase variability and sample size. The majority of dives were to the trial depth of 40 m (80 %). However, maximum dive depth was up to 53 m due to the sea lions occasionally briefly diving below the feeding tubes at the start of dives.

Variable calculation

For the purposes of calculating AMR and ODBA, a dive cycle for a single dive trial was defined to commence with the start of the dive and continued through the post-dive surface interval until $s\dot{V}_{O_2}$ returned to within 5 % of pre-dive MRs. A dive bout consisted of a series of dives, the brief post-dive surface intervals between dives, and the

longer post-diving surface interval until the $s\dot{V}_{O_2}$ returned to within 5 % of pre-dive MRs. $s\dot{V}_{O_2}$ was calculated across the entire dive bout and divided by total dive bout duration to yield average metabolic rate (AMR). Previous research has shown that the relationship between heart rate and $s\dot{V}_{O_2}$ is linear over a complete single dive cycle or dive bout (i.e., AMR), but not over the dive portion only (i.e., DMR as per Young et al. 2011). Therefore we chose to use AMR calculated over the single dive cycle or dive bout in our analyses.

To calculate ODBA, we first smoothed each axis of acceleration with a 3-s running mean to calculate the static acceleration (Shepard et al. 2008; Wilson et al. 2006). The static acceleration (smoothed data) was subtracted from the unsmoothed acceleration, resulting in dynamic acceleration. The absolute value of dynamic acceleration was then summed across surge, sway, and heave axes to yield instantaneous ODBA at 20 Hz over the entire dive trial. Exact dive start time and dive end time were extracted from the TDR, and instantaneous ODBA was averaged over each single dive cycle or dive bout and matched to the corresponding AMR measurement.

Statistical analysis

Data were analyzed within a repeated measures framework using linear mixed-effects models (LME) in R 2.3.0 (Gałecki and Burzykowski 2013; Pinheiro and Bates 2000; Zuur et al. 2009). LME models utilize individual animal variation relative to the mean of the population while correcting for repeated measurements within and among animals. Animal was treated as a random effect that controlled for repeated measures and allowed inferences from the sample population to the wild population.

LME comparisons of linear models require that any models being compared are significantly linear (i.e., intercept and slope significantly different from zero). First, the significance of the slope and intercept was determined using a conditional ANOVA F-Test for both the null model (i.e., ODBA vs. AMR with no fixed factors) and models that included a fixed effect (e.g., ODBA vs. AMR with trial type as a potential fixed factor). The intercepts were significantly different from zero for all of the models tested; therefore we only report results from the ANOVA tests in reference to the significance of the slope. Likelihood ratio tests (LRT) with the fixed effect model hierarchically nested within the null model without fixed effects were used in a stepwise approach to compare models and determine if inclusion of combinations of potential fixed factors was significantly better than models with fewer fixed effects (including the null model).

Within LME analysis on linear models, additive fixed factors can only change the intercepts, but multiplicative factors (which indicate an interaction between the factor and ODBA) change both intercept and slope. The simpler additive model (+dive type) is accepted unless the multiplied factor (×dive type) is significantly better as determined using an LRT test. None of the models had significant interactions between the fixed factor and ODBA; therefore, only the intercepts are different on the same model. Tukey post hoc tests with Bonferroni adjusted P values were used to compare the means between multiple levels within significant fixed factors (mvtnorm and multcomp; R libraries).

Fixed effects that were tested as potential significant model factors to explain variation in the relationship between ODBA and AMR included dive type (single dive, bout of short dives, bout of long dives), cumulative food fed, and maximum dive depth (< or >50 m). For both bouts of short dives and bouts of long dives, we also tested the number of dives in a bout as a fixed factor. We also tested cumulative dive duration (<10, 11–20, 21–30 min) and single dive cycle duration or dive bout duration (<10, 11–20, 21–30, 31–40, >40 min). However, cumulative dive duration depended upon trial type since all single dives had shorter dive durations than cumulative bout dive durations. Therefore, we converted cumulative dive duration into percent of dive cycle spent submerged (total dive duration/total dive cycle duration ×100). For dive bouts, this was calculated as the cumulative dive duration divided by the cumulative dive bout duration until within 5 % of MRs. We tested the percent of the dive cycle spent submerged (<50 or >50 %) as a fixed factor for the relationship between ODBA and AMR.

We also tested the potential effect of anaerobic metabolism on the relationship between ODBA and AMR. The only way to directly determine if a dive uses anaerobic or aerobic metabolism is to measure post-dive plasma lactate levels, which is extremely difficult to do on freely diving animals (Ponganis et al. 1993; Shaffer et al. 1997). Therefore, we inferred whether the dives were anaerobic or aerobic based on comparisons between the observed dive durations and the 3.0 min cADL of Steller sea lions (Gerlinsky et al. 2013). Specifically, we separated all dives into categories of "≤3.0 min cADL" or ">3.0 min cADL" to create a fixed factor termed "cADL type". The minimum dive time for a single dive was 3.5 min; therefore all single dives were categorized as ">cADL". While the individual dive durations within a dive bout varied, we used average dive duration within each dive bout ("mean dive duration") to provide a single reference value versus cADL for dive bouts. Mean dive duration was only used for this comparison to cADL type; all other calculations and analysis were done on the actual observed individual dive durations within each bout.

