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REVIEW

Physiological constraints and energetic costs of diving behaviour in marine mammals: a review of studies using trained Steller sea lions diving in the open ocean

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Abstract Marine mammals are characterized as having physiological specializations that maximize the use of oxygen stores to prolong time spent under water. However, it has been difficult to undertake the requisite controlled studies to determine the physiological limitations and trade-offs that marine mammals face while diving in the wild under varying environmental and nutritional conditions. For the past decade, Steller sea lions (*Eumetopias jubatus*) trained to swim and dive in the open ocean away from the physical confines of pools participated in studies that investigated the interactions between diving behaviour, energetic costs, physiological constraints, and prey availability. Many of these studies measured the cost of diving to understand how it varies with behaviour and environmental and physiological conditions. Collectively, these studies show that the type of diving (dive bouts or single dives), the level of underwater activity, the depth and duration of dives, and the nutritional status and physical condition of the animal affect the cost of diving and foraging. They show that dive depth, dive and surface duration, and the type of dive result in physiological adjustments (heart rate, gas exchange) that may be independent of energy expenditure. They also demonstrate that changes in prey abundance and nutritional status cause sea lions to alter the balance between time spent at the surface acquiring oxygen (and offloading CO_2 and other metabolic by-products) and time spent at depth acquiring prey. These new insights into the physiological basis of diving behaviour further our understanding of the potential scope for behavioural responses of marine mammals to environmental changes, the energetic significance of these adjustments, and the consequences of approaching physiological limits.

Keywords Diving physiology · Steller sea lions · Metabolism · Foraging

The need to study diving metabolism

Marine mammals are well known for being able to remain submerged for extended durations. The early studies of marine mammals (mainly phocid or "true" seals) investigated the anatomical features by which they managed to do so. These include adaptations for withstanding the intense pressures experienced at depth and greater relative on-board oxygen stores than their terrestrial counterparts, which allows them to remain active during submergence breath-holding. For example, elevated oxygen storage is present in both circulating haemoglobin and the myoglobin of their locomotor muscle tissues (Kooyman 1985).

Marine mammals also possess a series of physiological specializations that allow them to maximize the use of these oxygen stores and prolong their time submerged (Davis and Williams 2012; Andersen 1966; Butler and Jones 1997). These are traditionally grouped into a set of physiological adjustments known as the "dive response", comprising apnea, peripheral vasoconstriction, and bradycardia. In the face of low blood oxygen pressure (PO_2), apnea maximizes the use of oxygen stores by delaying the impulse to return to the surface to breathe. The reduction of blood flow to "non-essential" tissues limits their local rates of oxygen consumption (and may also assist in myoglobin

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store utilization within constricted muscle groups; Davis et al. 2004). Bradycardia is required to maintain central blood pressure in light of these adjustments to peripheral blood flow. These physiological and anatomical adaptations are widespread among marine mammals—although not always to the same degree (Mottishaw et al. 1999; Davis 2014).

The common response of reduced heart rate and restricted blood flow observed in early studies of diving physiology suggested that energy expenditure (i.e., metabolism) while diving was low—certainly lower than for active terrestrial mammals. The diving metabolic rate (DMR) has been directly measured in a few pinniped species, but rarely under conditions that approach natural diving in the wild, and often under conditions that are euphemistically characterized as "forced diving" (e.g., Irving et al. 1935; Scholander et al. 1942). Although forced diving experiments provided novel and useful insight into marine mammal diving physiology, they likely represented an extreme example of the dive response that does not occur frequently in nature (in fact, some have referred to these experiments as demonstrations of the "fear response"). We now appreciate that the dive response is not an automatic reflex, but rather a graded adjustment that is under some degree of voluntary control (Butler 1988; Butler and Jones 1997).

