Activity and diving metabolism correlate in Steller sea lion *Eumetopias jubatus*

Andreas Fahlman[1],*, Rory Wilson[2], Caroline Svärd[1], David A. S. Rosen[1], Andrew W. Trites[1]

[1]Marine Mammal Research Unit, Fisheries Centre, Room 247, AERL—Aquatic Ecosystems Research Laboratory,
University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada
[2]Biological Sciences, University of Wales Swansea, Swansea SA2 8PP, UK

ABSTRACT: Three Steller sea lions *Eumetopias jubatus* were trained to participate in free-swimming, open-ocean experiments designed to determine if activity can be used to estimate the energetic cost of finding prey at depth. Sea lions were trained to dive to fixed depths of 10 to 50 m, and to re-surface inside a floating dome to measure energy expenditure via gas exchange. A 3-axis accelerometer was attached to the sea lions during foraging. Acceleration data were used to determine the overall dynamic body acceleration (ODBA), a proxy for activity. Results showed that ODBA correlated well with the diving metabolic rate (dive + surface interval) and that the variability in the relationship ($r^2 = 0.47$, linear regression including Sea lion as a random factor) was similar to that reported for other studies that used heart rate to estimate metabolic rate for sea lions swimming underwater in a 2 m deep water channel. A multivariate analysis suggested that both ODBA and dive duration were important for predicting diving metabolic cost, but ODBA alone predicted foraging cost to within 7 % between animals. Consequently, collecting 3-dimensional acceleration data is a simple technique to estimate field metabolic rate of wild Steller sea lions and other diving mammals and birds.

KEY WORDS: Marine mammal · Acceleration · Foraging cost · Respirometry · Field research

INTRODUCTION

Determining the metabolic rates of free-living, air-breathing divers (mammals, birds and reptiles) has been an active area of study over the last 3 decades. Respirometery has been a standard straight-forward means to measure energetic costs when animals come ashore (e.g. to provision juveniles or during courtship). However, it has been far more challenging to measure metabolic rates of animals while diving at sea.

A number of methods have been used to estimate the at-sea metabolic rates of diving animals. The doubly-labelled water technique gives an integrated measure of metabolism over finite periods of time. However, this method is expensive, labour intensive and cannot differentiate the metabolic cost of different activities such as diving versus surface swimming (Costa 1988). Measuring the duration of dives and linking these values with available oxygen stores can provide a rough estimate of the metabolic cost of diving, but cannot determine variation in metabolic rate within and between dives.

Heart rate has also been used as a proxy for estimating metabolic rate of diving animals while foraging (Green et al. 2003, Froget et al. 2004). A few studies have used heart rate to estimate the metabolic cost for various activities, such as diving, resting at the surface, travelling, etc., during a foraging trip (Green et al. 2003, Froget et al. 2004). Calibration experiments relating heart rate and the rate of oxygen consumption ($\dot{V}_{O_2}$) have shown great promise for estimating the metabolism of animals walking on land from heart rate

measurements (Fahlman et al. 2004), but have also shown limitations related to physiological state such as fasting (Fahlman et al. 2004), type and level of activity (Nolet et al. 1992) and season. Attempts have been made to correlate heart rate with metabolic rate in aquatic animals, with inconclusive results (McPhee et al. 2003, Halsey et al. 2007).

There are a number of logistical problems associated with measuring heart rate in the field over longer periods, such as the effects of surgical implantation of the datalogger (Haulena et al. 2005) and the difficulty of accurately detecting peaks of the electrocardiogram signal (Fahlman unpubl. obs.). In addition, adequate calibration studies are essential given the complexity of the bradycardia and tachycardia response in diving endotherms (Butler & Jones 1997) and the pressure-related changes in gas exchange in mammals (Kooyman & Sinnett 1982, Bostrom et al. 2008). Despite these problems, attempts have been made to estimate field (Green et al. 2003, Froget et al. 2004) and diving metabolic rates (Green et al. 2007) from heart rates, but none have been tested for animals diving for >1 to 2 min or for animals diving deeper than 2 m. Clearly, a simple and accurate method that can be validated for animals performing realistic dives is needed to determine the metabolic costs of foraging according to circumstance.

Movement requires energy, which means that energy expenditure might be estimated using an appropriate transducer that monitors movement. This has been explored in penguins, humans and pinnipeds (e.g. Kumahara et al. 2004, Williams et al. 2004, Wilson et al. 2008). Williams et al. (2004), for example, estimated total energy expenditure of Weddell seals *Leptonychotes weddellii* by determining the metabolic cost for an average diving stroke, and assuming that stroke amplitude and underwater swimming speed do not vary within a seal. Unfortunately, this method for estimating metabolic rate will not work with most animals (including diving mammals) that change the amplitude and frequency of limb motion to modulate travel speed (Webb & Keyes 1982), resulting in substantial variations in energy expenditure with speed (Bainbridge 1958). A possible solution is to record triaxial dynamic acceleration given that greater limb movement will result in greater acceleration, which should correlate with energy expenditure in species with more variable swimming patterns (Wilson et al. 2006, 2008).