We also investigated the relationship between cumulative dive duration, AMR, ODBA, and cumulative recovery

Table 2 Summary of dive characteristics for single dives, bouts of short dives, and bouts of long dives in trained Steller sea lions, including number of dives per trial type

Dive type	No. dives	Dive duration (min), mean (±s.d.)			Surface interval duration (SI, min), mean (±s.d.)		
		Individual dive	Cumulative dive	Dive bout (dives + SIs) or single dive cycles	Individual SI	Final SI	Cumulative SI
Single dive	1	4.3 ± 0.8	NA	10.2 ± 1.4	NA	6.0 ± 1.0	NA
Bout of short dives	10, 12	1.6 ± 0.3	18.7 ± 1.7	30.3 ± 2.4	0.6 ± 0.10	4.7 ± 1.0	11.7 ± 1.2
Bout of long dives	4–6	4.6 ± 1.1	19.5 ± 3.4	33.3 ± 5.9	2.6 ± 0.8	5.5 ± 0.9	13.9 ± 2.9

Mean values are presented (±s.d.) for individual dive durations, cumulative dive durations (submergence time only) for dive bouts, and duration of complete dive bouts (cumulative dive duration plus multiple surface intervals and final SI), or single dive cycles (1 dive followed by final surface interval). Average individual surface intervals between dives in dive bouts (individual SI), the final post-dive recovery periods (final SI), and cumulative SI for dive bouts (sum of individual and final SI) are also detailed

duration to examine the effect of submergence duration on recovery duration (i.e., post-dive surface interval duration). Cumulative recovery duration included the final post-dive surface interval (i.e., final SI in Table 2) and any surface intervals within a dive bout (i.e., individual SI, Table 2). The potential relatedness between dive duration and dive type excluded testing dive type as a fixed factor when dive duration was the dependent variable. When the dependent variable was categorical (i.e., comparing mean ODBA among dive types without testing a linear relationship), LME model comparison was analogous to performing repeated measures ANOVA with the important addition of accounting for random effects.

The main goal of our analyses was to derive statistically significant predictive equations of AMR from ODBA for different dive behaviors. However, it was also important to understand the associated error with those predictions. The error of predictive equations is not constant, with a minimum value at the mean ODBA and increasing toward both tails. The error of LME models is infrequently reported and varies widely in the manner of its calculation. For this study, we calculated the average percent error based on the model residuals (as described in Young et al. 2011) for comparisons with other studies. We calculated the average percent error by dividing the mean absolute fixed residual by the median predicted AMR value. We then multiplied this by 100 to calculate a percent error. This calculation of error takes into account the inclusion of individual sea lion as a random factor, as well as the repeated measures framework of the models. Standard error of the estimated AMR (s.e.e.$_{calibration}$) was calculated using the minimum, mean, and maximum ODBA for each model (Eq. 10 in Green et al. 2001; Lyons et al. 2013; Eq. A2 in Young et al. 2011; Zar 2010). The s.e.e. incorporates residual error as well as additional error terms for the error associated with random effects and fixed factors. Relative s.e.e. (s.e.e.$_{calibration}$ %) was also calculated as a percentage of the estimated AMR for the minimum, mean, or maximum ODBA value.

We conducted post hoc power analysis in R using the Prwr function within the nlmeU package (Gałecki and Burzykowski 2013). Ideally, power analysis should be conducted a priori. Realistically, logistics and available animals, especially with marine mammals, often limit sample size and time available to collect data. Caution should be used in interpreting the observed post hoc power values because post hoc observed power is a re-expression of a *P* value and therefore does not add new information to the statistical analysis (Gałecki and Burzykowski 2013; Hoenig and Heisey 2001; Thomas 1997). However, post hoc power analysis can still provide insight into interpretation and more importantly refining experimental designs for future studies.

Results

Differences in dive characteristics

The main purpose of the analysis was to determine the ability of ODBA to predict AMR, while taking into account the potential effect of differences in dive behavior. The characteristics of the different dive types resulted in a range of dive durations (per dive and cumulative over a bout), inter-dive surface intervals, and post-dive recovery periods (summarized in Table 2). As previously noted (and illustrated in Fig. 1a), cumulative dive duration was confounded with dive type. Mean cumulative dive duration was 18.7 ± 1.7 min for bouts of short dives and 19.5 ± 3.4 min for bouts of long dives. Durations for single dives (mean = 4.3 ± 0.8 min) were always shorter than for dive bouts (Table 2). Hence, when we tested the effect of cumulative dive duration on the predictive ODBA relationship, we did not also include dive type as a factor (Fig. 1c).

