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Transiting to depth disrupts overall dynamic body acceleration and oxygen consumption rate in freely diving Steller sea lions

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ABSTRACT: Previous research has presented contradictory evidence on the ability of overall dynamic body acceleration (ODBA) to predict mass-corrected oxygen consumption ($s\dot{V}O_2$) in air-breathing diving vertebrates. We investigated a potential source of these discrepancies by partitioning the ODBA–$s\dot{V}O_2$ relationship over 3 phases of the dive cycle (transiting to and from depth, bottom time, and post-dive surface interval). Trained Steller sea lions *Eumetopias jubatus* executed 4 types of dives to 40 m (single dives, long-duration dive bouts of 4–6 dives, short-duration dive bouts of 10 or 12 dives, and transit dives with minimal bottom duration). Partitioning single dives by dive phase showed differing patterns in the ODBA–$s\dot{V}O_2$ relationship among dive phases, but no significant linear relationships were observed. The proportion of the dive cycle spent transiting to and from the surface was a significant predictive factor in the ODBA–$s\dot{V}O_2$ relationship, while bottom duration or post-dive surface interval had no effect. ODBA only predicted $s\dot{V}O_2$ for dives when the proportion of time spent transiting was small. The apparent inability of ODBA to reliably predict $s\dot{V}O_2$ reflects differences in the inherent relationships between ODBA and $s\dot{V}O_2$ during different phases of the dive. These results support the growing body of evidence that ODBA on its own is not a reliable field predictor of energy expenditure at the level of the single dive or dive bout in air-breathing diving vertebrates likely because ODBA (a physical measure) cannot account for physiological changes in $s\dot{V}O_2$ that occur during the different phases of a dive cycle.

KEY WORDS: Diving behaviour · Metabolic rate · ODBA · Dive phase · Pinniped

INTRODUCTION

Animals must acquire sufficient energy to meet their nutritional needs and offset their costs of foraging in order to survive. The amount of prey required by marine mammals is a central concern for considerations of species conservation and resource competition with humans. Bioenergetic and ecological models that can predict required prey resources depend on reliable estimates of energy expenditure during different activities such as diving or resting (e.g. Winship et al. 2002).

A scientific standard for measuring energy expenditure in mammals is to calculate the rate of oxygen consumption ($\dot{V}O_2$) using gas respirometry (see Appendix 1 for abbreviations). Unfortunately, it is not possible to measure $\dot{V}O_2$ directly in most wild pinnipeds, with the exception of phocids that surface in ice holes (e.g. Castellini 1992). Consequently, energy expenditure in free-ranging pinnipeds has tradition-

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*Corresponding author: b.volpov@oceans.ubc.ca ally been measured indirectly using the doubly labelled water (DLW) or heart rate methods (for a review, see Butler et al. 2004). A disadvantage of the DLW method is that it only provides a mean metabolic estimate (i.e. combining activities on land, swimming, and diving) that must be acquired over a defined time interval due to the biological half-life of the chemicals used (Costa & Gales 2003, Butler et al. 2004, Sparling et al. 2008). Heart rate has been used to measure activity-specific metabolic rate in the field with reliable success (Boyd et al. 1999, Butler et al. 2004, Fahlman et al. 2004, Ponganis 2007). However, this method requires laboratory calibrations prior to field use, and presents numerous technical challenges, and the relationship between energy expenditure and oxygen consumption may be affected by specific behaviours, or be sensitive to physiological and digestive states in pinnipeds (Williams et al. 1991, Boyd et al. 1995, Webb et al. 1998, Young et al. 2011a,b).

More recently, 3-dimensional body acceleration has emerged as a potential physical proxy for energy expenditure in marine mammals (Boyd et al. 2010, Halsey et al. 2011b, Dalton et al. 2014, Ydesen et al. 2014). Common indices of 3-dimensional body acceleration include overall dynamic body acceleration (ODBA; Wilson et al. 2006) and flipper stroke frequency (Hays et al. 2004, Williams et al. 2004, Maresh et al. 2015). The use of acceleration-based variables as a proxy for energy expenditure is based on the Newtonian principle that energy is the potential to do work (King et al. 2004, Gleiss et al. 2011). In theory, more body movement should result in higher rates of energy expenditure, but the exact mechanisms of how muscular tissue is linked to metabolic energy and mechanical work are still unclear (Gleiss et al. 2011). An advantage of using data from accelerometers is that the datalogger is relatively small, inexpensive, and can be integrated into other electronic tags, such as time-depth recorders. Another advantage of using accelerometers is the potential to measure 3 variables simultaneously from one datalogger including ODBA, prey capture attempts (Viviant et al. 2010, Watanabe & Takahashi 2013, Volpov et al. 2015a), and flipper stroke rate (Hays et al. 2004, Williams et al. 2004, Maresh et al. 2015).

Applying the ODBA method requires calibration studies that are specific to each species and circumstance to determine the strength and specific nature of the relationship between ODBA and $\dot{V}O_2$. Previous calibration studies have shown mixed results that cast doubt on the ability of ODBA to predict $\dot{V}O_2$ in diving, air-breathing vertebrates. ODBA has been shown to be a good predictor of $\dot{V}O_2$ in diving Steller sea lions (Fahlman et al. 2008b, 2013) and sea turtles (Halsey et al. 2011a), and has been shown to correlate to DLW turnover in wild northern fur seals (Jeanniard du Dot et al. 2016). However, reanalysis of Fahlman et al. (2008b) has raised questions on the strength and reliability of ODBA's predictive power (Halsey et al. 2011c), and ODBA has been shown to be a poor predictor of $\dot{V}O_2$ in cormorants (Halsey et al. 2011c) and northern fur seals (Dalton et al. 2014).

A subsequent study in Steller sea lions directly tested for differences in the ODBA–$\dot{V}O_2$ relationship among single dives and 2 types of dive bouts made by animals trained to dive untethered in the open ocean (Volpov et al. 2015b). Results showed that ODBA could predict $\dot{V}O_2$ in Steller sea lions over a complete dive cycle (dives and associated surface intervals) when data from all dive types (single active dives, short-duration dive bouts, and long-duration dive bouts) were combined. However, there were no significant relationships between $\dot{V}O_2$ and ODBA when data within each dive type were analyzed separately. Volpov et al. (2015b) concluded that ODBA was not suitable for estimating $\dot{V}O_2$ in the field due to substantial error and inconclusive effects of dive type. The reason for a lack of a relationship between ODBA and $\dot{V}O_2$ in earlier studies might have been because partitioning the data set resulted in a reduced range of ODBA values or because ODBA and $\dot{V}O_2$ was averaged over a complete dive cycle.

Dive cycles consist of different 'phases' that can be broadly categorized into time spent at the surface, at depth, and transiting to and from depth. Averaging ODBA and $\dot{V}O_2$ values across different phases of a dive cycle may dilute any inherent differences within the phases, thereby lowering the overall predictive power. For example, peaks in instantaneous ODBA values (i.e. ODBA at a given point in real-time) of Steller sea lions diving to 40 m (see Fig. 4 in Volpov et al. 2015b) were generally greater than while resting at the surface, while mean ODBA values did not differ substantially. It is further hypothesized that the ODBA–$\dot{V}O_2$ relationship might differ among these phases due to differences in the type of physical activity and associated physiological adjustments. Therefore, partitioning ODBA and $\dot{V}O_2$ by dive phases may yield distinct relationships that predict $\dot{V}O_2$ better than single models fit to data averaged over the complete dive cycle.

It was also hypothesized that underlying behavioural differences in the proportion of time spent in each dive phase create differences in mean ODBA and $\dot{V}O_2$ between dive types, leading to an apparent overall statistical relationship where no underlying physio-mechanical relationship exists. Behavioural differences potentially included several factors such as differences in body movements during swimming or resting, orientation of the seals' body and flipper stroke patterns. This hypothesis would be supported if dive types (short-duration dive bout, long-duration dive bout, or single dive) differ in the proportion of time spent in each dive phase and if there is no clear ODBA–$\dot{V}O_2$ relationship within each dive phase. Finding both to be true would mean that previous 'overall' ODBA–$\dot{V}O_2$ relationships (i.e. over the dive cycle without separation by dive type) were likely due to differences in behaviour among different dive types, and not to any intrinsic relationship between ODBA and $\dot{V}O_2$ within different phases. As a consequence, the proportion of time in each dive phase should be a proportion factor in the ODBA–$\dot{V}O_2$ relationship over the dive cycle. Further research is thus needed to explicitly test the influence of dive phase on the potential ODBA–$\dot{V}O_2$ relationship.

The overall aim of our study was to investigate whether the ability of ODBA to predict $\dot{V}O_2$ in diving Steller sea lions could be improved by partitioning the data over different dive phases. There were 3 research objectives. First, we determined whether the proportion of time in each dive phase (transiting to and from depth, bottom time, and post-dive surface interval) varied among different dive types (short-duration dive bout, long-duration dive bout, or single dive). Second, our study determined whether there was an ODBA–$\dot{V}O_2$ relationship within each phase of a single dive cycle — transiting, bottom, or surface phase. Third, data from Volpov et al. (2015b) were reanalyzed to determine whether the proportion of time spent in each of the 3 dive phases could explain the poor or non-existent relationships they found between ODBA and $\dot{V}O_2$ for single dive cycles and dive bouts.