Quantifying the metabolism of marine mammals while diving is important beyond the realm of comparative physiology. The rate at which oxygen stores are depleted, together with the extent of these stores, allows an animal's aerobic dive limit (ADL) to be calculated. The ADL is the maximum time that an animal can remain submerged relying solely on aerobic metabolism (Kooyman et al. 1983). Although the transition between aerobic and anaerobic metabolism during diving is likely not a distinct switch, the ADL is a critical comparative parameter for investigating the ecological physiology and behaviour of marine mammals. It not only defines the physiological constraints and costs of different foraging patterns, but it is also integral to formulating optimal foraging strategies (Carbone and Houston 1996; Houston and Carbone 1992; Thompson and Fedak 2001).

In theory, determining the diving metabolism of a marine mammal is relatively straightforward; it can be estimated from the rate of oxygen consumption ($\dot{V}\mathrm{O}_2$) and carbon dioxide production ($\dot{V}\mathrm{CO}_2$) over a dive event using the standard techniques of flow-through respirometry. This entails having the animal breathe into a semi-enclosed container with a constant flow-through airstream upon returning to the surface after completing a dive. Consequently, the $\dot{V}\mathrm{O}_2$ and $\dot{V}\mathrm{CO}_2$ during the dive are inferred from data obtained during the post-dive surface interval (Hastie et al. 2006a; Reed et al. 1994, 2000; Scholander 1940).

However, actual measurements of diving metabolism are sparse. This is partly because it is highly challenging to measure in wild animals—a notable exception being Weddell seals (*Leptonychotes weddellii*) that reliably surface in ice holes (Kooyman et al. 1980). It is equally logistically difficult to obtain these measures from trained animals in aquariums and similar facilities, given that pool depths cannot accommodate natural diving behaviour. While some novel tests have been undertaken measuring the metabolism of harbour seals (*Phoca vitulina*) swimming for extended linear distances in a pool, it is questionable whether this invokes the same physiological responses as diving to depth (Gallon et al. 2007; Sparling et al. 2007b). In particular, the effect that pressure has on the respiratory system may significantly alter physiology, including how gases are managed (Scholander 1940; McDonald and Ponganis 2013; Fahlman et al. 2009). Furthermore (as discussed later), once these operational impediments have been solved, the actual calculation of metabolic rate while diving from gas exchange data is not as straightforward as it would first appear, and there are still varying opinions on how to experimentally estimate the actual energy cost.

To attempt to address this paucity of data, we undertook a risky venture: we decided to study the diving metabolism of trained Steller sea lions (*Eumetopias jubatus*) away from the confines—and security—of a traditional laboratory or aquarium setting. Sea lions (otariids) had, of course, been trained to operate freely in the open ocean before. However, these were California sea lions (*Zalophus californianus*), and most endeavours had been undertaken by military organizations for security rather than research purposes (although a group at Moss Landing started a research program in 2005). In 2004, we began relocating trained female Steller sea lions from the Vancouver Aquarium (where they had been raised since pups) to the University of British Columbia's Open Water Research Station, based at a marina in Port Moody, British Columbia. The concept was to bridge the gap between the types of largely uncontrolled studies that could be conducted with wild animals in their natural environment and controlled experiments conducted with trained animals in an artificial (and physically restricted) environment.

The Open Water Station is unique in that researchers can measure physiological, behavioural, and ecological variables during controlled experiments using sea lions diving unrestrained in the open ocean environment. Although under trainer control, the sea lions perform dives to depths and for durations similar to wild animals (Merrick and Loughlin 1997), and can make foraging and oxygen management decisions analogous to their wild counterparts.

The objectives of the research program were to:

1. Measure the energetic cost of diving.
2. Investigate the relationship between individual physiology and diving capacity.
3. Investigate the physiological mechanisms that underpin dive behaviour.
4. Test specific optimal foraging theories for diving mammals.
5. Develop and test proxies for energy expenditure that could be used to measure the energy expenditure of diving in wild sea lions.

It might seem that the first goal—measuring the energetic cost of diving—was the most straightforward to address; but as we describe, defining and quantifying an animal's metabolism while submerged is complex. As will become apparent (and which was clear in hindsight), the actual cost of diving is variable, and can be affected by the intensity and type of subsurface activity, the dive depth, the dive and surface duration, and the physiological and nutritional state of the individual, all of which are often interacting factors. Hence, the major goal of our program developed into gleaning an understanding of how these parameters affect the cost (and underlying physiology) of diving, rather than being focused on producing a single, unrepresentative value for "the" cost of diving.