Cumulative recovery duration (i.e., cumulative surface interval duration) differed among dive types in a similar fashion. Cumulative recovery was shorter for
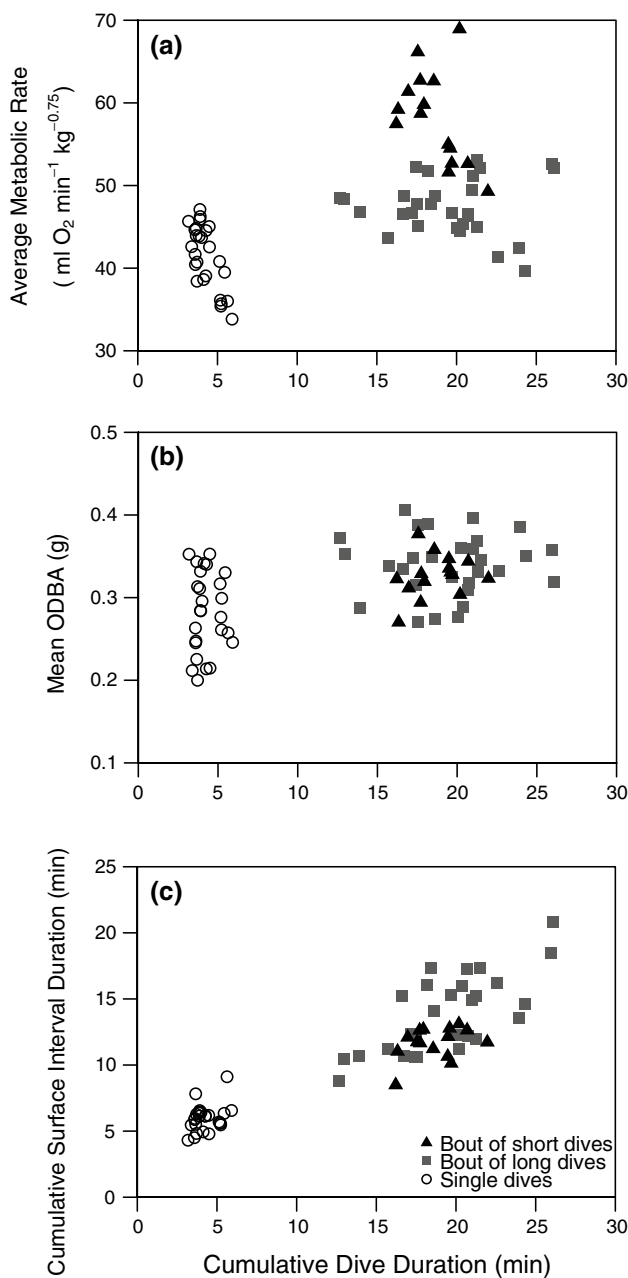
Fig. 1 Changes in **a** average metabolic rate (AMR i.e., rate of oxygen consumption over the complete dive bout), **b** overall dynamic body acceleration (ODBA), and **c** cumulative surface interval duration in relation to cumulative dive duration in Steller sea lions. The sea lions executed single dives, bouts of long duration dives (4–6 dives per bout), or bouts of short duration dives (10 or 12 dives per bout). ODBA and AMR were averaged over the complete single dive cycle or dive bout

single dives (6.0 ± 1.0 min) than for bouts of either short dives (11.7 ± 1.2 min) or long dives (13.9 ± 2.9 min, LRT = 112.86, P < 0. 0001, Table 2). Mean percent of cycle spent submerged also differed among dive types (LRT = 135.39, P < 0.0001). The mean percent of dive

cycle spent submerged was similar for bouts of short dives (61.6 ± 2.7 %) and bouts of long dives (58.4 ± 3.6 %, Tukey, P = 1.0), but was significantly shorter for single dives (41.7 ± 4.6 %, Tukey, P = 0.001).
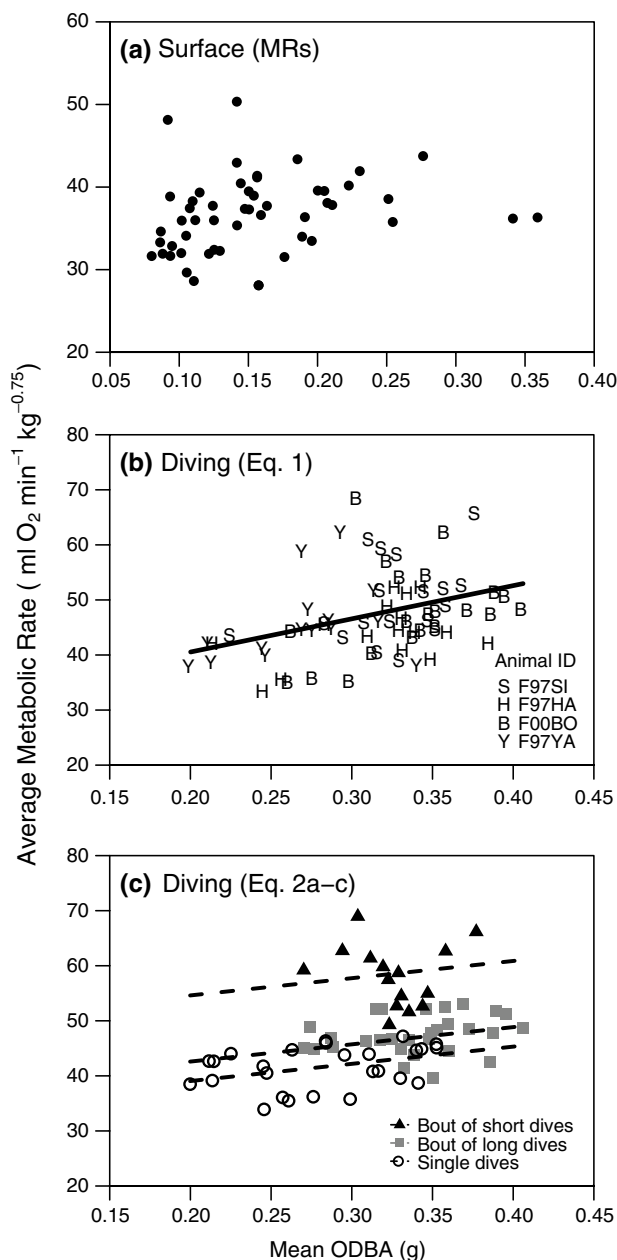
Relationship between ODBA and rates of oxygen consumption

Pre-dive metabolic rate at the surface (MRs) ranged from 28.1 to 50.3 ml O_2 min^{-1} $kg^{-0.75}$ and the corresponding surface ODBA ranged from 0.08 to 0.36 g (mean = 0.16 ± 0.06 g). The relationship between ODBA and MRs was not linear (ANOVA, P = 0.09, Fig. 2a), apparently due to changes in ODBA that were not reflected by similar changes in MRs.