MATERIALS AND METHODS

Data were collected in 2011–2013 on 4 trained female Steller sea lions housed at the University of British Columbia's Open Water Research Station (Port Moody, BC, Canada; see Table 1). Animals were aged 11–14 yr, and were previously trained to freely dive in the open ocean. All animal work was conducted voluntarily under trainer control using positive reinforcement techniques and authorized under UBC Animal Care Permit A11-0397.

Dive behaviour and water temperature were measured with a time-depth recorder attached to a tight fitting harness worn by the sea lions (TDR, 1 Hz, 0.5 × 3.3 × 4.4 cm, SU-05272, ReefNet). Water temperature was measured to assess whether thermoregulation potentially impacted $\dot{V}O_2$, presumably if animals were outside their thermal neutral zone (TNZ). Three-dimensional body movement was measured with an accelerometer mounted between the shoulders on a harness (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). Static acceleration was calculated by smoothing each axis of acceleration with a 3-s running mean (Wilson et al. 2006, Shepard et al. 2008). Next, static acceleration was subtracted from the unsmoothed acceleration to estimate the dynamic acceleration for each axis. Finally, the absolute value of dynamic acceleration was summed across surge, sway, and heave axes to yield instantaneous ODBA at 20 Hz over the entire dive trial (Wilson et al. 2006, Shepard et al. 2008).

Rates of oxygen consumption ($\dot{V}O_2$) were measured using open-circuit gas respirometry in a 100 l dome floating at the surface of the water, as previously detailed elsewhere (Hastie et al. 2006). Air was drawn through the dome at a rate of 475 l min^{-1} (500H mass flow generator and controller, Sable Systems). Oxygen and carbon dioxide concentrations were measured from a dried subsample of the excurrent airstream (Sable FC-1B and CA-1B analyzers), averaged every 0.5 s, and recorded onto a laptop computer. Oxygen consumption rates were calculated from O_2 and CO_2 concentrations as described in Withers (1977; their Eq. 3b) using Warthog Systems Lab Analyst (M. Chappell, UC Riverside, CA, USA). There is no consensus among studies as to whether metabolic rate scales intra-specifically with body mass, and if so which exponent to employ (Schmidt-Nielsen 1975, West & Brown 2005, White & Seymour 2005, Savage et al. 2007). Given the range of body mass within and among animals over the 3-yr study (see Table 1), we employed a mass-corrected oxygen consumption (s$\dot{V}O_2$) using an exponent of 0.75.

Animals were fasted overnight prior to a trial. During diving trials, animals were fed 20 g pieces of Pacific herring *Clupea pallasii* within the respiratory dome at the surface and also through 1 or 2 PVC pipe feeding stations at 40 m, depending on trial requirements. Animals consumed 2.9 to 14.5 kg total of herring during the entire dive trial, which took approximately 45–60 min, including time spent travelling to the dive site.

Trial protocols

The present study combined original data from previously published research (see Table 2) (Goundie et al. 2015, Volpov et al. 2015b). The metabolic cost of resting inactive at the surface (MRs) was calculated from a period of stable rate of oxygen consumption (2.0 ± 0.5 minutes) while animals were calmly floating at the surface immediately prior to the first dive of each trial. For all dive types, post-dive $s\dot{V}O_2$ was measured until $s\dot{V}O_2$ returned to within 5% of pre-dive levels (MRs) for that specific trial.

Overall, there were 5 different dive types used in our study, with all dives to 40 m depth (Fig. 1). Transit dives occurred when the sea lions went directly to and from a single feeding station with a goal of no bottom time. Transit dives included primarily only ascent and descent with minimal (<10 s) bottom duration (Fig. 1A, see below for $s\dot{V}O_2$ calculations and details). For single stationary dives — designed to limit movement at depth — sea lions dove to a single feeding station, where they remained for the entire bottom time (Fig. 1B). Single active dives occurred when sea lions dove to 2 feeding stations spaced ~9 m apart that were designed to increase physical movement at depth and simulate more natural foraging behaviour by having the sea lions constantly swim between stations (Fig. 1B). Both types of single dives had a total dive (submergence) duration goal of ~4–6 min. Single dives were defined as a single submergence event followed by complete metabolic recovery at the surface (defined below). In comparison, dive bouts are a series of dives, with inter-dive surface intervals too short for complete $s\dot{V}O_2$ recovery, followed by a final recovery surface interval. For this study, both short-duration and long-duration dive bouts were used. Short-duration dive bouts included 10 or 12 dives per bout with 1–2 min dive duration goal per dive (Fig. 1C). Long-duration dive bouts included 4–6 dives per bout with 4–6 min dive duration goal per dive (Fig. 1D; both dive bouts originally presented in Volpov et al. 2015b). Long- versus short-duration dive bouts refers to the duration of individual dives within a dive bout, and not to the cumulative duration of a

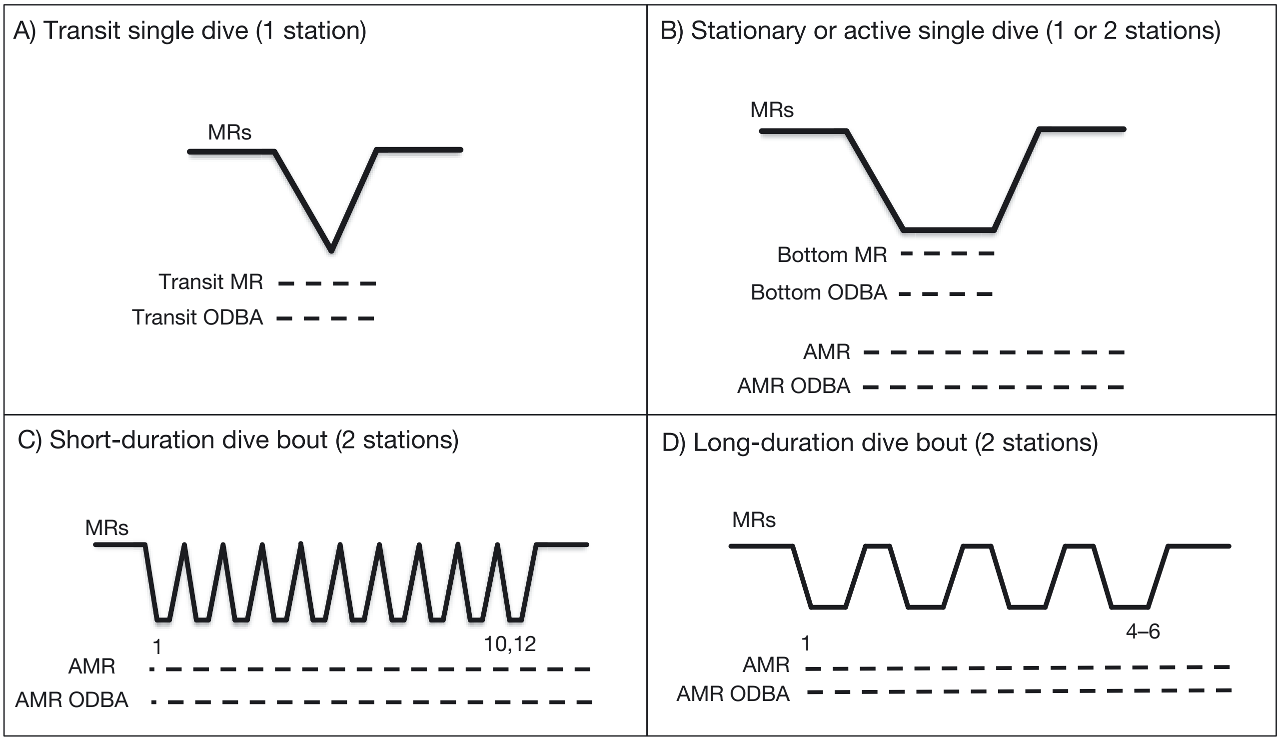

Fig. 1. Schematic of trial types executed by trained Steller sea lions diving to 40 m depth. Trial types included resting at the surface prior to diving (MRs, A–D), single dives with 1 feeding station (stationary, B), single dives with 2 feeding stations (active, B), transit dives with minimal bottom duration (A), short-duration bouts with an individual dive duration goal of 1–2 min dive duration (10, 12 dives per bout, C), and long-duration bouts with an individual dive duration goal of 4–6 min (4–6 dives per bout, D). Transit dives (i.e. bounce dives) included primarily only ascent and descent with minimal (<10 s) bottom duration (A). Active dives included 2 feeding stations, and stationary dives and transit dives included 1 feeding station (B). MRs was measured before each trial. Overall dynamic body acceleration (ODBA) and mass-corrected oxygen consumption rate ($s\dot{V}O_2$) were averaged over corresponding dive phases as indicated by dashed lines. AMR: average metabolic rate

dive bout or the number of dives per bout (Table 2, Fig. 1). Both dive bout types were behaviourally controlled by the trainers to have similar cumulative dive (submergence) durations (19–20 min) and only differ in the number of dives per bout and individual dive durations. Each animal completed multiple replicates of each dive type (see Table 1).