The following review is not a synopsis of the field of diving physiology, as many excellent comprehensive surveys already exist (e.g., Kooyman 2002; Davis 2014; Butler and Jones 1997). Rather, it attempts to describe the progress and discoveries made in exploring the complex interaction between diving physiology and behaviour of Steller sea lions.

Experimental set-up

While the experimental manipulations conducted over the last decade have become more complex, the general experimental set-up has changed little from its initial conception (Hastie et al. 2006b). When not undertaking studies, the sea lions stay in flow-through holding pens with adjacent haul out space at a local marina. They are trained each day by professional husbandry staff from the Vancouver Aquarium using positive reinforcement. The sea lions are usually maintained on an ad libitum diet, composed primarily of herring (*Clupea pallasii*), and supplemented with vitamins and other prey species. All husbandry and experimental protocols are approved by the Animal Care Committees of the University of British Columbia and the Vancouver Aquarium. It is important to note that all research conducted at the Open Water Research Station is done voluntarily by the sea lions, and they can end a dive trial at any point that they choose.

The sea lions are weighed each morning on a platform scale prior to their first meal. When working in the open ocean, they are outfitted with a custom, tight-fitting harness that makes the animal more visible underwater. The harness holds a VHF transmitter in case the animal wanders from the study area, and also permits the temporary attachment of additional experimental equipment, including time-depth recorders, accelerometers, heart-rate monitors, etc.

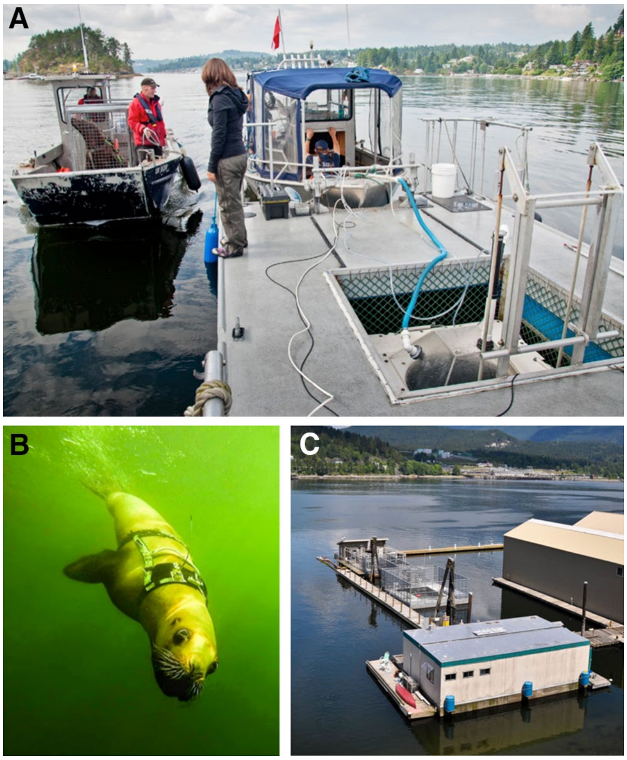

Fig. 1 Photograph of the experimental set-up for diving trials. **a** Sea lions are trained to dive between a respirometry dome situated in the middle of the floating barge (foreground) to the bottom of feeding stations that deliver 20-g pieces of fish to specific depths. A research boat (seen in the *background*) carries the associated respirometry equipment and support personnel. Sea lions are transported to the dive trial site on a separate vessel (seen on *left*). **b** When performing trials in the open water, the sea lions carry assorted scientific and safety equipment on a custom-fit harness. **c** Aerial view of the Open Water Station in Port Moody, BC, showing the laboratory (foreground) and flow-through water pens for sea lions. When not actively participating in trials, the animals interact daily in the adjacent waters with training and research staff