Mean AMR of all dives types combined (47.6 ± 7.4 ml O_2 min^{-1} $kg^{-0.75}$, 70 data points,) was 23 % greater than mean MRs (36.7 ± 4.1 ml O_2 min^{-1} $kg^{-0.75}$, 52 data points, LRT = 68.35, P < 0.0001). Mean ODBA for all dives combined was 0.316 ± 0.05 g, double the mean ODBA when at the surface. Therefore, we analyzed the relationship between ODBA and AMR while diving separately from when the animals were resting at the surface prior to diving.

We first calculated the model for predicting AMR from ODBA alone (without dive type as a fixed factor). This "generic" model (that combined all dive types into a single model) was significantly linear (slope ANOVA, F = 10.77, P = 0.0017, Eq. 1, Table 3; Fig. 2b). The "generic" model (Eq. 1, Fig. 2b) is the null model counterpart to Eqs. 2a–c (Fig. 2c; Table 2). However, there was a significant difference in AMR among dive types (LRT = 90.37, P < 0.0001). Mean AMR was highest for bouts of short dives (58.18 ± 5.6 ml O_2 min^{-1} $kg^{-0.75}$) compared to bouts of long dives (47.44 ± 3.5 ml O_2 min^{-1} $kg^{-0.75}$) and single dives (41.4 ± 3.9 ml O_2 min^{-1} $kg^{-0.75}$). Mean ODBA also varied significantly by dive type (LRT = 33.65, P < 0.0001). Mean ODBA was similar for over bouts of long dives (0.34 ± 0.04 g) and bouts of short dives (0.33 ± 0.03 g, Tukey, P = 1.0), but significantly lower over single dives (0.28 ± 0.05 g, Tukey, P = 0.001).

Cumulative dive duration also had an effect on both AMR and ODBA. Across all dive types, both AMR and ODBA were higher in dive trials with longer cumulative dive durations (Fig. 1a, LRT = 42.69, P < 0.0001; Fig. 1b, LRT = 30.03, P < 0.001, cumulative dive duration tested as a binned fixed factor). However, this result could have been driven by the inclusion of single dives, which had shorter dive durations across a narrower range that did not overlap with the other dive types. However, for a given cumulative dive duration, AMR was greater for bouts of short dives compared to bouts of long dives, while mean ODBA did not differ by bout type (Fig. 1a, b).

Fig. 2 The relationship between overall dynamic body acceleration (ODBA) and average metabolic rate while Steller sea lions were **a** measured as MRs while resting on the surface or **b, c** as AMR while diving to 40 m. The relationship between ODBA and metabolic rate was not linear when the sea lions were resting on the surface (**a**), but was significant when they were diving (**b, c**). The relationship between ODBA and AMR was linear when data from all dives were combined (**b** *solid line*) but the inclusion of dive type as a significant model factor indicated that the relationship varied among bouts of short dives, bouts of long dives, and single dives (**c** *dashed lines*)

These observed differences in the differences in AMR and ODBA between dive types were reflected by the fact that the best statistical model for predicting AMR from ODBA included dive type as a fixed factor (LRT = 104.07,

$P < 0.0001$, Fig. 2c; Table 3 Eq. 2a–c, $n = 70$ data points). This indicates that the relationship between AMR and ODBA differed when animals executed single dives, bouts of long dives, or bouts of short dives. However, when each dive type was analyzed separately, the slopes were not significantly linear for the bouts of short dives (ANOVA, $P = 0.59$, $n = 15$ data points, Eq. 3), the bouts of long dives (ANOVA, $P = 0.09$, $n = 29$ data points, Eq. 4, Table 3), or single dives (ANOVA, $P = 0.09$, $n = 26$ data points, Eq. 5, Table 3).

We examined additional potential fixed factors in a stepwise modeling approach on the relationships between ODBA and AMR. We focused the model selection on the fixed factors that were most pertinent to the research objectives and were experimentally manipulated (dive type, number of dives per bout, dive duration, dive cycle, or dive bout duration). Next, we tested secondary factors that were not intentionally manipulated, but potentially varied among trial types (cumulative food fed, maximum depth). While cumulative dive duration and number of dives per bout significantly improved the null model (i.e., no fixed factor), these models were not significantly better than those that included only dive type as a fixed factor. None of the other potential fixed factors significantly improved the null model or the model with dive type as a fixed factor. As previously noted, cumulative dive duration was inter-related with dive type because all single dives were shorter in duration than the cumulative dive duration of both types of dive bouts. However, cumulative dive duration still did not improve the model that included dive type when dive bout data were examined without single dives.

Overall, the model with dive type as a fixed factor was statistically the best model at predicting AMR (Eq. 2a–c, Table 3). Additionally, the average percent residual error was less for the model that separated the dive types (Eq. 2a–c, 7 %, Table 3) than for the generic null model (Eq. 1, 11 %). A single average percent residual error could only be calculated for the model that included dive types as a factor because the predictive equations for individual dive types (Eq. 2a–c, Table 3) are all derived from the same statistical model, with different predictive equations for each level (i.e., dive type) of the fixed factor. The standard error of the estimated AMR (s.e.e.$_{calibration}$ %) at the minimum ODBA of 0.200 was greatest for single dives (32 %) and bouts of long dives (30 %) compared to the bouts of short dives (23 %) or generic dive model (5 %, Table 3; as calculated in Eq. 10 in Green et al. 2001; Table S1 in Young et al. 2011; Zar 2010). Values of s.e.e. $_{calibration}$ % calculated using the mean, minimum, and maximum ODBA values decreased slightly as ODBA increased (Fig. 3; Table 4), but did not vary greatly within the same model due to the narrow range of ODBA.