Mass-corrected metabolic rate ($s\dot{V}O_2$) for each dive type was calculated as described below and in Fig. 1. Metabolic rates for the transit dives were calculated as the increase in oxygen consumption above MRs divided by submergence duration (transit MR; Fig. 1A). Mean cost of transit was calculated as the mean $s\dot{V}O_2$ for all transit dives for that animal only. Bottom MR for each single dive was calculated by subtracting the mean cost of transit (calculated from all transit dives) per animal from the total cost of that individual dive (submerged portion only, not dive cycle; see Eq. 1 in Goundie et al. 2015). This allowed the separate cost of the bottom portion of the dive to be calculated for all of the single dives per animal (Fig. 1B). In estimating the metabolic cost of each dive phase, we assumed that metabolic rate for each phase was consistent across different dive types within the same animal (see Goundie et al. 2015).

A dive cycle (for either single dives or dive bouts) started from the beginning of the first dive and continued until the $s\dot{V}O_2$ during the post-dive surface interval returned to within 5% of pre-dive MRs (when the sea lion's gas balance was deemed to have recovered to pre-dive levels). Average metabolic rate (AMR) for single dives was calculated as the total oxygen consumption post-dive divided by the duration of the dive cycle from the start of dive until post-dive surface interval $s\dot{V}O_2$ was within 5% of MRs (i.e. over a dive cycle with all dive cycles combined; Fig. 1B). AMR for dive bouts was calculated as the total volume of oxygen consumed for the entire dive bout divided by the total dive bout duration that included cumulative dive duration, inter-dive surface intervals, and final post-dive surface interval until recovery (i.e. all dives + all surface intervals; Fig. 1C,D).

For single dives only, the linear relationship between ODBA and $s\dot{V}O_2$ was tested separately within each dive phase. Matching mean ODBA measures for each dive phase were obtained directly from all single dives by partitioning the instantaneous ODBA accordingly between phases with the aid of TDR data. The precise start and end times for the dive descent, bottom phase, and ascent were extracted from the TDR, and the post-dive surface interval duration was defined to match that used for the metabolic analysis. Graphs of the raw surge (forward) acceleration verses depth verified time alignment of dataloggers, including alignment of specific dive phases for all trials. Instantaneous ODBA was averaged over each time period for each individual dive or each dive bout and matched to the corresponding $s\dot{V}O_2$ measurement (i.e. ODBA and $s\dot{V}O_2$ were always calculated over the same time periods; Fig. 1). For example, instantaneous ODBA for a transit dive only was averaged from the start of the dive until the animal reached the surface (i.e. submergence only; Fig. 1A). Instantaneous ODBA was averaged over the bottom phase only to yield bottom ODBA, and instantaneous ODBA was separately averaged over the dive cycle to obtain AMR ODBA. There were no transit dives from animal F00BO in this analysis because the accelerometer malfunctioned on these dives, making it impossible to calculate bottom MR for this animal (transit MR and bottom MR was only calculated if transit dives were available for that specific animal). There was only 1 transit dive for F97YA, but we felt this was sufficient to calculate transit MR and, subsequently, bottom MR.

Statistical analysis

Although there were 5 dive types in total, each research objective only used a subset of relevant dive types (i.e. all 5 dive types were not tested together simultaneously). First, we tested whether the proportion of time spent in each dive phase (transit duration, bottom duration, and post-dive surface interval duration) varied among different dive types with each dive phase tested separately. This is because if the proportion of time spent in each dive phase did not differ between dive types, then it would not explain why dive type was a model variable in our previous analyses. For this first analysis, dive type was tested as a fixed factor with 3 levels (single dives with active and stationary combined into 1 dive type, short-duration bouts, or long-duration bouts). Second, the present study determined whether there are predictive ODBA–$s\dot{V}O_2$ relationships when a single dive cycle is partitioned into dive phases. This second analysis used single stationary dives, single active dives, and transit dives. Activity level (stationary versus active) was tested as an additional fixed factor for the relationship over the bottom phase and over the dive cycle.

Third, our study investigated whether the proportion of time spent in each dive phase could explain the poor ODBA–$\dot{V}O_2$ relationship over the dive cycle in both single dives and dive bouts by re-analyzing data from Volpov et al. (2015b). This new analysis expanded on previous research by testing the proportion of the dive cycle in each dive phase as a fixed factor with all dive types from Volpov et al. (2015b) combined (single active dives, long-duration bouts, and short-duration bouts). Unfortunately, it was not possible to directly compare the predictive strengths of dive type versus dive phase proportion as fixed factors because preliminary analysis revealed that time in each dive phase differed significantly among dive types (therefore the 2 factors were confounded). For this third analysis, the fixed factor of the proportion of time in each dive phase was grouped into 3 categorical levels using the minimum value, lower quartile (Q1), upper quartile (Q3), and maximum value as divisors (i.e. the 3 levels: minimum value to <Q1, ≤Q1 to <Q3, ≥Q3 to maximum value; see Table 4). For example, the fixed factor of the proportion of the dive cycle spent transiting had 3 levels defined as 4.6 to <7.4 %, ≥7.4 to <15.7 %, and ≥15.7 to 34.5 % transit; see Table 4). Cumulative food consumed per trial (from start of boat loading until end of dive trial) was also tested as a categorical factor on all models for all research objectives with food grouped by quartiles (see Table 4).

Data were analyzed with linear mixed-effects models (LME; lme package, Pinheiro & Bates 2000, Zuur et al. 2009), which accounted for repeated measures within and among animals in R version 2.6.1 and 3.1.2 (Gałecki & Burzykowski 2013, R Core Development Team 2015). Animal ID was treated as a random effect, which potentially allowed inferences from the sample population to be applied to the wild population (Pinheiro & Bates 2000, Zuur et al. 2009). Hierarchically nested LME models were compared using likelihood ratio tests (LRT) with the fixed effect model nested within the model without any fixed effects (null model). A stepwise model comparison approach was employed to select whether inclusion of specific predictive factors was better than the simpler model (including the null model with no fixed factors). Tukey post hoc tests with Bonferroni-adjusted p-values compared the means between multiple levels within significant fixed factors (mvtnorm and multcomp; R libraries). To compare the means among groups without testing for a linear relationship, LMEs with a categorical dependent variable were used (i.e. analogous to a repeated-measures ANOVA with a random factor added). All means are reported ±SD and significance was set at $\alpha = 0.05$. All models were tested for normally distributed errors, homogeneity of the variance, and normality using the methods described in Pinheiro & Bates (2000) and Zuur et al. (2009), and met the assumptions of LMEs.

RESULTS

Dive characteristics

Sample sizes for dive types are presented in Table 1. The dive characteristics — such as dive duration, surface interval, and recovery time — for each of the dive types used in our study (transit dives, stationary and active single dives, short and long dive bouts) are presented in Table 2. Mean dive duration did not significantly differ between active single dives (2 feeding stations) and stationary single dives (1 feeding station; 4.2 ± 0.77 versus 3.8 ± 0.12 min, LRT = 1.89, p = 0.17). However, mean bottom duration was significantly longer in the active compared with the stationary dives (3.5 ± 0.73 versus 2.9 ± 0.11 min, LRT = 6.60, p = 0.01). Despite this difference, post-dive surface interval duration was also similar between active and stationary single dives (6.0 versus 6.4 min, LRT = 0.02, p = 0.87).

Table 1. Animal ID, age, and body mass at the start of trials, mass deviation during trials (±SD), and number of dives per trial type (n = 90 dives total, n = 57 MRs total) for 4 adult female Steller sea lions. Trial types included resting at the surface prior to diving (MRs), single dives with 1 feeding station (stationary), single dives with 2 feeding stations (active), transit dives with minimal bottom duration (i.e. ascent and descent only), short-duration bouts (10–12 dives per bout), and long-duration bouts (4–6 dives per bout)

Animal ID	Age (yr)	Mass (kg) Mean	Mass (kg) ±SD	Trial type: Resting at surface (MRs)	Single dive (stationary)	Single dive (active)	Transit single dive	Short-duration bout	Long-duration bout
F97SI	14	220	14.2	17	3	7	3	4	8
F97HA	14	168	3.7	13	3	7	3	4	5
F00BO	11	148	5.4	15	3	7	0	5	9
F97YA	11	207	5.4	12	3	6	1	2	7
Total				57	12	27	7	15	29

Table 2. Summary of dive characteristics for dives executed by Steller sea lions diving in the open ocean to 40 m. Trial type, number of feeding stations, number of dives per trial type, dive durations (dur.), bottom phase durations, and surface durations are presented (means ± SD are shown). Dive durations are submergence time only and were cumulative over bouts. Surface intervals (SI) for single dives and dive bouts are also described. Dive types are described in Fig. 1. Ind. dive: mean dive duration for dives within a dive bout or single dive durations as appropriate; Ind. SI: mean surface intervals within a dive bout; Final SI: the final post-dive recovery period only; Cumulative SI: sum of individual SI and final SI for a dive bout; NA: not applicable