The actual experimental trials are undertaken in nearby, deep-water fjords that provide the necessary water depth and isolation. Sea lions are transported to these study sites on-board a modified transport boat. A second research boat carries scientific equipment, personnel, and a research platform to the selected dive site (Figs. 1, 2). The 6.0 × 3.1-m platform contains a 150 L floating respirometry dome in the centre that is attached to flow generators and O_2 and CO_2 analysers that continuously feed data into a laptop computer. Below the respirometry dome is a nylon enclosure with a trap door that assists to

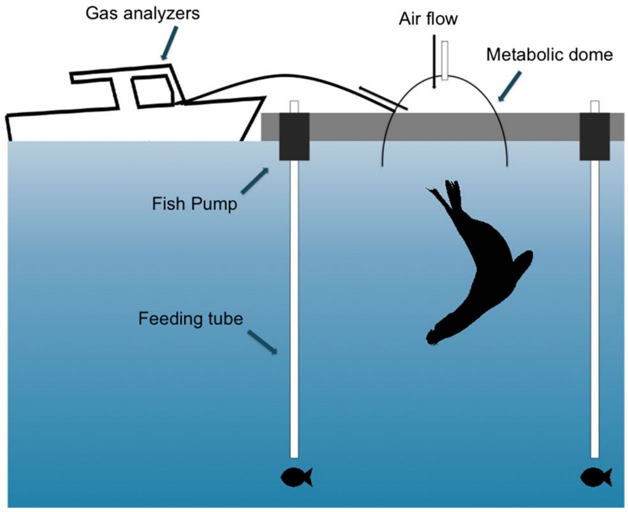

Fig. 2 Schematic (not to scale) of typical set-up for diving experiments at the Open Water Station with Steller sea lions. A floating platform holds the respirometry dome, and is connected to gas analyzers and flow generators on an accompanying research vessel. The platform also has a nylon-webbed enclosure (not shown) that can be used to encourage the sea lions to remain at the surface (but does not physically restrict them). The sea lions are trained to dive between the respirometry dome and the bottom of a pair of PVC tubes placed at desired depths (feeding stations). Pieces of fish are alternately pumped to the bottom of the two tubes at given rates to represent different quality prey patches (which may also be at different depths). Dive durations can be either chosen by the sea lion or controlled by fish delivery or light signals at depth

behaviourally contain (but not forcibly confine) the sea lions for extended periods at the surface. Lengths of PVC tubes are fitted together and lowered off the side of the platform to desired depths, usually between 10 and 50 m, to make subsurface feeding stations. Water pumps deliver 20-g pieces of fish to depth at selected rates, thereby controlling the depth (and durations if required) of the sea lions' dives. Prior to 2007, only a single feeding station was used, but later studies used two stations (~6 m apart) with alternating food delivery to stimulate swimming at depth, as well as enable tests for the effects of choices of depth and/or prey field quality (number of fish per minute) on behaviour and physiology. The set-up allows the trained sea lions to perform dives similar to their wild counterparts; Steller sea lions in the wild generally dive for less than 2 min and 90 % of their dives are shallower than 50 m (Loughlin et al. 2003, 1987).

As detailed later, various experimental protocols can be employed to alter the characteristics of a dive depending on the specific scientific goals. For example, dive durations can be either determined by the sea lions or controlled by the researchers, via either a light cue at the end of the feeding tubes or cessation of fish delivery. Similarly, interdive surface intervals can be determined by the sea lion or controlled by the researchers using training cues and food reinforcement. Video cameras at depth and at the surface allow staff to observe the behaviour of the sea lions throughout the trials.

The logistics of this experimental set-up (e.g., the high level of training, the time to run a single trial) inherently limit the number of individual sea lions that can be used in any set of experiments. This, in turn, limits statistical power, including the ability to make inferences about the population as a whole. This can be partly overcome by appropriate experimental design and use of repeated-measures and mixed-effect model statistics (Zuur et al. 2009). The fact that many of the studies use the same group of individuals adds to our ability to compare the results among studies and, therefore, to derive conclusions regarding the physiological and behavioural effects of different experimental conditions.