The goal of our study was to use acceleration as a proxy for activity and attempt to estimate the metabolic rate over a complete dive event (dive + surface interval) in freely diving Steller sea lions *Eumetopias jubatus*. We sought to derive an equation to predict the metabolic rate of sea lions from measured acceleration

and dive characteristics (dive depth and duration) using trained sea lions voluntarily diving to depths from 10 to 50 m.

MATERIALS AND METHODS

Sea lions. Experiments were conducted between October 2006 and August 2007 with 3 female Steller sea lions housed in a specially designed floating pen located in a coastal inlet in British Columbia, Canada. The pen allowed access to seawater and provided a base for research in the surrounding waters. The sea lions freely chose to cooperate with all data collection and were never restrained during any of the experimental trials. Two of the sea lions (F97HA and F97SI) were 9 yr old, and the third was 6 yr old (F00BO). Body mass (M_b) of each sea lion was measured daily; average M_b values (±SD) for data are reported in Table 1.

Experimental procedure and measurement of diving oxygen consumption. All experiments were conducted under permits from Sea lion Care Committees of the University of British Columbia and the Vancouver Aquarium. All trials were performed in the morning, at least 16 h and up to 20 h postprandial. Prior to the daily trials, each sea lion was weighed (±0.5 kg) and fitted with a webbing body harness that held an accelerometer (see following subsection) and a VHF transmitter (used to locate the sea lion in the event of it leaving the trial area). The sea lions were transported in a 22 ft boat from their holding pen to the trial areas, where they dove from a floating respiratory dome to an underwater feeding tube placed at a predetermined depth (see following subsection). A second 22 ft research boat carrying the respirometry equipment and towing a floating barge was anchored in the trial area. The barge contained a rectangular hole into which a cage (152 × 152 × 250 cm) was placed in the water, covered by the floating respirometry dome. The cage floor could be opened to allow the sea lion to enter and breathe in the dome. The cage made it possible to voluntarily contain the sea lion for short periods of time to measure metabolic rate while the sea lions were inactive at the surface. While the sea lions were within the cage, their activity varied between trials. Our values were therefore by definition neither resting nor basal estimates of metabolic rate, but rather an estimate for a sea lion with varying activity level at the surface, which we called surface metabolic rate (MR_S).

A floating transparent Plexiglas dome (either 100 or 200 l internal volume) enabled collection of respiratory gases and determination of the rate of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$)

using flow-through respirometry. A mass flowmeter (Flow Kit Model 500H, Sable Systems Int.) pulled $475 \, l \, min^{-1}$ through the dome. This mass flowmeter automatically corrected flow rates to standard temperature and pressure (STP). A subsample of this gas was passed via a canister of anhydrous $CaSO_4$ (W. A. Hammond Drierite) to a paramagnetic O_2 (FC-1B O_2, Sable Systems Int.) and an infrared CO_2 analyzer (CA-10A, Sable Systems Int.). Data were sampled at 2 Hz and saved to a laptop.

The gas analyzers were calibrated before and after each experiment using ambient air (20.94 % O_2) and 1.0 % CO_2 in N_2 from a commercial mixture (Praxair). Temperature (°C) and humidity (%) of the excurrent gas were measured using a commercial sensor (Springfield Precise Temp., Springfield Precision Instruments Inc.). Average ± SD respirometer temperature was 17.9 ± 4.9°C (range: 9.9 to 25.0°C), humidity was 73 ± 16 % (range: 46 to 100 %), and barometric pressure was 101.92 ± 0.5 kPa (range: 101.2 to 103.2 kPa). Measuring the humidity of the excurrent air made it possible to correct flow to STP dry (STPD).

The accuracy of the respirometry system was determined by simultaneous N_2- and CO_2-dilution tests (Fedak et al. 1981, Fahlman et al. 2005), and showed that the differences between the observed and expected values were within 4 %. Addition of CO_2 confirmed that minimal amounts of CO_2 were lost by dissolving in the seawater (Fahlman et al. 2005). The effective volume of the system was either 120 or 220 l, including the volume of the respirometer and the plastic hose to the analyzers. With a flow rate of $475 \, l \, min^{-1}$, this gave time constants of 0.25 and 0.46 min, respectively. The time required to reach a 95 % fractional transformation to a new steady state was 3.2 times the time constant, or 48 and 90 s, respectively (Fahlman et al. 2004).

A tube and pump system allowed delivery of fish (frozen herring) to various depths at different rates (0 to 12 fish min^{-1}) that simulated food patches of varying densities. For a dive trial, the sea lion was instructed to enter the respirometry dome and the cage door was closed. The sea lion stayed in the dome for 6 min while MR_S was measured. The duration was extended if steady values of O_2 and CO_2 were not recorded during the last 2 min of this period. During MR_S measurements, the water temperature at the surface was quite variable, but within the thermoneutral range for this species (Rosen & Trites 2003). The sea lions were at least 16 h postabsorptive, but the activity inside the dome was highly variable.