Trial type	Feeding stations	No. dives	Mean dive duration (min)				Mean surface duration (SI, min)			Source
			Ind. dive	Cumulative dive	Cumulative bottom	Dive bout or single dive cycles	Ind. SI	Final SI	Cumulative SI	
Resting at surface (MRs)	NA	NA	NA	NA	NA	NA	2.1 ± 0.5	NA	NA	Volpov et al. (2015b); Goundie et al. (2015)
Transit single dive	1	1	0.8 ± 0.1	NA	0.10 ± 0.1	6.0 ± 1.9	NA	5.1 ± 1.9	NA	Goundie et al. (2015)
Single dive (stationary)	1	1	3.8 ± 0.1	NA	2.9 ± 0.1	10.3 ± 1.6	NA	6.4 ± 1.6	NA	Goundie et al. (2015)
Single dive (active)	2	1	4.2 ± 0.8	NA	3.5 ± 0.7	10.2 ± 1.4	NA	6.0 ± 1.0	NA	Volpov et al. (2015b); Goundie et al. (2015)
Short-dur. dive bout	2	10, 12	1.6 ± 0.3	18.7 ± 1.7	9.5 ± 1.6	30.3 ± 2.4	0.6 ± 0.10	4.7 ± 1.0	11.7 ± 1.2	Volpov et al. (2015b)
Long-dur. dive bout	2	4-6	4.6 ± 1.1	19.5 ± 3.4	15.7 ± 4.4	33.3 ± 5.9	2.6 ± 0.8	5.5 ± 0.9	13.9 ± 2.9	Volpov et al. (2015b)

Transit dives were experimentally designed to have minimal bottom duration through the use of trainer behavioural control and positive reinforcement. Mean dive duration for the transit dives was only 0.8 min, with a bottom duration of only 0.10 ± 0.1 min (Table 2), which was significantly lower than for single stationary dives (LRT = 100.47, $p < 0.0001$) or single active dives (LRT = 60.16, $p < 0.0001$). As previously noted, the short- and long-duration bouts differed in the number of dives per bout and individual dive durations, but intentionally had similar cumulative dive durations (19–20 min) and cycle durations (30–33 min; Table 2). The design of similar cumulative dive durations allowed us to focus on differences due to number of dives per bout or individual interbout dive durations. While cumulative dive times were similar, the long-duration bouts had significantly greater cumulative bottom duration (15.7 ± 4.4 min) compared with the short-duration bouts (9.5 ± 1.6 min, LRT = 25.0, $p < 0.0001$), which was a result of differences in time spent transiting.

Mean water temperature at depth was 7.9 ± 1.8°C and ranged from 6.0 to 16.4°C. The TNZ has not been measured on Steller sea lions, but the TNZ for the sympatric California sea lion has been shown to be 6.4–22.4°C resting or swimming in a pool (Liwanag et al. 2009). Additionally, 93% of all mean temperatures per dive trial were greater than 6.4°C. Consequently, it is unlikely that water temperature affected the present study's results.

Cumulative food fed per trial ranged from 2.9 to 13.5 kg (mean = 7.0 kg). The wide range of food fed during trials was a result of the positive reinforcement and trainer control used to elicit the 4 different dive types, and the varying duration of dives themselves. Cumulative food fed was not a significant factor in any of the models presented below. Consequently, the short duration of the trials (<60 min) coupled with the fact that animals did not consume bulk meals and that sea lions can potentially partially defer digestion while diving (Rosen et al. 2015), all suggest that the heat increment of feeding (HIF; Rosen & Trites 1997) did not confound our study results (see 'Discussion' for more details).

Mean proportion of time in each dive phase for single dives and dive bouts

Our study investigated whether the proportion of time spent in each dive phase varied among single dives, short-duration bouts, or long-duration bouts by comparing the mean proportions within each dive type (i.e. we were comparing mean proportions only, not testing for linear relationships). Overall, the proportion of time spent in each dive phase significantly differed among single active dives, long-duration bouts, and short-duration bouts for the transit phase (LRT = 182.85, $p < 0.0001$; Fig. 2A, see Table 1 for sample sizes), bottom phase (LRT = 49.35, $p < 0.0001$; Fig. 2B), and post-dive surface phase (LRT = 129.89, $p < 0.0001$; Fig. 2C).

Post hoc Tukey tests showed that the mean proportion of the dive cycle spent in the transit phase significantly varied among all 3 dive types (Tukey, $p < 0.001$ for all comparisons), such that short-duration bouts had the greatest proportion of the dive cycle spent transiting (29.0 ± 2.9%), followed by long-duration bouts (10.5 ± 3.2%) and single dives (7.5 ± 1.6%; Fig. 2A). The proportion of the dive cycle spent in the bottom phase was significantly greater for long-duration bouts (47.0 ± 4.7% Tukey, $p < 0.001$) than for single dives or short-duration bouts (31.3 ± 4.7%, 34.3 ± 4.3% respectively, Tukey, $p = 0.53$; Fig. 2B). The proportion of the dive cycle spent at the surface during the post-dive surface interval differed significantly among all 3 dive types (Tukey, short versus long: $p < 0.03$, single versus long: $p < 0.001$, single versus short: $p < 0.001$; Fig. 2C). The proportion was greatest for single dives (58.3 ± 4.6%), followed by long-duration bouts (41.6 ± 3.6%) and then short-duration dive bouts (38.4 ± 2.7%). Overall, the significant differences in the proportion of time spent in each dive phase provided initial evidence that dive phase may impact the overall ODBA–$s\dot{V}O_2$ relationship over the dive cycle, and thus provided justification to investigate the relationship in more detail.

Partitioning ODBA–$s\dot{V}O_2$ into dive phases for single dive cycles

Mean ODBA significantly differed among dive phases in single dives including MRs, transit, and bottom phases (LRT = 66.59, $p < 0.001$; Table 3, Fig. 3, see Table 1 for sample sizes). Mean $s\dot{V}O_2$ also differed among these 3 dive phases (LRT = 60.52, $p < 0.0001$; Table 3). Mean ODBA and $s\dot{V}O_2$ across the entire dive cycle also significantly differed from any of its component dive phases (i.e. MRs, transit, bottom, dive cycle; LRT ODBA = 85.46, $p < 0.0001$; LRT $s\dot{V}O_2 = 60.52$, $p < 0.0001$).

For single dives, there were no significant linear relationships between ODBA and $s\dot{V}O_2$ for the transit phase (Fig. 3A), bottom phase (Fig. 3B), post-dive surface phase (Fig. 3C), or over the complete single dive cycle (Fig. 3D), all due to non-significant slopes (i.e. slopes were not different from zero). Level of activity (active or stationary) was not a significant explanatory factor in the predictive analyses for either the bottom phase or the complete dive cycle (LRT = 2.13, $p = 0.71$), so that data for single dives with 1 feeding station (stationary) were combined with single dives with 2 feeding stations (active) for all subsequent analyses.

Although there were no significant linear relationships, partitioning single dives by dive phase clearly showed differing patterns in the plots of ODBA–$s\dot{V}O_2$ among dive phases (Fig. 3). Notably, during the post-dive surface phase, $s\dot{V}O_2$ displayed a relatively low range in values (28–50 ml O_2 min^{-1} $kg^{-0.75}$), while the range in ODBA was large (0.08–0.35 *g*; Fig. 3, Table 3). In contrast, the transit phase of the dive was characterized by large ranges in $s\dot{V}O_2$ (22–148 ml O_2 min^{-1} $kg^{-0.75}$), but small ranges in ODBA (0.24–0.32 *g*). The large variation in transit MR values were not clustered by animal, and were also not likely influenced by date-specific environmental variables as all transit dives per animal were collected on the same date.

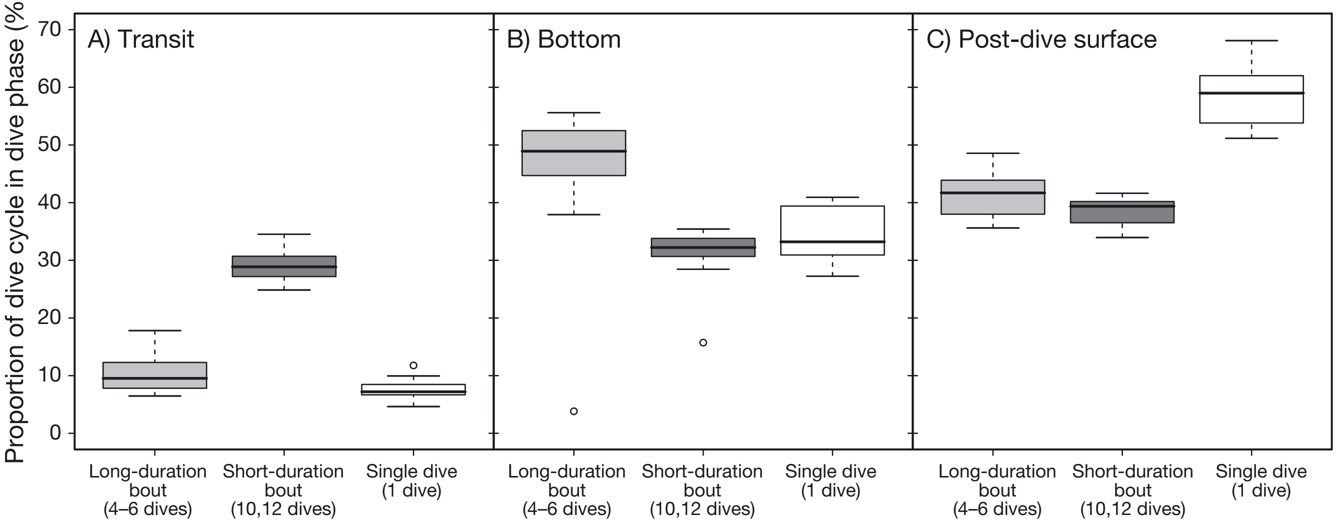

Fig. 2. Mean proportion of time spent by the Steller sea lions in each dive phase for single dives (active and stationary combined) and both types of dive bouts. The proportion of the dive cycle spent in each dive phase significantly differed among single dives, short-duration bouts, and long-duration bouts for (A) transit, (B) bottom, and (C) post-dive surface interval phases. See Table 1 for sample sizes per dive type. Box plots show the median, minimum, maximum, and quartiles of each dive type