Finally, despite its ground-breaking design, we recognize the inherent limitations of the experimental set-up. As these are trained sea lions kept under human care, their behaviour and life history are not identical to their wild counterparts, and certain aspects of their physiology may also differ. For example, the study animals are free of disease and injury, are non-breeding, and while they are accustomed to regular diving and swimming in the open ocean, it is not on the same schedule as wild sea lions (although see Gerlinsky et al. 2013). It is also worth noting that, at the end of the day, our sea lions do not have to forage to survive. While the open water design differs from the "elongated pool" protocol (e.g., Sparling and Fedak 2004) by incorporating the effects of depth and pressure, it is limited in the amount of activity (number of dives) the animals will perform while still reliably collecting respirometry data (i.e., returning to the dome). Although using trained animals under these controlled conditions permits testing a range of specific physiological, behavioural, and environmental effects, this set-up cannot reproduce completely "natural" behaviours that can be observed through measuring the energy expenditure of wild pinnipeds (Kooyman et al. 1980; Iverson et al. 2010). As with all manipulative experiments, studies are designed and interpreted with these considerations in mind.

Calculating the cost of diving

On first consideration, it would not seem overly complicated to calculate an animal's metabolism while diving given accurate measures of O_2 consumption and CO_2 production. However, one difficulty is that, unlike terrestrial mammals, the gas exchange related to physical activity is temporally removed from the measurement of that consumption. This is because, in diving mammals, the actual O_2 consumption occurs at depth away from the respirometry dome, and can only be replenished (and CO_2 off-loaded) after the dive has been completed.

The most common measure of metabolism while submerged is diving metabolic rate (DMR). For single dives, DMR can be quantified from the excess (above resting levels) volume of O_2 consumed (VO_2) and CO_2 expelled (VCO_2) that occurs post-dive, which is measured until the point when the animal has returned to its resting state. The definition of "resting state" is, in itself, open to interpretation. For practical and scientific reasons, we use the stable rate of oxygen consumption ($\dot{V}O_2$) while the sea lions are resting, inactive at the water's surface prior to any diving activity, and with minimal food reinforcement (to minimize the potential effect of the heat increment of feeding; HIF) as our "baseline" measure. This may or may not coincide with classically defined resting metabolic rate, and so we adopted the nomenclature of "metabolic rate at the surface" (MRs, Fig. 3a) (Fahlman et al. 2008b).

This additional post-dive $\dot{V}O_2$ and $\dot{V}CO_2$ above MRs levels are thought to represent the aerobic metabolism during the dive. The VO_2 consumed during the submerged portion of the dive can, therefore, be estimated by subtracting the post-dive increase in $\dot{V}O_2$ from the MRs. The total energetic cost of a dive can then be calculated as the total additional oxygen consumed, while DMR can be calculated by dividing the total cost by the submergence time (Fig. 3a).

It is vitally important that the animal has sufficient time to completely recover between dives, or the true DMR will be underestimated by failing to capture all post-dive excess $\dot{V}O_2$. In theory, pre-dive MRs and post-dive MRs should be identical. However, in a subset of our studies, we found that the pre-dive MRs was elevated in relation to post-dive MRs. This may be due to natural physiological variation, or it may be due to behavioural and physiological anticipation of diving causing an elevation in pre-dive MRs.

The importance of an animal returning to steady state is a vital consideration when measuring DMR of sea lions performing dive bouts, as they often do in the wild. Dive bouts consist of multiple dives interspersed with relatively brief inter-dive surface intervals, followed by an extended post-dive surface recovery period at the end of the bout. The inter-dive surface intervals are too short for complete gas exchange (i.e., animals do not return to resting state and carry over some level of oxygen debt). As a result, the $\dot{V}O_2$ must be determined over the entire dive bout (Boutilier et al. 2001). In fact, a dive bout (in contrast to single dives) could be operationally defined as a series of dives with incomplete physiological recovery in between. Hence, DMR for dive bouts is calculated from the total additional $\dot{V}O_2$ during both the brief inter-dive surface intervals and