Each sea lion was instructed to swim to the end of the feeding tube that was placed at a predetermined depth (10, 15, 20, 30, 40, or 50 m). The dive duration was determined by the sea lion, and each sea lion was held in the dome after each dive until its metabolic rate had returned to predive levels. This sequence of a dive and surface interval was repeated for between 1 and 8 dives during each trial (1 trial d^{-1}).

Fish were delivered at a predetermined, constant rate for each trial. To ensure that sea lions were not naïve to the required dive parameters during a trial, each sea lion was trained at each depth for 5 to 7 d prior to collecting any data. A total of 141 dives was analyzed, of which most were to 10 or 50 m (Table 1).

The average $\dot{V}_{O_2}$ for each dive and subsequent surface interval (1 dive cycle) was estimated by integrating the instantaneous oxygen consumption rate over the entire post-dive surface interval and dividing this by the dive cycle duration (Sparling & Fedak 2004, Hastie et al. 2006). We used an entire dive cycle (dive + surface interval) as an estimate for diving metabolic rate (DMR). All surface intervals in a dive series were >240 s.

The water temperatures at the surface and at the end of the feeding tube were monitored during each trial using remote temperature loggers (Onset Computer Corp.). Temperatures at the surface ranged from 6.0 to 16.6°C, while temperatures at depth ranged from 7.9 to 17.3°C.

Acceleration and estimation of activity. An accelerometer (JUV Elektronik; $65 \times 36 \times 22$ mm, mass 35 g) that recorded triaxial acceleration (0 to 6 g, 1 g = 9.8 m s^{-1}) at 16 Hz was attached to the sea lion's harness. The logger was calibrated by rotating the unit through defined combinations of pitch and roll and converting all voltages to gravitational force.

Overall dynamic body acceleration (ODBA, g) was estimated as described in Wilson et al. (2006, 2008), with the static acceleration for each axis computed from the running mean over a 2 s interval (Shepard et al. 2008). Subsequently, the static acceleration, or smoothed data, was subtracted from the corresponding unsmoothed data, resulting in an estimate of dynamic acceleration. In other words, the gravity resulting from

Table 1. *Eumetopias jubatus*. Average body mass (M_b), total number of trials and number of dives to each depth for the 3 Steller sea lions

Sea lion	M_b (kg)	No. of trials	No. of dives per depth (m)							Total dives
			10	15	20	25	30	40	50	
F97SI	215.4 ± 3.4	9	24	4	3	–	21	2	–	54
F97HA	162.6 ± 2.8	8	12	–	3	1	2	–	21	39
F00BO	141.8 ± 2.7	11	18	3	–	–	1	–	26	48
Total		28	54	7	6	1	24	2	47	141

the relative position of the datalogger was removed from the data such that the resulting value only related to the movement of the sea lion. Finally, the absolute value for each of the 3 axes was summed into a value of ODBA, or activity. The average ODBA for the dive and subsequent surface interval (dive cycle) was used to compute an average activity for the dive cycle. This allowed us to account for differences in activity during the surface period.

Data assessment and statistical analysis. Mixed models regression using a compound symmetry covariance structure to deal with the correlation within sea lions (Littell et al. 1998) was used to determine the best predictive model for the relationship between $\dot{V}_{O_2}$ (dependent variable) and 4 experimental variables (ODBA, dive duration, dive depth, M_b) as independent fixed covariates. Initially, a univariate analysis on each independent variable was performed, and only those variables with p < 0.20 (Wald's tests) were considered in the multivariate analysis. Stepwise techniques were used to search for the best model. The likelihood ratio test was used to determine significance of parameters between nested models. In this test, significance was defined by increases in the log-likelihood (LL) values of the models (i.e. significantly smaller negative LL values). The models were analyzed and corrected for departures from normality, outliers and linearity. Statistical analyses were performed using S-plus 2000 (Lucent Technologies). Acceptance of significance was set at p < 0.05, and 0.05 < p < 0.1 was considered to be important enough to warrant investigation or consideration. All values are reported as means (±SD) unless otherwise specified.

RESULTS

Rate of oxygen consumption

Mean MR_S in water increased proportionally between individuals with M_b. The minimum and maximum MR_S observed were 0.91 l and 2.23 l O_2 min^{-1}, respectively. Mean (±SD) respiratory exchange ratio (RER, $\dot{V}_{CO_2}\,\dot{V}_{O_2}^{-1}$) during the period in the dome before the first dive was 0.90 ± 0.09 for the 3 sea lions *Eumetopias jubatus*, and individual mean values ranged between 0.79 and 0.96. During diving, mean RER was 0.84 ± 0.09, and there were no systematic changes with depth.