Table 3 Equations for mixed-effect linear models relating overall dynamic body acceleration (ODBA) to average metabolic rate (AMR) for Steller sea lions undertaking different set of diving behaviors in the form (AMR = a•ODBA + b)

Eq.	Model description	Fixed factor	Slope		Intercept		Avg. %	s.e.e.$_{calibration}$ %
			a	(±s.e.m)	b	(±s.e.m)	Error	Min ODBA
1	All dives (generic)	None	60.3*	(18.4)	28.5	(5.8)	10.6 %	4.8 %
2a	All dives (specific)	Dive type (short)	31.3*	(12.4)	48.3	(6.3)	6.8 %	23.1 %
2b		Dive type (long)	31.3*	(12.4)	36.2	(5.2)	6.8 %	29.6 %
2c		Dive type (single)	31.3*	(12.4)	32.7	(7.3)	6.8 %	32.3 %
3	Bout of short dives only	None	−34.0	(61.5)	69.4	(18.8)	Not linear	Not linear
4	Bout of long dives only	None	41.2	(23.3)	33.5	(6.9)	Not linear	Not linear
5	Single dives only	None	27.2	(15.3)	33.7	(4.4)	Not linear	Not linear

The "generic" model included data from all dives, but no fixed factors (Eq. 1). When dive type was included as a fixed factor the relationship differed significantly among dive types (Eq. 2a–c, Fig. 2c) and from Eq. 1, but the relationships were not significantly linear when each dive type was analyzed separately (Eqs. 3–5). Model slopes and intercepts (±s.e.m) are presented along with number of dives per bout (* indicates significantly linear slope and intercept). Average percent error of the each model was calculated with Eq. A2 from Young et al. 2011. Standard error of the estimated AMR (s.e.e.$_{calibration}$ %) at the minimum ODBA was calculated with Eq. 10 from Green et al. 2001. Equations 2a–c are from a single model with a significant fixed factor for each dive type, thus having identical slopes, but significantly different intercepts. Equations 3–5 are from separate models that do not include any fixed factors
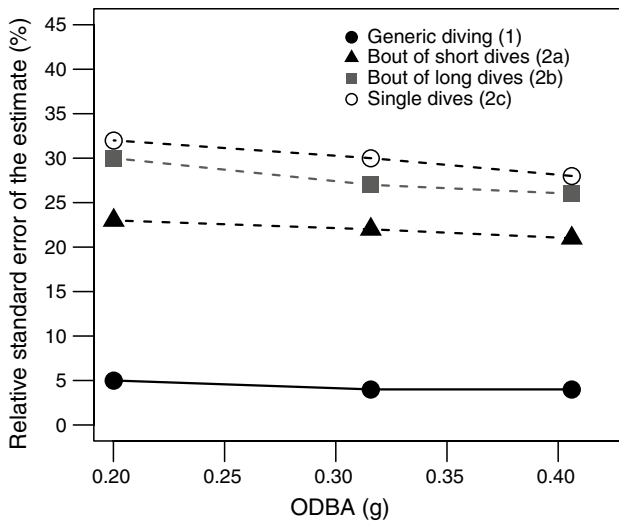
Fig. 3 Relative standard error of the estimated AMR from ODBA (s.e.e.$_{calibration}$ %) was calculated using the minimum (0.200), mean (0.316), and maximum (0.406) ODBA over the single dive cycle or dive bout using Eq. 10 in Green et al. 2001. s.e.e.$_{calibration}$ % was expressed as a percentage of the estimated AMR for each model as in Eq. A2 in Young et al. 2011. s.e.e.$_{calibration}$ % values decreased slightly as ODBA increased, but did not vary greatly within the same model due to the narrow range of ODBA

Oxygen depletion and recovery duration

We also tested whether physiologically significant levels of oxygen depletion were being incurred, as demonstrated by differences in recovery durations and individual dive durations in relation to cADL. As previously noted, the mean cumulative recovery duration for bouts of long dives was greater than for bouts of short dives or for single dives (Table 2; Fig. 1c).

Bouts of short dives and bouts of long dives had similar final post-dive surface intervals at the end of a bout, and the difference in cumulative recovery durations between bouts was mostly due to differences in the duration of individual surface intervals within a dive bout (Table 2). The longer mean cumulative recovery duration indicates that the bouts of long dives incurred greater levels of oxygen depletion.

We also tested "cADL type" as a fixed factor within the LME models to explore the potential effects of aerobic vs. anaerobic metabolism. All of the single dive durations were > 3.0 min, the estimated cADL (Gerlinsky et al. 2013), and all 15 bouts of short dives had mean dive durations within a bout that were <cADL. For the bouts of long dives, 28 bouts were classified as having the mean dive duration within a dive bout >3.0 min (>cADL), but 1 bout was marginally classified as <cADL (mean dive duration for 6 dives = 2.91 min). Including cADL type as a fixed factor did improve the null model (Eq. 1, LRT = 74.36, $P < 0.0001$), but was not better than the model that included dive type (Eq. 2a–c, LRT = 26.67, $P = 0.0001$). Further, adding dive type and cADL type as fixed factors simultaneously was not significantly better than adding only dive type as a fixed factor (LRT = 6.3, $P = 0.39$).