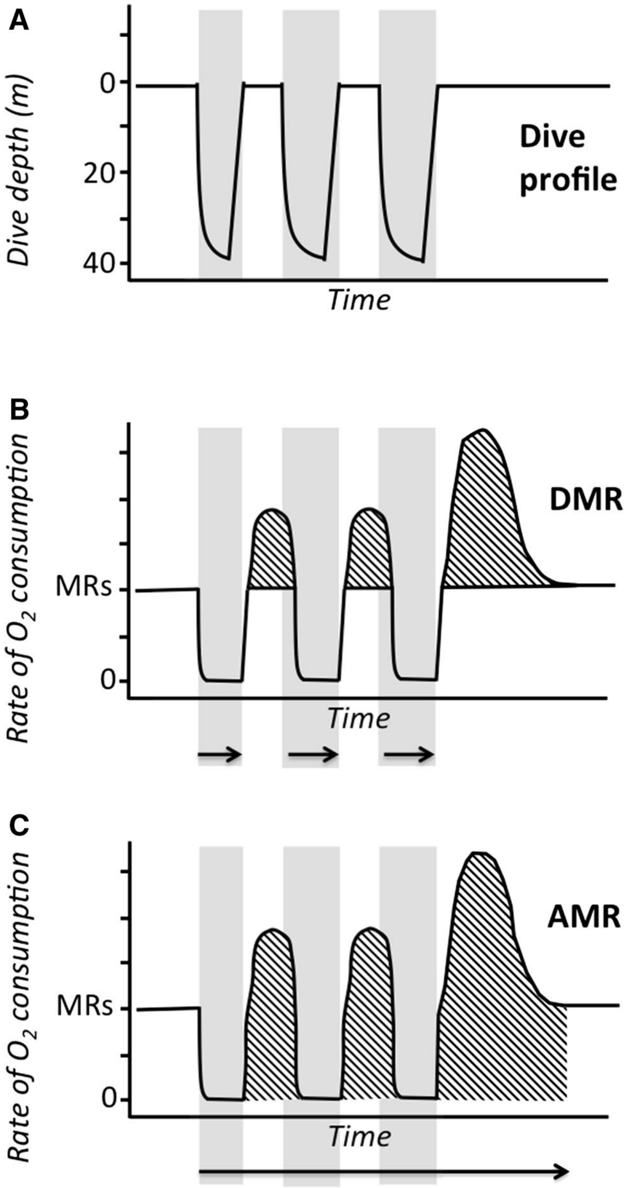

Fig. 3 Schematic representing measurement of diving metabolic rate (DMR) and average metabolic rate (AMR) of diving sea lions from recorded changes in spontaneous oxygen consumption. **a** Represents a theoretical series of three dives to 40 m, with submergence periods indicated by the *grey bars*. DMR **b** is measured as the post-dive increase in total oxygen consumption above resting (MRs) levels (identified by the striped areas) divided by the actual submergence time (identified by *arrows*). AMR **c** is calculated from total oxygen consumption (integrated above "zero") from the start of the dive until the rate of oxygen consumption reaches the original steady state (MRs), divided by the time from the start of the dive until recovery is reached. These measures can be applied to either single dives (which are followed by complete recovery) or bouts of multiple dives. As individual dives within a dive bout are not physiologically independent (due to incomplete oxygen recovery), only a single value for either DMR or AMR can be obtained for a given bout

the final post-dive recovery, divided by the total submergence time. As each dive in the bout is not physiologically independent, only a single estimate of DMR, calculated across all dives in the bout, can be obtained (thereby inherently limiting statistical power).

While DMR may seem a logical way to measure the cost of diving, it makes the assumption that the dive and the time at the surface (both inter-dive surface intervals and post-dive recovery periods) are independent events. In other words, it assumes that the post-dive metabolic rate is simply the sum of the direct cost of the submerged portion of the dive cycle and resting surface rate. Evidence suggests that this is not physiologically accurate (Fedak 1988; Kooyman and Ponganis 1998; Reed et al. 1994). This has led to the calculation of an alternate measure, often referred to as "average metabolic rate" (AMR). For AMR, the total volume of oxygen consumed is averaged over the entire dive cycle (submergence and inter-dive and post-dive surface times). Unlike DMR calculations, it does not attempt to separate the "surface resting" and "diving" portions of oxygen consumption measured during the post-dive surface intervals. Rather, AMR entails integrating the total volume of oxygen consumed and converting it to a rate by dividing over the length of the dive cycle. The dive cycle is the time from the start of the first dive to the end of the recovery period (when rates of oxygen consumption return to baseline levels; Fig. 3b). AMR can be calculated for both single dives and dive bouts although, as with DMR, only a single value can be calculated for a single dive bout.