Table 3. Summary of mean ± SD oxygen consumption (s$\dot{V}O_2$; ml O_2 min^{-1} kg$^{-0.75}$) and overall dynamic body acceleration (ODBA; *g*) across dive phases for single dives executed by 4 Steller sea lions. Single dives with 1 feeding station (stationary) were combined with single dives with 2 feeding stations (active) because they were not statistically different. NA; not applicable

Dive phase	Dive type	s$\dot{V}O_2$	ODBA	Figure
Resting at surface (MRs)	NA	36.4 ± 4.6	0.15 ± 0.06	Fig. 3A
Transit	Single	73.1 ± 40.8	0.29 ± 0.03	Fig. 3B
Bottom (active + stationary)	Single	46.9 ± 13.8	0.34 ± 0.14	Fig. 3C
Dive cycle (active + stationary)	Single	41.8 ± 3.5	0.28 ± 0.07	Fig. 3D

The pattern of ODBA over the bottom phase of single dives showed an apparent bimodal split at ~0.2–0.3 *g* ODBA, but adding binned bottom duration as a fixed factor did not yield a linear relationship over the bottom phase (LRT = 0.31, p = 0.98; Fig. 3). Additionally, the bimodal pattern could not be attributed to individual animal or active versus stationary dive types. It remains unclear what underlying mechanism was contributing to this bimodal split of ODBA.

Proportion of time in each dive phase as a fixed factor for single dives and dive bouts

Based on differences in proportion of time spent in each phase (Fig. 2) and the ODBA and s$\dot{V}O_2$ trends within each dive phase (Fig. 3), the present study investigated whether accounting for the proportion of time spent in each dive phase could be used to develop a predictive ODBA–s$\dot{V}O_2$ equation. Specifically, the present study tested whether categorizing all dive types by the proportion of time spent in a given dive phase (separately for transit, bottom, post-dive surface phases) would result in significant predictive ODBA–s$\dot{V}O_2$ relationships compared with when all dives were separated only by dive type (single dives, long-duration bouts, and short-duration bouts).

As previously noted, the proportions of time in each dive phase were grouped into categorical fixed fac-

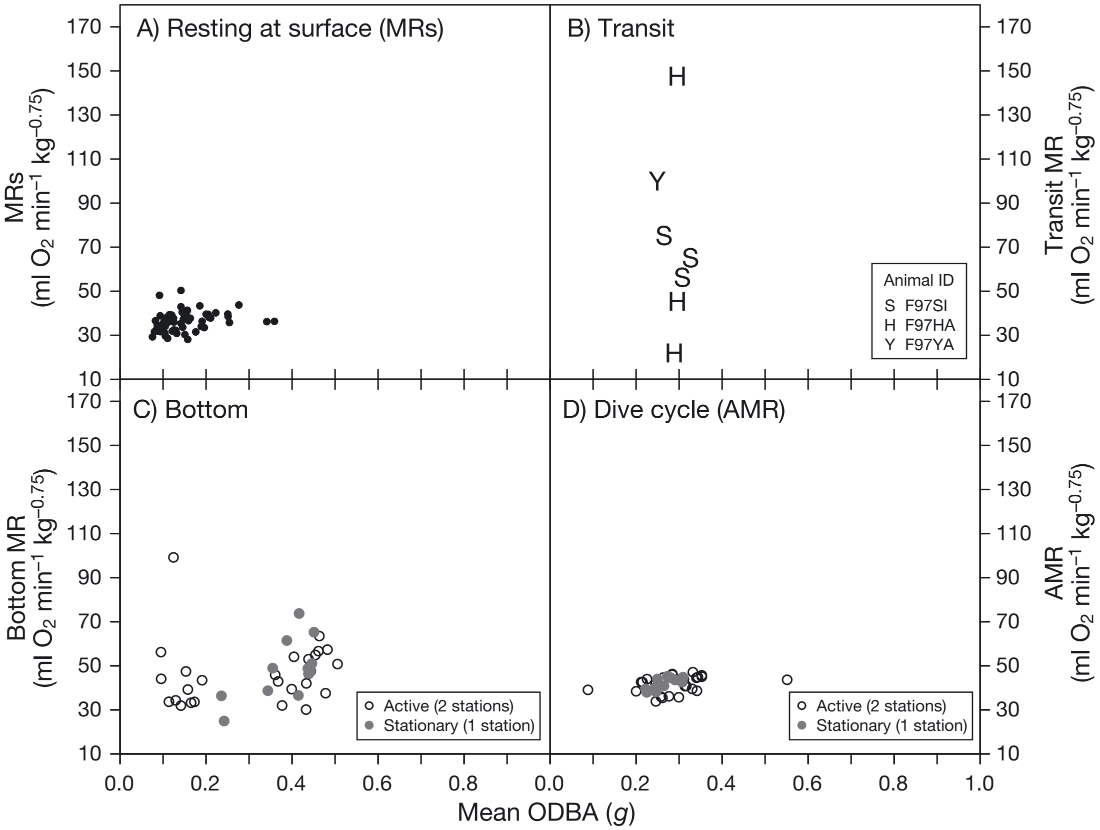

Fig. 3. Relationship between overall dynamic body acceleration (ODBA) and mass-corrected metabolic rates (s$\dot{V}O_2$) calculated for each dive phase of a single dive for Steller sea lions (A) resting on the surface, (B) transiting to or from depth, (C) over the bottom phase of the dive, and (D) over the dive cycle. Partitioning the ODBA–s$\dot{V}O_2$ relationship into dive phases for single dives showed no significant linear relationships for any dive phase, and active dives did not differ from stationary dives (C,D). See Fig. 1 for description of different metabolic rates

Table 4. Summary of the quartiles used to group the food consumed and the percent of time spent by the Steller sea lions in each dive phase. Percent of time in each dive phase (transit, post-dive surface interval, or bottom) was grouped into categorical fixed factors based on the range and lower (Q1) and upper (Q3) quartiles of each variable. For each fixed factor tested, the groups were set at <Q1, ≥Q1 to <Q3, and ≥Q3. Cumulative food fed was also tested as a fixed factor grouped by quartiles for Figs. 2 to 4. The cumulative food consumed per trial differed among dive trials, as indicated by the individual lines in the table

Fixed factor	Min	Q1	Q3	Max	Figure
Cumulative food consumed (kg)	5.0	6.3	7.6	13.5	Figs. 2,4
Cumulative food consumed (kg)	2.9	5.5	7.0	13.5	Fig. 3
Transit (%)	4.6	7.4	15.7	34.5	Fig. 4A
Post-dive surface interval (%)	34.0	39.5	55.4	68.1	Fig. 4B
Bottom (%)	31.7	31.7	48.0	55.6	Fig. 4C

tors based on quartiles (Table 4). All of the panels in Fig. 4 are the identical data points of the same dives, but each panel is coded in greyscale differently by the fixed factor of interest (1 data point for each dive). The null model (i.e. generic model of all data points the same and with no fixed factors) was the same for all panels in Fig. 4 and was significantly linear (ANOVA, slope: $p = 0.0013$, intercept: $p < 0.001$). For comparison, Fig. 4D illustrates dive type as a fixed factor (Volpov et al. 2015b). Volpov et al. (2015b) showed inconclusive results of whether dive type was a meaningful factor and concluded that ODBA was an unreliable predictor of $s\dot{V}O_2$. Consequently, LME model lines were not plotted in Fig. 4D for comparison with the current data, but are available elsewhere (see Figs. 2b,c in Volpov et al. 2015b).

Only the proportion of time in the transit phase was a significant predictive factor in the overall ODBA–$s\dot{V}O_2$ relationship over a dive cycle; neither post-dive surface interval nor bottom phase proportion significantly impacted the relationship as fixed factors. When the data were examined for each level of transit (%) separately, the