Relationships between dive duration, depth, ODBA and diving metabolic rate

The overall mean dive duration was 3.02 ± 1.58 min (range from 0.6 to 7.0 min) and increased with depth from 2.33 ± 1.22 min at 10 m to 4.29 ± 1.46 min at 50 m (Table 2; $F_{1,139} = 73.6$, p < 0.01). To account for differences in M_b between sea lions, we used a conservative mass exponent for marine mammals ($M_b^{0.75}$) to derive mass-specific metabolic rates as $s\dot{V}_{O_2} = \dot{V}_{O_2} \cdot$ kg$^{-0.75}$. When the diving data were analyzed separately from the surface resting values, there was a significant correlation between mass-specific dive metabolic rate (sDMR, ml O_2 min^{-1} kg$^{-0.75}$) and ODBA (p < 0.05, LL = –563.2, 1 df). Depth was not a significant covariate (p > 0.1, LL = –566.2, p > 0.4), but there was a trend for a slight negative correlation between dive duration and sDMR (p < 0.1, LL = –565.2) (Fig. 1). There was a significant positive correlation between ODBA and dive duration (p < 0.01) and a negative correlation with depth (p < 0.01). Both ODBA and dive duration warranted inclusion in a multivariate model (p < 0.01, LL = –559.3) whereby:

$$sDMR = 0.0287 + 0.0303 \times ODBA - 0.00118 \times \text{Dive duration} \tag{1}$$

Analyzing all data ($s\dot{V}_{O_2}$, sDMR and mass-specific surface metabolic rate [sMR_S] together) showed that neither dive depth (p > 0.9) nor dive duration (p > 0.3) correlated with $s\dot{V}_{O_2}$. However, there was a significant positive correlation between ODBA and $s\dot{V}_{O_2}$ such that:

$$s\dot{V}_{O_2} = 0.0248 + 0.0308 \times ODBA \tag{2}$$

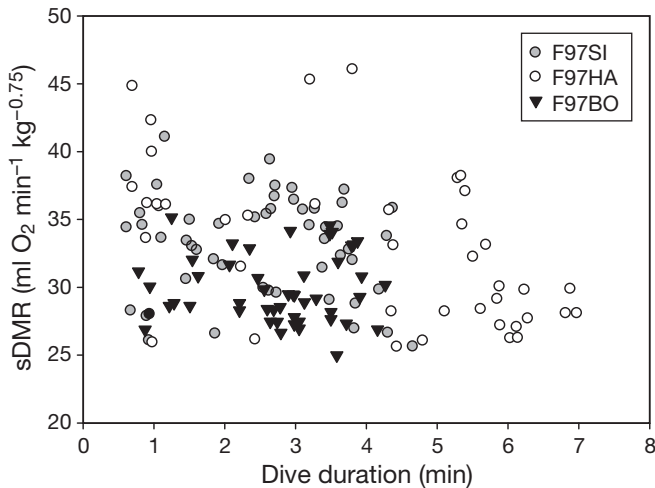There were no differences in slopes or intercepts between sMR_S and sDMR

Table 2. *Eumetopias jubatus*. Average ± SD dive duration (min) and diving metabolic rate (DMR, l O_2 min^{-1}) per depth, and average ± SD surface metabolic rate (MR_S, l O_2 min^{-1}) before diving, of 3 Steller sea lions

Dive depth (m)	F97SI	F97HA	F00BO	Grand mean
Dive duration				
10	2.50 ± 1.22	2.31 ± 1.60	2.13 ± 0.90	2.31 ± 0.18
15	1.38 ± 0.91	——	1.75 ± 0.54	1.57 ± 0.26
20	2.21 ± 0.44	1.81 ± 0.56	——	2.01 ± 0.28
25	——	1.08	——	1.08
30	2.84 ± 1.15	0.98 ± 0.01	2.93	2.25 ± 1.10
40	——	6.04 ± 0.27	——	6.04
50	——	5.28 ± 1.46	3.31 ± 0.55	4.30 ± 1.39
DMR				
10	1.80 ± 0.24	1.69 ± 0.24	1.23 ± 0.09	1.57 ± 0.30
15	2.09 ± 0.15	——	1.28 ± 0.08	1.69 ± 0.58
20	1.95 ± 0.16	1.53 ± 0.11	——	1.74 ± 0.30
25	——	1.65	——	1.65
30	1.87 ± 0.14	1.51 ± 0.45	1.39	1.59 ± 0.25
40	——	1.36 ± 0.02	——	1.36
50	——	1.37 ± 0.27	1.21 ± 0.11	1.29 ± 0.11
MR_S	1.73 ± 0.17	1.49 ± 0.41	1.02 ± 0.07	1.41 ± 0.36

Fig. 1. *Eumetopias jubatus*. Dive duration versus mass-specific diving metabolic rate (sDMR, ml O_2 min^{-1} kg$^{-0.75}$) for 3 Steller sea lions (F97SI, F97HA and F00BO). Dive metabolic rate was corrected using a mass exponent of 0.75