To clarify, DMR and AMR are (in our usage) alternate means of calculating the rate of oxygen consumption during either single dives or a mean value over a dive bout consisting of a series of submergences. There are pros and cons to estimating the energetic cost of diving as either DMR or AMR. DMR is theoretically a more "direct" cost of the actual submergence time, but makes the questionable assumption that post-dive rates of oxygen consumption are simply the sum of the exertion of the previous activity and the costs of resting at the surface. DMR is also more dependent on the measure of MRs; if MRs is elevated, DMR will be underestimated. In comparison, AMR does not make the assumption of physiological independent between post-dive MRs and the costs of the previous physical exercise. It is not as susceptible to errors induced by elevated pre-dive MRs, as it is calculated on the total observed rates of oxygen consumption. However, it is highly susceptible to errors induced by inaccurate estimates of the recovery time. As AMR is based on the total oxygen consumption over the entire dive cycle, miscalculations in the recovery period will proportionally affect the measure (e.g., incorrectly long recovery times will proportionally decrease the apparent AMR by increasing the denominator).

It is also important to note that the estimated recovery time is a useful physiological measure in its own right. As later discussed, it can provide valuable information on post-dive gas exchange rates and can be used to examine the effect of diving duration on foraging efficiency over a complete dive cycle. Finally, when comparing published studies, it is important to note the specific formula used to calculate diving metabolism, as the terms DMR and AMR have been variously used to denote a variety of calculations. For clarity in this review, DMR will always refer to the rate of oxygen consumption calculated for the submerged portion of the dive and AMR will refer to the average metabolic rate over the entire dive cycle.

Evidence for hypometabolism while submerged

One of the first studies conducted at the Open Water Research Station using two Steller sea lions appeared to confirm the general marine mammal model that metabolism was depressed during diving (Hastie et al. 2007). This initial study employed a relatively straightforward set-up: the animal undertook single dives, of a controlled (but variable) duration (60–200 s), to a submerged target positioned at depth (between 5 and 30 m). Each trial involved single dives followed by a post-dive recovery. The results indicated that DMR was only 55–57 % of MRs, and neither dive duration nor depth was a significant predictor of DMR in the resulting statistical model.

These results provided the first estimates of DMR for Steller sea lions and showed that this species can exhibit a marked decrease in oxygen consumption while submerged relative to surface rates. These results were similar to those reported for California sea lions (Hurley and Costa 2001), and would appear to support Scholander's (1940) original hypothesis that marine mammals reduce their metabolic rate during diving to help increase foraging efficiency.

However, there were suggestions that our early results (Hastie et al. 2007) did not accurately reflect the metabolism of sea lions while diving. One concern was that the sea lions, despite an extensive preliminary training period, were not completely comfortable with the experimental protocols. Average pre-dive MRs (~1.64 L O_2 min^{-1}) were slightly higher compared with subsequent studies (and measured recovery periods slightly shorter), potentially leading to underestimates of the costs of the dives (see earlier discussion on potential errors in calculating DMR). On a related note, there was concern that a lack of familiarity with the experimental protocols—specifically that the animals did not control dive duration—may have induced a "maximum" dive response, similar to (although less dramatic than) the effect reported for the early "forced" diving experiments (Jobsis et al. 2001).

A more general concern related to the fact that metabolism was not measured under "realistic" conditions. The dives were relatively short, the sea lions performed only single dives and not dive bouts, and their activity at depth was minimal. As a result, the effect of predictability and control on physiological response, dive duration, activity level, and the differences between single dives and dive bouts were explored in subsequent studies.