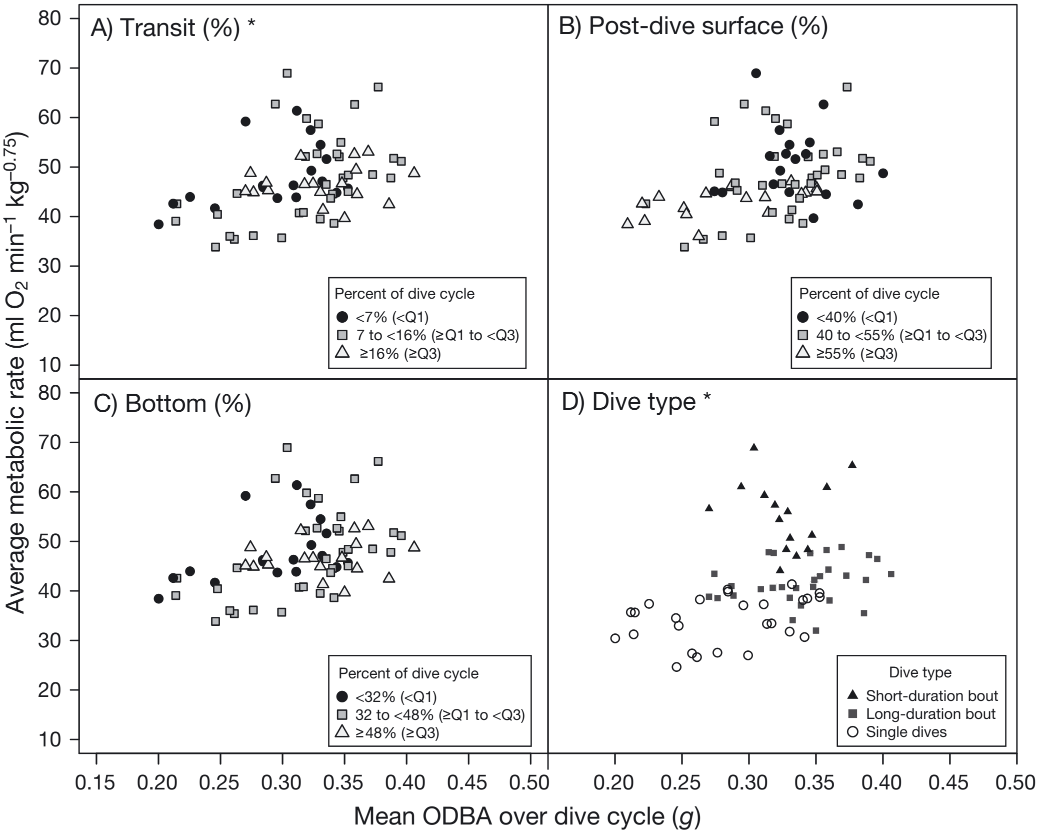

Fig. 4. Relationship between overall dynamic body acceleration (ODBA) and average metabolic rate (AMR) while Steller sea lions were executing single active dives, short-duration bouts, or long-duration bouts. The percentages of time in each dive phase (transit, post-dive surface, or bottom) were grouped into categorical fixed factors based on quartiles (Table 4). The proportion of time in the transit phase (A) was a significant predictive factor (*), but neither post-dive surface interval (B) nor bottom phase proportion (C) significantly impacted AMR. Each panel shows the same data points with different fixed effects tested within LME models. (D) Dive type as a significant (*) fixed factor; plotted from Volpov et al. (2015b) for comparison

ODBA–s$\dot{V}O_2$ relationship was significantly linear only within the <7% transit category (slope p = 0.004). The relationship was not significantly linear for dives with ≥7 to <16% transit (slope p = 0.08) or for dives with ≥16% transit (slope p = 0.08; Fig. 4A). The levels for post-dive surface intervals or bottom phase were not examined separately because the fixed factor was not significant for these variables.

DISCUSSION

Measuring the level of physical activity (e.g. ODBA) has been proposed as a means of estimating energy expenditure in pinnipeds, such as Steller sea lions. However, previous ODBA–$\dot{V}O_2$ calibration experiments on Steller sea lions freely diving in the open ocean (Fahlman et al. 2008b, 2013, Volpov et al. 2015b) investigated the relationship over the entire dive or dive cycle with inconclusive results (Halsey et al. 2011c). Our study investigated whether the mixed results in the ability of ODBA to reliably predict s$\dot{V}O_2$ and the apparent effect of dive type in Steller sea lions was due to different inherent relationships between dive type and dive phases of a dive cycle. Results showed that the relationship between ODBA and s$\dot{V}O_2$ differed across the 3 dive phases (transiting to and from depth, bottom time, and post-dive surface interval), but the relationship was not statistically linear in any individual phase (Fig. 3).

Results also showed that the time spent in different phases differed among dive types (i.e. single dives, long-duration dive bouts of 4–6 dives, short-duration dive bouts of 10–12 dives, and transit dives with minimal bottom duration; Fig. 2), and that these differences significantly impacted the ODBA–s$\dot{V}O_2$ relationship over the dive cycle (Fig. 4). The variable that had the greatest effect on the ODBA–s$\dot{V}O_2$ relationship over the dive cycle was the proportion of time spent transiting to or from depth, such that the ability of ODBA to predict s$\dot{V}O_2$ held only for dives with minimal transiting time. However, even this relationship was potentially limited by the small sample size of transit dives.

Proportion of time spent per dive phase differs among dive types

The hypothesis that the previously reported differences in the ODBA–s$\dot{V}O_2$ relationship among dive types was due to differences in the characteristics of these dives was dependent on the supposition that the experimental dive types did, in fact, differ in such behaviours. Our findings are consistent with this. Our results show that the proportion of time spent in each dive phase was key to whether there was a significant ODBA–s$\dot{V}O_2$ relationship, and that other studies had not accounted for this. In our case, the 3 dive types differed in the proportion of time spent in each of the dive phases (Fig. 2), which suggests that dive phase may impact the overall ODBA–s$\dot{V}O_2$ relationship over a dive cycle. Such findings warranted further investigation into the ODBA–s$\dot{V}O_2$ relationship within individual phases of a complete dive cycle to examine its potential effect on the overall predictive relationship.

Partitioning ODBA–s$\dot{V}O_2$ by dive phase shows divergent patterns

ODBA may have been a poor predictor of s$\dot{V}O_2$ if the range of ODBA values used in our regression model was too narrow. Previous research suggests that calculating an average ODBA over a dive cycle reduces the range of ODBA values (Volpov et al. 2015b). However, the range of our values of average ODBA for sea lions diving to 1 or 2 feeding stations (0.07–0.55 *g*, all dive types) was wider than in previous studies for the same animals that used either 1 feeding station (~0.15–0.40 *g*, Fahlman et al. 2008b, ~0.11–0.45 *g*, Fahlman et al. 2013) or 2 feeding stations (0.20–0.41 *g*, Volpov et al. 2015b). The wide range in ODBA values was also apparent when calculated over the dive cycle for single dives (range = 0.09–0.55 *g*; Fig. 3C). Thus, it seems unlikely that the range of measured ODBA values was too narrow to predict s$\dot{V}O_2$ if a relationship actually existed between the 2.

A second feeding station was added to increase the physical movement of the sea lions and increase the range of ODBA during the bottom phase of their dives. However, sea lions unexpectedly had lower ODBA values when foraging between 2 feeding stations than while feeding at a single station (Fig. 3). Anecdotal evidence from a video camera mounted at depth showed that the sea lions occasionally made tight circles around a single feeding station, which would have potentially increased activity and energetic costs for dives that were designed to be mostly stationary (Wilson et al. 2013). However, the number of feeding tubes was not a significant factor in the LME models, indicating that potential differences between active and stationary dives did not impact our results. Additional research with a larger sample size is needed to fully explore the effect of the level and type of movement at depth on ODBA.

ODBA was unable to predict $s\dot{V}O_2$ during the bottom portion of dives. This was due in large part to the sea lions producing a wide range of ODBA values during the bottom phase of the dive that were associated with only a small range of $s\dot{V}O_2$ values. There was also a similar (but inverse) disconnect between ODBA and $s\dot{V}O_2$ when the sea lions were resting at the surface. In contrast to the transit phases of the dives, the surface and bottom phases of the different dives displayed a wide range of ODBA values associated with a narrow range of $s\dot{V}O_2$ measurements. Despite the dive type name, none of the sea lions appeared to exert themselves during the transit portions of the dives (i.e. transit dives were 'easier' for the animals relative to the other dive types tested). Their times to descend and ascend were consistent among all dive types (range ~20–35 s each) and varied little (descent mean = 21 ± 4 s, ascent mean = 24 ± 5 s). Mean speeds of descent (1.90 m s^{-1}) and ascent (1.67 m s^{-1}) in our study were all within the range of mean transit speeds observed in wild New Zealand sea lions *Phocarctos hookeri* and Galapagos sea lions *Zalophus wollebaeki* (1.24–1.99 m s^{-1}, Crocker et al. 2001, Villegas-Amtmann et al. 2008), indicating that the physical activity pattern for transiting in the present study was likely comparable to that in wild otariids. The stereotypical physical movement of the sea lions in the present study during transiting likely led to their ODBA values consistently falling within a narrow range (Fig. 3B).

A previous study (Fahlman et al. 2008b) with the same Steller sea lions examined the transiting phase in more detail and also found very stereotypical transiting patterns. Fahlman et al. (2008b) found that ODBA on descent was only high in the first 5 m (indicating active swimming) and decreased with depth. In contrast, ODBA on ascent was higher and more variable, indicating more active swimming. These behavioural differences observed in Fahlman et al. (2008b) translated into differences in ODBA, which was 0.131 *g* during the descent phase and 0.353 *g* during the ascent, which would yield an average value similar to the transit dives reported in our study (0.29 *g*; Table 3).

While stereotypic movement may explain the consistent ODBA values during the transit phases of all dives, it does not explain the wide range of associated $s\dot{V}O_2$ values. We hypothesize that the pattern of variation in $s\dot{V}O_2$ with little variation in ODBA that occurred while transiting most likely reflects differences in the degree of metabolic suppression the sea lions experienced among dive types. Although not specifically analyzed in our study, previous studies have shown that $\dot{V}O_2$ decreases with dive duration (Fahlman et al. 2008a, Hindle et al. 2010). Therefore, the sea lions in our study may have exhibited greater metabolic suppression for comparatively longer single dives than shorter transit dives, resulting in a wider range of $s\dot{V}O_2$ without corresponding changes in ODBA. The observation that ODBA remains mostly constant during extreme changes in $s\dot{V}O_2$ during transit dives further highlights how ODBA may be unable to account for physiological changes that occur during diving.