(p > 0.1, ANCOVA) (Fig. 2). Eq. (2) yielded predicted $\dot{V}_{O_2}$ values that agreed well with the observed data, with an overall error of 0.2% [(predicted – observed)/ predicted × 100], a range of 23.8 to –46.8% and an
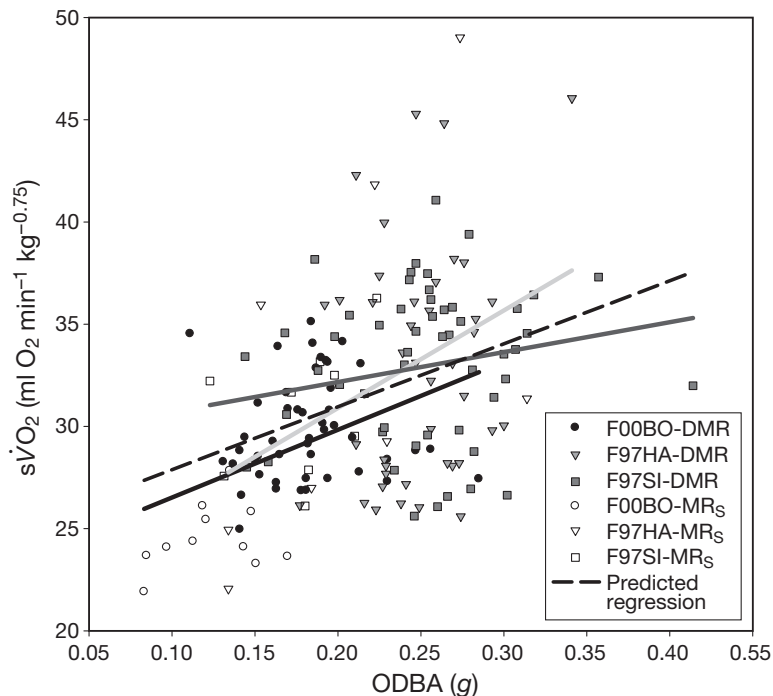

Fig. 2. *Eumetopias jubatus*. Overall dynamic body acceleration (ODBA, *g*) versus mass corrected O_2 consumption rate (s$\dot{V}_{O_2}$, ml O_2 min^{-1} kg$^{-0.75}$) for 3 Steller sea lions (F97SI, F97HA and F00BO) during diving (DMR—diving metabolic rate) or while confined to the metabolic dome at the surface (MR$_S$—surface metabolic rate). Closed symbols are for sea lions diving, while open symbols are for sea lions resting at the surface. Predicted relationships (from Eq. 2) are shown for each sea lion (solid lines) and for all sea lions combined (dashed line)

absolute mean error of 11.1%. The partial residuals were randomly distributed against all covariates, and there were no departures from normality. To test the sensitivity of the regression model, data were sequentially removed from each sea lion and the model was re-fit with the same covariates. Average error for all sea lions (Eq. 2) was 0.6% (range from 7.2 to –3.4%).

Changes in ODBA during descent and ascent

To determine the activity levels during the descent and ascent phase, ODBA was plotted against depth (Fig. 3). All dives examined showed similar patterns between sea lions. During descent, there was an initial increase in ODBA during the first 5 m, followed by an exponential decline falling below 0.2 *g*. This indicated that Steller sea lions glide passively as they descend beyond 5 m. During the ascent phase, on the other hand, ODBA was much higher and more variable, indicating active swimming (Fig. 3). There was also a slight positive correlation between ODBA and depth during ascent (p < 0.05) (Fig. 3).

DISCUSSION

Using activity to predict diving metabolic rate

Our main objective was to determine if an estimate of activity could be used to predict metabolic cost in Steller sea lions. Our experimental design allowed us to test sea lion diving to depths of up to 50 m, which was within the dive range most commonly observed in the wild (>95% of all dives in adult female Steller sea lions throughout the year are to depths <50 m; Merrick & Loughlin 1997). Thus, our data are particularly relevant for this age class and species. Our results corroborate previous studies using movement as a proxy for metabolic rate, adding to existing evidence indicating the effectiveness of acceleration dataloggers for examining costs incurred in free-living marine mammals.