Discussion

While rates of oxygen consumption are considered the "gold standard" for estimating energy consumption of marine mammals, it is not possible to directly measure oxygen consumption in the field with the exception of the few pinniped species that reliably surface in ice holes (e.g., Bengtson and Stewart 1992; Castellini 1992). Therefore,

Table 4 Relative standard error of the estimated AMR (s.e.e._calibration %) was calculated using the minimum (0.200), mean (0.316), and maximum (0.406) ODBA over the single dive cycle or dive bout using Eq. 10 in Green et al. 2001

Eq.	Model description	Fixed factor	At minimum ODBA = 0.200 s.e.e._calibration %	At mean ODBA = 0.316 s.e.e._calibration %	At max ODBA = 0.406 s.e.e._calibration %
1	All dives (generic)	None	5	4	4
2a	All dives (specific)	Dive type (short)	23	22	21
2b		Dive type (long)	30	27	26
2c		Dive type (single)	32	30	28

s.e.e._calibration % was expressed as a percentage of the estimated $s\dot{V}_{O_2}$ for each model as in Eq. A2 in Young et al. 2011

additional methods are needed that can predict energy consumption of free-ranging animals. Previous research has yielded mixed results on the ability of ODBA to predict rates of oxygen consumption, especially in diving air-breathing vertebrates. Compared to the previous validation experiments, our study examined the relationship between ODBA and $s\dot{V}_{O_2}$ with Steller sea lions diving in the open ocean under conditions of increased movement at depth, increased number of dives per bout, and potentially increased oxygen depletion.

The relationship between ODBA and MRs

Our results showed that ODBA was unable to predict MRs at the surface prior to diving. The lack of relationship was certainly not due to a lack of variability in the ODBA data, but may have been due to the source of that variation. While all of the animals appeared to be resting at the surface (~2 min) prior to diving (as evident by steady $s\dot{V}_{O_2}$), this did not necessarily translate into minimal instantaneous ODBA. For example, occasional rapid and brief headshakes or other similar apparently minor movements at the surface caused substantial peaks in instantaneous ODBA without corresponding increases in instantaneous $s\dot{V}_{O_2}$. This occasional but substantial disassociation between ODBA and $s\dot{V}_{O_2}$ likely resulted in the collapse of any (potential) predictive relationship while sea lions were at the surface.

The conclusions of past studies of the ability of ODBA to predict metabolic rate at the surface and whether this relationship differs from that while diving are mixed, even among studies conducted on the same animals. Fahlman et al. (2008b) reported that the relationship between ODBA and MRs was linear, and not different from the relationship between ODBA and AMR over single dive cycles. A subsequent, larger study (which incorporated the 2008 data) also found a linear relationship between ODBA and MRs, but determined that it was distinct from the relationship between ODBA and AMR during single dives (Fahlman et al. 2013). It is difficult to discern whether the differences between the results of these previous studies were due to

either a larger dataset or differences in statistical approach and interpretation of results. In contrast to both of these earlier studies, our data failed to find a linear relationship between ODBA and MRs despite the increased statistical power from adding a greater number of data points and, more importantly, adding a fourth animal (Zar 2010; Zuur et al. 2009). The fact that the potential relationship between ODBA and MRs is inconsistent, even when applied to controlled experiments under similar conditions, casts doubt on its predictive capacity when applied to free-ranging animals at the surface that exhibit an even wider range of surface behaviors.

Predicting rates of diving oxygen consumption from ODBA

The different dive types performed by the sea lions in our study provided a range of values for both ODBA and AMR. Both mean AMR and ODBA differed significantly among dive types, with dive bouts having greater mean ODBA and higher mean AMR than single dives. Bouts of short dives had a much higher AMR at a given ODBA than bouts of long dives. However, while the bouts of short dives had approximately twice as many ascent and descents as the bouts of long dives, the number of dives per bout was not the source of the observed differences in the relationship between ODBA and AMR by dive type. Alternately, the difference was potentially due to greater metabolic depression influenced by extended dive durations within the bouts of long dives.

This range in ODBA and AMR allowed us to formulate predictive linear models. Our generic statistical model revealed a linear relationship between ODBA and AMR when data from all dives were combined (Eq. 1, Fig. 2b). However, including dive type provided a stronger predictive model, indicating a statistical difference in the nature of the relationship among dive types (Eq. 2a–c, Fig. 2c). Yet, while the predictive relationship that incorporated dive type was statistically significant, there were no significantly linear relationships between ODBA and AMR for any dive type when analyzed separately (Eq. 3–5, Table 3).

This apparent inconsistency could reflect that there are separate underlying relationships between ODBA and AMR for each dive type, but we lacked enough statistical power to detect it after separating dive types (type II error). Alternately, concurrent changes in the physiology of the sea lions (such as thermoregulation and digestion) could have reduced the predictive capacity within dive types. Finally, the statistical significance of the generic predictive model may have been a spurious consequence of differences in mean ODBA and AMR between dive types. In this case, the lack of predictive power within dive types is a natural consequence of the inherent disconnect between physical activity and gas exchange in diving vertebrates.

Quantitatively, incorporating dive type into the predictive model resulted in reduced statistical power. While sample sizes were smaller within each dive type (15–29 points per dive type) compared to the data that combines all dives ($n = 70$ points, Table 1), post hoc power analysis showed that we had medium observed power of 0.39 to detect observed differences in dive type (Eq. 2a–c). Within each dive type, the post hoc observed power to detect a significant slope was 0.08 for bouts of short dives (Eq. 3), 0.42 for bouts of long dives (Eq. 4), and 0.42 for single dives (Eq. 5). It is therefore possible that the nonsignificant slopes in Eqs. 3–5 were due to the lack of power, especially for bouts of short dives. However, caution should be used in interpreting these post hoc power values because power was collected from the sample data (Gałecki and Burzykowski 2013; Hoenig and Heisey 2001; Thomas 1997). Rather, these power values are primarily valuable as a guide for future research. While additional research with more animals and larger sample sizes within each dive type would help clarify whether a linear relationship exists within each isolate dive type, one has to be careful not to fall into the trap of collecting so much data that significant correlations are inevitable regardless of the weak effect size.