Although there were no linear relationships between ODBA and $s\dot{V}O_2$ within each dive phase (Fig. 3), the differing patterns in these measures among dive phases provides valuable clues as to why ODBA overall is a poor predictor of energy expenditure over a complete dive cycle. A complete dive cycle is made up of 3 phases — each with apparent divergent patterns in the $s\dot{V}O_2$ and ODBA relationship, as well as different mean values for both ODBA and $s\dot{V}O_2$. Calculating ODBA over a complete dive cycle essentially 'averages' these different relationships, which potentially explains the absence of any overall ODBA–$s\dot{V}O_2$ relationship over the course of a dive cycle.

Proportion of time spent transiting disrupts ODBA–$s\dot{V}O_2$ over the dive cycle

The absence of a relationship between ODBA and $s\dot{V}O_2$ due to the lack of relationships within each phase of a dive (Fig. 3) does not explain why the relationship differed among experimental dive types in the Volpov et al. (2015b) study that showed dive type as a significant factor in the predictive relationship. We now suspect that this result may be due to the fact that dive types differ in the proportion of time spent in each phase of the dive, and that each phase differs in its average ODBA and $s\dot{V}O_2$. We tested this by re-examining all dive types together and setting the proportion of dive phase as a categorical factor, and found that the proportion of time spent transiting was an important factor when all experimental dive types were considered together (Fig. 4A). However, examining each category of transiting (i.e. <7 %, ≥7–<16 %, or ≥16 %) separately revealed only 1 statistically linear relationship for dives that have <7 % of the dive cycle spent transiting, but none for dives with a greater transiting proportion (Fig. 4A). This is important because it suggests that dive types that have proportionally more transiting, such as short-duration bouts (29.0%), would be less likely to have linear ODBA–$s\dot{V}O_2$ relationships compared with long-duration bouts (10.5%) or single dives (7.5%; Fig. 2). This is especially relevant when free-ranging populations are considered, given that the experimental dives with poorest predictive power due to a higher proportion of time spent transiting (short-duration dive bouts) are most similar to those dive durations observed in free-ranging populations (92–89% of dives are <4.0 min and <50 m; Merrick & Loughlin 1997).

ODBA is a poor predictor of $s\dot{V}O_2$: physiological and physical explanations

The potential link between physical activity and energy expenditure is complicated in breath-hold divers that expend energy and physically move without being able to simultaneously resupply oxygen stores. Marine mammals evoke a dive response that uses a suite of physiological factors to regulate energy expenditure and dive duration (Butler 1982, 1988, Butler & Jones 1997, Davis et al. 2004). The results from our study add to a large body of evidence suggesting plausible reasons why ODBA on its own is a poor predictor in air-breathing vertebrates, including the influence of environment, thermoregulation, digestion increasing $s\dot{V}O_2$, metabolic suppression, and a temporal disconnect between gas exchange and physical activity (King et al. 2004, Gleiss et al. 2011, Halsey et al. 2011a,b,c).

Additional physiological factors that alter $s\dot{V}O_2$ without changing physical activity, such as thermoregulation or digestion, could also disrupt the potential ODBA–$s\dot{V}O_2$ relationship. The HIF in Steller sea lions resting on land onsets at approximately ≥1 h and peaks with a doubling of metabolism at ~4 h following a 4 kg meal (Rosen & Trites 1997, Secor 2009). However, we do not feel that HIF affected $s\dot{V}O_2$ in the present study. The animals in our study consumed smaller 20 g pieces of food over <60 min instead of ingesting bulk meals, as in Rosen & Trites (1997). Additionally, recent research has shown that Steller sea lions can partially defer digestion while foraging (Rosen et al. 2015). Specifically, the increase in metabolism associated with HIF when sea lions were diving was only 46% of the increase seen in pre-dive, and post-dive MRs were greater in the animals fed 1 h before a dive trial compared with animals fasted overnight, indicating that the additive effect of digestion was reduced or partial during diving under normal nutritional conditions. The fact that level of food intake was not a significant fixed factor also supports our contention that HIF did not confound our results. Similarly, as the majority of water temperatures during the trials were within the TNZ for the related California sea lion, there is no reason to believe that thermoregulation substantially impacted our results.

There is also growing evidence that the potential relationship between ODBA and $s\dot{V}O_2$ could be disrupted by physical factors including drag, buoyancy, and gliding behaviour (King et al. 2004, Gleiss et al. 2011, Halsey et al. 2011b,c). Steller sea lions are negatively buoyant and primarily glide while descending on 40 m trained dives (see Fig. 3B in Hindle et al. 2010). Anecdotal evidence from animal-borne video cameras in our study also show that Steller sea lions can descend to 40 m with only ~2–3 flipper stokes. Theoretically, the degree to which the animal is gliding has a greater effect on its metabolic costs ($s\dot{V}O_2$) than it does on ODBA because active flipper stroking requires greater energy than passive gliding, but the physics being measured (i.e. downward movement) would be roughly similar. Fahlman et al. (2008b) estimated that gliding during descent resulted in ~9% energetic savings, a benefit that was offset by increased swimming during ascent. Differences in gliding behaviour may account for our results that showed little variation in ODBA and larger variation in $s\dot{V}O_2$ (Figs 3 & 4). While it is possible that gliding behaviour disrupted any potential link between ODBA and $s\dot{V}O_2$, additional research is needed to comprehensively explore the influence of gliding on this relationship.

Future studies could explore additional metrics of ODBA, including integration or total ODBA values, to determine whether these metrics relate to $\dot{V}O_2$ better than mean ODBA. However, it is possible that the diving physiology associated with air-breathing vertebrate divers does not have a predictable relationship with ODBA, regardless of the exact type of ODBA.

CONCLUSIONS

Our study indicates that ODBA on its own may not be able to predict $s\dot{V}O_2$ in air-breathing divers, as proposed by others (Halsey et al. 2011c). Our results support the hypothesis that behaviour (measured as dive phase or dive type) does indeed impact the predictive ability of ODBA.

The apparent role of dive type in altering the relationship between ODBA and $s\dot{V}O_2$ observed in previous studies was likely due to differences in the time spent in different dive phases, and the divergent relationships between ODBA and $s\dot{V}O_2$ within each of these phases. The proportion of the dive cycle spent transiting had the strongest effect on the potential ODBA–$s\dot{V}O_2$ relationship. A relationship between ODBA and $s\dot{V}O_2$ was only apparent in dives that had low levels of transiting (<7% of total dive cycle). For sea lions that spent a higher proportion of time transiting to or from depth (such as short-duration bouts typical of wild Steller sea lions), ODBA on its own failed to accurately predict $s\dot{V}O_2$. Partitioning the ODBA–$s\dot{V}O_2$ relationship by dive phases also did not improve the ability of ODBA to predict energy expended by diving sea lions despite the increased range of ODBA values used in our study. Overall, our results support the growing body of evidence that ODBA on its own is a poor predictor of energy expenditure in air-breathing diving vertebrates at the level of the single dive or dive bout because ODBA (a physical measure) cannot account for physiological changes in $s\dot{V}O_2$ that occur as part of the dive response.

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LITERATURE CITED

Boyd IL, Woakes AJ, Butler PJ, Davis RW, Williams TM (1995) Validation of heart rate and doubly labelled water as measures of metabolic rate during swimming in California sea lions. Funct Ecol 9:151–160

Boyd IL, Bevan RM, Woakes AJ, Butler PJ (1999) Heart rate and behavior of fur seals: implications for measurement of field energetics. Am J Physiol Heart Circ Physiol 276: 844–857

Boyd IL, Bowen WD, Iverson SJ (2010) Marine mammal ecology and conservation: a handbook of techniques. Oxford University Press, Oxford

Butler PJ (1982) Respiratory and cardiovascular control during diving in birds and mammals. J Exp Biol 100:195–221

Butler PJ (1988) The exercise response and the 'classical' diving response during natural submersion in birds and mammals. Can J Zool 66:29–39

Butler PJ, Jones DR (1997) Physiology of diving of birds and mammals. Physiol Rev 77:837–899

Butler PJ, Green JA, Boyd IL, Speakman JR (2004) Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. Funct Ecol 18:168–183

Castellini MA (1992) Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. J Exp Biol 165:181–194

Costa DP, Gales NJ (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol Monogr 73:27–43

Crocker DE, Gales N, Costa D (2001) Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). J Zool 254:267–277

Dalton AJM, Rosen DAS, Trites AW (2014) Season and time of day affect the ability of accelerometry and the doubly labeled water methods to measure energy expenditure in northern fur seals (*Callorhinus ursinus*). J Exp Mar Biol Ecol 452:125–136

Davis RW, Polasek L, Watson R, Fuson A, Williams TM, Kanatous SB (2004) The diving paradox: new insights into the role of the dive response in air-breathing vertebrates. Comp Biochem Physiol Part A 138:263–268

Fahlman A, Handrich Y, Woakes AJ, Bost C-A, Holder R, Duchamp C, Butler CJ (2004) Effect of fasting on the V_{O2}–f_h relationship in king penguins, *Aptenodytes patagonicus*. Am J Physiol Regul Integr Comp Physiol 287: 870–877

Fahlman A, Svärd C, Rosen DAS, Jones DR, Trites AW (2008a) Metabolic costs of foraging and the management of O_2 and CO_2 stores in Steller sea lions. J Exp Biol 211: 3573–3580