For Steller sea lions foraging at sea, there are 2 distinct behaviours: breath-hold diving, or breathing at the surface. For both of these behaviours, the activity level should be important in determining the metabolic rate. Our estimate of MR$_S$ is not an estimate of the basal metabolic rate of the sea lion, but rather it is an estimate of the metabolic cost while remaining relatively inactive at the
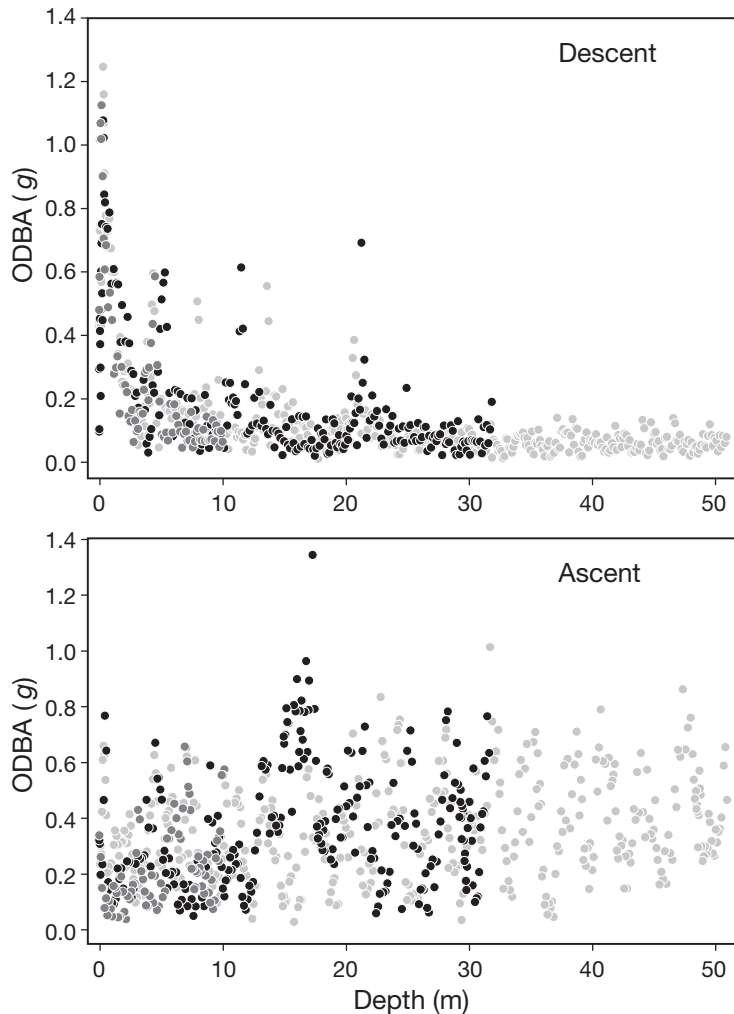
Fig. 3. *Eumetopias jubatus*. Overall dynamic body acceleration (ODBA, *g*) versus depth (m) during descent or ascent for representative dives of 3 Steller sea lions descending to 10, 30, or 50 m. Dark grey: dives to 10 m; black: to 30 m; light grey: to 50 m

water surface, i.e. not actively swimming. There was good agreement between ODBA and sMR$_S$, which did not differ significantly from the relationship between ODBA and sDMR. Therefore, Eq. (2) provides a predictive equation for all activities except active travel at the surface, which was not tested, while the sea lions are at sea with a small error between animals. However, the effect of dive duration or other diving related changes that may affect metabolic rate, e.g. body temperature, body condition, etc., is not accounted for in Eq. (2) and should be verified in future studies.

The variability we found in the relationship between ODBA and s$\dot{V}_{O_2}$, as crudely assessed by the correlation coefficient ($r^2 = 0.47$, linear regression including Sea lion as a factor) was similar to that found using the heart rate technique for king penguins *Aptenodytes patagonicus* swimming underwater in a water channel

($r^2 = 0.46$; Halsey et al. 2007). The heart rate technique has shown great promise for estimating the energetic cost of breath-hold diving, and the difference between measured and predicted $\dot{V}_{O_2}$ is commonly within a few percent with errors ranging from 40 to 90 % for individual estimates (Fahlman et al. 2004). Despite the wide range of body masses of the 3 sea lions we used in our study, the errors reported were much smaller (–3.9 to 7 %) and showed good agreement for the entire group (Fig. 2). This suggests that this method may be used for estimating the metabolic rates for individual sea lions with errors <10 %. It is also possible that this technique can partition metabolic cost for various underwater activities such as active swimming versus gliding (see following subsection).

Comparing ODBA with other techniques used to estimate DMR by activity

To our knowledge, only 1 previous study has successfully developed a method that showed a relationship with DMR. A study of Weddell seals showed that the locomotor cost of a dive was directly proportional to the number of flipper beats during a dive (Williams et al. 2004). This agrees with the idea that animal activity correlates well with energetic cost. Our method is similar as it assumes a relationship between activity and metabolic rate. However, using ODBA has a number of added benefits.

Williams et al. (2004) used stroke frequency rather than the actual force or amplitude of each stroke. The energetic cost of a flipper stroke is related to the actual force produced. As stroking patterns (force and amplitude) may differ between dives and within a dive (i.e. strokes for forward motion versus turning), this could alter the locomotor cost and increase variability.