Concurrent physiological changes that alter $s\dot{V}_{O_2}$ independent of activity would serve to weaken any potential relationship between ODBA and AMR. For example, sea lions that are outside their thermoneutral would be expected to change their $s\dot{V}_{O_2}$ without a corresponding increase in ODBA. While the thermal neutral zone (TNZ) has not been directly measured for Steller sea lions, our water temperatures (mean = 7.7 ± 1.3 s.d., 70 % >6 °C) were similar to TNZ estimates for California sea lions (6.4–22.4 °C, Liwanag et al. 2009)—suggesting that our animals were unlikely to be outside their TNZ zone for prolonged periods during our diving trials. Similarly, the heat increment of feeding (HIF) has been shown to substantially increase $s\dot{V}_{O_2}$ of Steller sea lions while resting on land, starting at ≥ 1 h (estimated from Fig. 1) and peaking at approximately 4 h after a 4 kg meal (Rosen and Trites 1997). Although our

trials were much shorter than this 4-h peak time (≤ 60 min), there is still the possibility of a smaller digestive effect. However, recent research conducted at the same facility as our study found evidence that Steller sea lions partially defer digestion during diving (Rosen et al. 2015). Therefore, the facts that the trial durations were short, that animals were fed 20 g increments instead of a bulk meal, and that cumulative food fed was not a significant factor in the LME models suggest that HIF's potential effect on the relationship between ODBA and $s\dot{V}_{O_2}$ was minimal.

There are also a number of reasons to expect that the lack of relationship between ODBA and AMR when dive types were analyzed individually reflect a biological reality. First, despite our changes in study design to better mimic natural foraging patterns, the ODBA range in our study (0.20–0.41 g) was surprisingly similar to that reported in previous studies with these same sea lions executing a combination of single dives and dive bouts (estimated from graphs, ~0.11–0.45 g, Fig. 2b, Fahlman et al. 2013; ~0.15–0.40, Fig. 2, Fahlman et al. 2008b)—even with the addition of a second feeding tube at depth to increase physical movement. While it is possible that the second feeding tube did not substantially increase the activity of the sea lions in our study, it is also possible that the mathematical averaging of ODBA masked changes in behavior. Similarly, averaging over the complete dive cycle or dive bout—including the surface interval with lower associated ODBA—effectively reduced the range of mean ODBA. Unfortunately, this averaging was necessary so that the time periods for ODBA and AMR would match. Previous work demonstrated that the linear relationship between AMR and heart rate was only present over a single dive cycle or dive bout with post-dive surface intervals included (Young et al. 2011). This supports the theory that single dive cycles or dive bouts are complete physiological units that should not be divided into surface and submerged phases (Fedak et al. 1988; Kooyman and Ponganis 1998).

To explore the possible suppressing role of using mean ODBA, we plotted instantaneous ODBA verses dive depth for each dive type on representative trials from animal F97SI and found that instantaneous ODBA while diving was greater than instantaneous ODBA at the surface (Fig. 4). While patterns in instantaneous ODBA differed between dive types, mean ODBA was similar among the dive types of the representative trials (0.32–0.35 g, Fig. 4b, d, f). We note, however, that this analysis should only be interpreted as a representative example because instantaneous ODBA varied greatly within and among trials and animals.

Further evidence that ODBA may not accurately reflect levels of physical activity in a diving mammal is the lack of differences in ODBA observed between bouts of long dives and bouts of short dives, The bouts of short dives did not have greater mean ODBA values than the bouts of
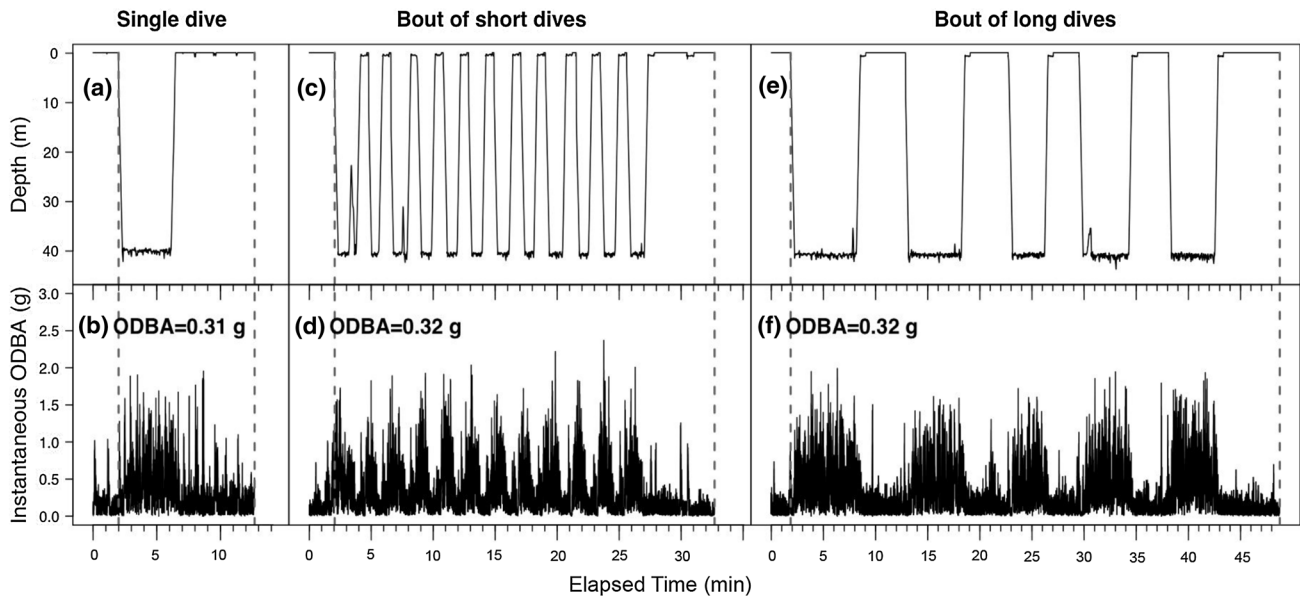
Fig. 4 Changes in instantaneous ODBA and dive depth for representative single dives (**a**, **b**), bouts of short dives (**c**, **d**), and bouts of long dives (**e**, **f**) on animal F97SI. Mean OBDA was averaged over the single dive cycle or dive bout (as indicated by *dashed lines*), start-ing with the first dive and continuing through the final surface interval until $s\dot{V}_{O_2}$ returned to within 5 % of pre-dive metabolism. Although instantaneous ODBA patterns varied among dive types, mean ODBA was similar among the dive types of the representative trials (**b**, **d**, **f**)