Fahlman A, Wilson RP, Svärd C, Rosen DAS, Trites AW (2008b) Activity and diving metabolism correlate in Steller sea lion *Eumetopias jubatus*. Aquat Biol 2:75–84

Fahlman A, Svärd C, Rosen DAS, Wilson RP, Trites AW (2013) Activity as a proxy to estimate metabolic rate and to partition the metabolic cost of diving vs. breathing in pre-and post-fasted Steller sea lions. Aquat Biol 18: 175–184

Gałecki A, Burzykowski T (2013) Linear mixed-effects models using R: A step-by-step approach. Springer, New York, NY

Gleiss AC, Wilson RP, Shepard ELC (2011) Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. Methods Ecol Evol 2:23–33

Goundie ET, Rosen DAS, Trites AW (2015) Dive behaviour can predict metabolic expenditure in Steller sea lions. Conserv Physiol 3:cov052

Halsey LG, Jones TT, Jones DR, Liebsch N, Booth DT (2011a) Measuring energy expenditure in sub-adult and hatchling sea turtles via accelerometry. PLOS ONE 6:e22311

Halsey LG, Shepard ELC, Wilson RP (2011b) Assessing the development and application of the accelerometry technique for estimating energy expenditure. Comp Biochem Physiol Part A 158:305–314

Halsey LG, White CR, Enstipp MR, Wilson RP and others (2011c) Assessing the validity of the accelerometry technique for estimating the energy expenditure of diving double-crested cormorants *Phalacrocorax auritus*. Physiol Biochem Zool 84:230–237

Hastie GD, Rosen DAS, Trites AW (2006) Studying diving energetics of trained Steller sea lions in the open ocean. In: Trites AW, Atkinson S, DeMaster DP, Fritz LW, Gelatt TS, Rea LD, Wynne KM (eds) Sea lions of the world.

Alaska Sea Grant College Program, University of Alaska Fairbanks

Hays GC, Metcalfe JD, Walne AW, Wilson RP (2004) First records of flipper beat frequency during sea turtle diving. J Exp Mar Biol Ecol 303:243–260

Hindle AG, Young BL, Rosen DAS, Haulena M, Trites AW (2010) Dive response differs between shallow-and deep-diving Steller sea lions (*Eumetopias jubatus*). J Exp Mar Biol Ecol 394:141–148

Jeanniard du Dot T, Guinet C, Arnould JPY, Speakman JR, Trites AW (2016) Accelerometers can measure total and activity specific energy expenditures in free ranging marine mammals only if linked to time activity budgets. Funct Ecol, doi:10.1111/1365-2435.12729.

King AM, Loiselle DS, Kohl P (2004) Force generation for locomotion of vertebrates: skeletal muscle overview. IEEE J Oceanic Eng 29:684–691

Liwanag HEM, Williams TM, Costa DP, Kanatous SB, Davis RW, Boyd IL (2009) The effects of water temperature on the energetic costs of juvenile and adult California sea lions (*Zalophus californianus*): the importance of skeletal muscle thermogenesis for thermal balance. J Exp Biol 212:3977–3984

Maresh JL, Adachi T, Takahashi A, Naito Y and others (2015) Summing the strokes: energy economy in northern elephant seals during large-scale foraging migrations. Mov Ecol 3:22

Merrick RL, Loughlin TR (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can J Zool 75:776–786

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer-Verlag, New York, NY

Ponganis PJ (2007) Bio-logging of physiological parameters in higher marine vertebrates. Deep-Sea Res II 54: 183–192

R Core Development Team (2015) R: A language and environment for statistical computing, R Foundation for Statistical Computing. Vienna, Austria

Rosen DAS, Trites AW (1997) Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. Comp Biochem Physiol Part A 118A:877–881

Rosen DAS, Gerlinsky CD, Trites AW (2015) Evidence of partial deferment of digestion during diving in Steller sea lions (*Eumetopias jubatus*). J Exp Mar Biol Ecol 469: 93–97

Savage VM, Allen AP, Brown JH, Gillooly JF, Herman AB, Woodruff WH, West GB (2007) Scaling of number, size, and metabolic rate of cells with body size in mammals. Proc Natl Acad Sci USA 104:4718–4723

Schmidt-Nielsen K (1975) Scaling in biology: the consequences of size. J Exp Zool 194:287–307

Secor SM (2009) Specific dynamic action: a review of the postprandial metabolic response. J Comp Physiol B 179: 1–56

Shepard ELC, Wilson RP, Halsey LG, Quintana F and others (2008) Derivation of body motion via appropriate smoothing of acceleration data. Aquat Biol 4:235–241

Sparling CE, Thompson D, Fedak MA, Gallon SL, Speakman JR (2008) Estimating field metabolic rates of pinnipeds: doubly labelled water gets the seal of approval. Funct Ecol 22:245–254

Villegas-Amtmann S, Costa DP, Tremblay Y, Salazar S, Aurioles-Gamboa D (2008) Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. Mar Ecol Prog Ser 363:299–309

Viviant M, Trites A, Rosen DAS, Monestiez P, Guinet C (2010) Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. Polar Biol 33:713–719

Volpov BL, Hoskins AJ, Battaile B, Viviant M and others (2015a) Identification of prey captures in Australian fur seals (*Arctocephalus pusillus doriferus*) using head-mounted accelerometers: field validation with animal-borne video cameras. PLOS ONE 10:e0128789

Volpov BL, Rosen DAS, Trites AW, Arnould JP (2015b) Validating the relationship between 3-dimensional body acceleration and oxygen consumption in trained Steller sea lions. J Comp Physiol B 185:695–708

Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. Proc Natl Acad Sci USA 110:2199–2204

Webb PM, Andrews RD, Costa DP, Le Boeuf BJ (1998) Heart rate and oxygen consumption of northern elephant seals during diving in the laboratory. Physiol Zool 71:116–125

West GB, Brown JH (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. J Exp Biol 208:1575–1592

White CR, Seymour RS (2005) Allometric scaling of mammalian metabolism. J Exp Biol 208:1611–1619

Williams TM, Kooyman GL, Croll DA (1991) The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. J Comp Physiol B 160: 637–644

Williams TM, Fuiman LA, Horning M, Davis RW (2004) The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddelli*: pricing by the stroke. J Exp Biol 207:973–982

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity specific metabolic rate in free living animals: the case of the cormorant. J Anim Ecol 75: 1081–1090

Wilson RP, Griffiths I, Legg P, Friswell M and others (2013) Turn costs change the value of animal search paths. Ecol Lett 16:1145–1150

Winship AJ, Trites AW, Rosen DAS (2002) A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Mar Ecol Prog Ser 229:291–312

Withers PC (1977) Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. J Appl Physiol 42:120–123

Ydesen KS, Wisniewska DM, Hansen JD, Beedholm K, Johnson M, Madsen PT (2014) What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). J Exp Biol 217:2239–2243

Young BL, Rosen DAS, Haulena M, Hindle AG, Trites AW (2011a) Environment and feeding change the ability of heart rate to predict metabolism in resting Steller sea lions (*Eumetopias jubatus*). J Comp Physiol B 181: 105–116

Young BL, Rosen DAS, Hindle AG, Haulena M, Trites AW (2011b) Dive behaviour impacts the ability of heart rate to predict oxygen consumption in Steller sea lions (*Eumetopias jubatus*) foraging at depth. J Exp Biol 214: 2267–2275

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Verlag, New York, NY

Appendix 1. List of abbreviations

Term	Definition
ODBA	Overall dynamic body acceleration averaged over dive cycle or dive bout (*g*; 1 *g* = 9.81 m s^{-2})
$\dot{V}O_2$	Whole-animal oxygen consumption rate (ml O_2 min^{-1})
$s\dot{V}O_2$	Mass-corrected oxygen consumption rate (ml O_2 min^{-1} $kg^{-0.75}$)
MRs	Metabolic rate resting at the surface 2–3 min prior to diving (ml O_2 min^{-1} $kg^{-0.75}$)
SI	Post-dive surface interval
Single dive cycle	Single dive + subsequent SI until $s\dot{V}O_2$ within 5% of pre-dive MRs
Dive bout	Series of dives + inter-dive SI + final SI; SI within a dive bout does not return to within 5% MRs
Short-duration bout	10 or 12 dives per dive bout; goal of 1–2 min per dive (comparatively short individual dive durations)
Long-duration bout	4–6 dives per dive bout; goal of 4–6 min per dive (comparatively long individual dive durations)
Single stationary dive	1 dive to 1 feeding station for ~3 min bottom duration
Single active dive	1 dive to 2 feeding stations for ~3–5 min bottom duration
Transit dive	Single dive to 1 feeding station with goal of zero bottom duration (actual was <9 s)
Transit ODBA	Instantaneous ODBA averaged over the descent and ascent dive phases only
Transit MR	Metabolic rate over a transit dive ascent and descent only, calculated from $s\dot{V}O_2$ (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} $kg^{-0.75}$)
AMR ODBA	Instantaneous ODBA averaged over the single dive cycle or dive bout (dives + all SI)
Bottom MR	Metabolic rate over the bottom phase of a single dive calculated from $s\dot{V}O_2$ (ml O_2 min^{-1} $kg^{-0.75}$)
Bottom ODBA	Instantaneous ODBA averaged over the bottom phase only

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