There is no difference in forward acceleration (surge) when an animal is swimming or gliding at a constant speed, but there are differences in associated metabolic costs. However, flipper movement during active swimming results in different acceleration patterns in the upward/downward (heave) and side-to-side (sway) directions. Such patterns of forward movement can be distinguished by ODBA, because this is a measure of acceleration in 3 dimensions. For example, the descent duration for the dive to 50 m in Fig. 3 was 34.6 s and the ascent duration was 36.7 s. During a dive, the sea lion swam directly to and from the feeding tube to the

surface; therefore, the forward velocity was almost the same during descent and ascent. Despite this, ODBA was able to distinguish between passive gliding and active swimming. In addition to strokes, sea lions perform other activities that are related to propulsion, such as undulating movements similar to the dolphin kicks used by human swimmers during ascent. ODBA is a simple way to distinguish between and account for these different modes of movement in 3 dimensions. Additional advantages of using ODBA are that it is much easier to compute for large datasets compared to counting flipper beats or strokes, and it is insensitive to the direction of datalogger placement.

In a manner similar to that of the heart rate technique to estimate metabolic rates, it is possible that the relationship between metabolic rate and activity differs between species, and is influenced by sex, body condition and season. In appropriately controlled studies, the relationship between heart rate and $\dot{V}_{O_2}$ has been shown to change in birds fasting on land (Fahlman et al. 2004), but not while swimming underwater (Halsey et al. 2007). Reliable use of ODBA to estimate field metabolic rate will therefore require future studies to determine whether the relationship varies under different conditions.

Despite the common use of the heart rate technique to estimate metabolism (e.g. Froget et al. 2004), the relationships established between heart rate and $\dot{V}_{O_2}$ have been limited by the experimental set-up used to derive the equations, and have never been tested for animals diving for any length of time or to depths greater than a few meters (Halsey et al. 2007). Furthermore, the heart rate method relies on the assumption of a constant or systematically changing stroke volume (Froget et al. 2004) and fails to consider not only the huge variation that occurs in heart rate during and after dives as part of the dive response (Thompson & Fedak 1993, Andrews et al. 1997), but also that the level of gas exchange, or pulmonary shunt, changes with depth in mammals (Kooyman & Sinnett 1982). Systematic changes in stroke volume and heart rate have been demonstrated during forced dives in Weddell seals (Thornton et al. 2005), but were not apparent in the harbour seal *Phoca vitulina* during voluntary swimming underwater (Ponganis et al. 1990).

Methods that utilize activity measures (Williams et al. 2004, Wilson et al. 2006) circumvent many of the problems with the heart rate technique, and show great promise as a simple and affordable technique to obtain accurate activity budgets and estimate associated metabolic costs over long periods. As the storage capacities of dataloggers increase, it will be possible to use this method to determine the cost of activities and behaviours with finer scale resolutions (Wilson et al. 2008). Estimates of energetic costs are currently limited to those incurred over an entire dive cycle (dive and subsequent surface period). Obtaining additional data would allow common regression techniques to separate the metabolic costs associated with activity underwater and at the surface. For example, it would be possible to quantify the metabolic savings by the stroke-and-glide technique (see following subsection for an example) used by several diving species (Williams et al. 2000, Williams 2001).

sDMR, dive duration, dive depth and digestion while diving

It appears counterintuitive that depth, and thereby distance, would not affect diving cost. The extent of active transport and associated cumulative metabolic cost should increase as swimming distance increases. However, the ODBA indicated that, while the sea lions swam actively during the entire ascent, they were gliding passively as they descended below 5 m (Fig. 3). Passive gliding during descent has been observed in several other species and has been suggested to be an energy-conserving strategy. ODBA is particularly useful in this context as it can quantify (and account for) energy savings from variations in underwater behaviour.

For example, for dives to 10 m, the average ODBA was 0.259 *g* during descent and 0.212 *g* during ascent (Fig. 3). This was not very different from the average diving ODBA of 0.227 *g*, but was much higher than the average ODBA at the surface of 0.165 *g*. During dives to 50 m, ODBA was 0.131 *g* during the descent phase and 0.353 *g* during the ascent (the durations of the descent and ascent were almost identical at ~35 s each). This translated into a metabolic rate of 28.8 ml O_2 min^{-1} kg$^{-0.75}$ during descent and 35.7 ml O_2 min^{-1} kg$^{-0.75}$ during ascent (calculated using Eq. 2). While the gliding descent resulted in a metabolic savings of 9% as compared to the average dive (s$\dot{V}_{O_2}$ = 31.8 ml O_2 min^{-1} kg$^{-0.75}$), the metabolic cost of the ascent increased by 12%. Consequently, it appears that the metabolic savings by passive gliding during descent were similar to the additional cost of active swimming during ascent. This may explain why depth did not affect the metabolic cost of diving and shows how ODBA can be used to assess the metabolic cost of different phases of a dive.