long dives despite the fact that bouts of short dives included more ascents and descents for similar cumulative dive durations. In contrast, AMR was greater for bouts of short dives, likely caused by this greater physical diving effort. The fact that changes in transiting effort did not affect ODBA might reflect the fact that the maximum range of ODBA in diving Steller sea lions is finite and less flexible than $s\dot{V}_{O_2}$—an attribute that would depress its predictive power. This ties into the hypothesis that the physical movements of diving vertebrates are tempered while submerged (i.e., ODBA values reduced) compared to the physical movements at the surface (Halsey et al. 2011a, b). Future studies could potentially increase the ODBA range using experimental setups or trained behaviors that increased underwater activity, partition ODBA over different phases of the dive cycle, and explore other metrics of ODBA (such as an integral or total value).

Finally, the unavoidable temporal disconnect between physical activity while diving, tissue oxygen consumption (and associated circulatory adjustments), and gas exchange may preclude the ability of ODBA to predict AMR in air-breathing vertebrates as suggested in previous studies (Halsey et al. 2011a, b). This would likely be apparent in dives that exceeded and animal's aerobic dive limit, given the required additional post-dive biochemical processes required for full physiological recovery. All of the single dives had dive durations >3.5 min, substantially longer in duration than the 3.0 min cADL for this species (with some dive durations as much as twice the cADL). For the bouts of long dives, 97 % of the bouts had mean

individual dive durations greater than the cADL. In comparison, the individual dive durations within the bouts of short dives were all shorter than the cADL. Therefore, all of our sea lions ended their bouts of long dives and single dives with greater total O_2 depletion than during the bouts of short dives (although potentially to a greater extent with the bouts of long dives) and were possibly relying partly on anaerobic metabolism. This contention is supported by the differences seen in cumulative recovery durations. Cumulative recovery duration was greater following a bout of long dives compared to a bout of short dives of a similar cumulative dive duration (Fig. 1c). This potential increase in the degree of anaerobic metabolism and level of oxygen depletion among dive types likely contributed to the segregation of the relationship by dive type.

Assessing the error of using ODBA to predict $s\dot{V}_{O_2}$ and its field application

Unfortunately, there are no definitive means to quantify the error of LME predictive equations. The two methods we used to assess error of the calibration showed contrasting trends, but we encourage consideration of both error metrics in a complementary rather than competing manner. We focused on comparing error at the minimum ODBA because there were no large differences among the errors at the minimum, mean, or maximum ODBA values (Table 4). The calculation of average percent residual error of the model with dive type as a fixed factor (7 %) was

lower than that of the generic dive model that combined all dives (11 %; Table 3). In contrast, the s.e.e.$_{calibration}$ % metric for the generic dive model was much lower (5 %) than the model that segregated dive types (23–32 %). This was partially because the s.e.e. calculation for the model that included dive type incorporated 3 additional error terms for each level of the fixed factor The contrast between the error metric trends highlights the importance of transparent and multiple error comparison.

Overall, both of our predictive models had substantial error in predicting AMR from ODBA in diving Steller sea lions. The average percent residual errors were similar to the ~7 % error reported for the same animals executing single dives (Fahlman et al. 2008b). It was also similar to the average percent error for equations predicting AMR from heart rate over dive bouts (9 %), but lower than the error for single dive cycles (17 %, Young et al. 2011). Our estimates of s.e.e. also showed a similar wide range and variability of error by model type for equations predicting AMR from heart rate in diving Steller sea lions (4–22 %, Young et al. 2011). Considering together, our error estimates (5–32 % range of both methods) were similar to the error estimates derived with different calculations from the doubly labeled water method in northern fur seals, *Callorhinus ursinus* (+13 to −29 %, Dalton et al. 2014), swimming California sea lions, *Zalophus californianus* (+36 to 46 %, Boyd et al. 1995), or diving grey seals, *Halichoerus grypus* (−39 to +44 %, Sparling et al. 2008).

Overall, our results provide evidence that both supports and casts doubt on an underlying biological linear relationship between ODBA and AMR in diving sea lions. The generic model (excluding dive type) found an underlying statistical relationship between AMR and ODBA across dive types, as has been found in other studies. However, the importance of dive type as an explanatory factor, the considerable error associated with the predictive equation, and the lack of statistical relationships within each dive type indicate that ODBA is not suitable for estimating AMR in diving otariids under the conditions we tested. Continued research incorporating more dives per dive type, larger sample sizes, and a greater range of diving behaviors over longer times is needed to clarify whether there is a biologically relevant relationship between ODBA and AMR in diving otariids.

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