Previous work has suggested that diving mammals reduce their metabolic rate while diving, to a level below their resting value at the surface (Sparling & Fedak 2004). A univariate analysis of our Steller sea lion data suggested a negative trend between sDMR and dive duration (p < 0.1), with a significant increase in ODBA as the duration of the dive increased. We

therefore performed a multivariate analysis including both variables, and confirmed that both were important in predicting sDMR (Eq. 1). For example, for a short (0.6 min) or a long (7 min) dive both with a theoretical ODBA of 0.227 g (the average for all dives), Eq. (1) results in a 22% reduction in sDMR (34.9 to 27.3 ml O_2 min^{-1} kg$^{-0.75}$). A reduction in sDMR with dive duration agrees with studies with phocid seals, the bottlenose dolphin and the king penguin that used heart rate as an indicator of diving metabolic rate (Thompson & Fedak 1993, Williams et al. 1999, Froget et al. 2004), as well as a study directly measuring gas exchange in the grey seal *Halichoerus grypus* (Sparling & Fedak 2004).

Overall, sDMR was between 1 to 1.2 times sMR$_S$ for the majority of dives performed by Steller sea lions. However, our data also showed that sDMR for short dives (dives < 0.8 min, 33.6 ml O_2 min^{-1} kg$^{-0.75}$) was ~14% higher than the sMR$_S$ (28.8 ml O_2 min^{-1} kg$^{-0.75}$), but sDMR decreased to within sMR$_S$ as the dive duration increased. As the overall activity increased during longer dives it appears that this decrease was caused by a reduced metabolic rate during longer dives, but this warrants further study. In either case, sDMR was between 1 to 1.2 times sMR$_S$ for the majority of dives performed by Steller sea lions.

A decrease in DMR was also seen in grey seals (Sparling & Fedak 2004). However, the decrease in DMR in our study did not decrease exponentially as we previously measured for these sea lions (Fahlman et al. unpubl. obs.). In particular, the variability for short dives (<1 min) was much lower in the current study compared with our previous data (Fahlman et al. unpubl. data). This highlights the difference in experimental protocols. In our previous study, DMR was estimated during repeated dives of a continuous nature (Fahlman et al. unpubl. obs.). That is, following a pre-trial resting period where we estimated MR$_S$, the sea lions determined the duration of both the dive and the surface interval. In the current study, the duration of the surface interval was controlled by the researcher. During the previous study it was reported that the first and last dives in a series of repeated dives, respectively, had the lowest and highest estimated DMR. It was suggested that this was indirect evidence that the sea lions adjust tissue and blood P_{O_2} during a dive bout to enhance O_2 reloading at the surface to minimize time at the surface.

Even though there was a positive relationship between dive and surface interval duration in the previous study, there was large variability in surface interval duration (mean ± SD: 0.15 ± 0.18 min, range from 0.05 to 1.11 min) for short dives (<1 min). Thus, alterations in the surface duration can cause large differences in estimated DMR for a diving sea lion that does

not completely re-saturate tissue and blood O_2 stores during a surface interval. DMR estimates are therefore highly variable for short-duration dives when the sea lions dive continuously. In addition, as the sea lions do not fully restore O_2 stores during a dive bout, it may not be possible to assume independence between repeated dives in a bout. Consequently, the actual energetic cost of a dive may require a recovery type experimental design such as the one we used in the current study.

Our experimental trial began with the sea lions being at least 16 h post-absorptive. During each dive, the sea lions were free to dive to the end of the fish delivery tube and consume fish until they decided to return to the surface. At the surface, the sea lions were held inside the respirometry dome until the O_2 level had again returned to levels obtained before diving. Thus, each dive was independent, and there was no O_2 debt incurred between dives. However, sequential dives made the sea lions post-prandial as they were catching fish at depth (delivered down the tube from the surface) throughout the experiments. It was therefore important to determine if the sea lion began digesting food between dives, as this could have resulted in changes in the relationship or added to the variation.

The metabolic cost of sequential dives may have increased due to the effects of digestion on $\dot{V}_{O_2}$ (commonly called heat increment of feeding or specific dynamic action). If so, the increased consumption of O_2 would have reduced the aerobic dive duration. We investigated this by running the model on dive number (i.e. the order of dives). This analysis showed that DMR did not change with dive number when sea lion activity was accounted for ($F_{1,138}$ = 0.11, p > 0.1). Our finding concurs with the data reported by Sparling et al. (2007), who suggested that grey seals may defer metabolism until the end of a dive bout. These results are interesting and suggest that despite extended recovery (~6 to 8 min) between dives, digestion is prevented until the end of a dive bout. Thus, the effect of heat increment of feeding does not appear to have affected or confounded our metabolic data and estimates of DMR.

CONCLUSIONS

Previous studies have assumed that the metabolic rate during the surface interval is constant and equal to the measured resting rate (Hurley & Costa 2001, Sparling & Fedak 2004). The additional cost of diving, or true DMR, is thereby estimated by subtracting the expected volume of O_2 consumed related to MR$_S$ from the volume of O_2 consumed during the dive cycle.

However, this assumption is not valid given that there is considerable variability between animals in their activity during the surface interval, as well as between dives and days. ODBA appears to be a better means of estimating the energetic cost during a dive cycle (dive + subsequent surface interval) of Steller sea lions and other species, and should ultimately be able to partition the cost between true diving and resting at the surface with the collection of additional data.

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