Effect of dive duration and dive bouts

In our first study, the Steller sea lions did not demonstrate a relationship between DMR and dive duration (Hastie et al. 2007); however, the dive durations were only 3 min. In comparison, California sea lions showed larger decreases in DMR with dive durations of up to 7 min (Hurley and Costa 2001).

A subsequent study (Fahlman et al. 2008b) used three sea lions (two which were the same as the previous study) in dive trials that consisted of a series of repeated dives (2–15 dives) to a single feeding station at depths of 10–50 m. For dives where the sea lions chose both dive and inter-dive surface interval durations, DMR decreased exponentially with increasing dive duration. For dives longer than 1 min, DMR reached levels ~8 % lower than MRs.

Another follow-up study also investigated the potential metabolic differences between single dives and dive bouts in a trial that employed dive bouts composed of a set of up to five individual dives (Hastie et al. 2006a). Three sea lions dove to depths (5–30 m) with controlled dive times (40–200 s) similar to the earlier study that only measured metabolism over single dives (Hastie et al. 2007). However, in these trials, the inter-dive surface intervals between individual dives in the bout were limited (7–25 s) to simulate more natural dive bouts. Variation in dive duration and inter-dive surface intervals meant that the proportion of the dive cycle spent submerged ranged between 23 and 88 % (average = 75 %). While the study determined that diving metabolic rate was affected by dive activity (discussed later), it also determined that DMR decreased curvilinearly with dive depth once activity was considered. This relationship was not observed in the previous study that only employed single dives (Hastie et al. 2007).

It should not be surprising that single dives and dive bouts have different cost characteristics, given that they have different gas exchange dynamics. Inter-dive surface intervals during a dive bout represent "recovery" time, in which sea lions can off-load CO_2 and other metabolites from exercising tissues, and replenish on-board O_2 stores. Oxygen management during extended dives is complicated, involving peripheral, arterial, venous, and pulmonary circulatory adjustments (see McDonald and Ponganis 2013). It is unclear the degree to which diving mammals normally replenish their O_2 stores between dives in a bout, although a law of diminishing returns for oxygen uptake across a decreasing partial pressure gradient would suggest that it might be optimal for a sea lion to maintain some level of constant oxygen debt through a dive bout (Boutilier et al. 2001). Dive bouts, by definition, are characterized by inter-dive surface intervals that limit the extent of gas exchange and theoretically affect both dive behaviour and metabolic costs of subsequent dives. Therefore, the next set of trials specifically examined the effect of differing surface intervals on subsequent dive durations and their associated costs.

While these initial studies (Hastie et al. 2006a, 2007) highlighted the differences in cost between single dives and more natural dive bouts, a critical detail of the methodology was that both the dive durations and inter-dive surface intervals (for dive bouts) were controlled by the researchers and not the animals. A lack of control over dive durations may mean that the animals were responding to an uncertainty in submergence times by altering their physiological response compared with "natural" diving to maximize their potential submergence time. Hence, in the following study, the sea lions were allowed to control their dive duration.

The dive trials with three sea lions in the subsequent study (Fahlman et al. 2008b) consisted of either a single dive or a bout of repeated dives (2–15 dives) to a single feeding station at depths of 10–50 m. Two different diving protocols were used: 'spontaneous' dives where the trainers exerted no control over dive and inter-dive surface interval durations and 'conditioned' dives where the sea lions controlled the dive duration but were held at the surface between dives until the instantaneous rate of oxygen consumption returned to baseline levels. The conditioned dive bouts had imposed inter-dive surface intervals (1–8 min), such that they were, effectively, more similar to a series of single dives with near-complete gas exchange recovery between dives. In contrast, the inter-dive surface intervals (5–60 s) were much shorter for the spontaneous dives, such that they were equivalent to dive bouts in the previous studies.

Overall, the average DMR for all animals was 1.65 ± 0.66 L O_2 min^{-1}, which was lower compared with the previous study (Hastie et al. 2007), but still higher than the average MRs of 1.45 ± 0.44 L O_2 min^{-1}. The most striking result of this study was that DMR was significantly higher for spontaneous dive events as compared with conditioned dives (1.74 ± 0.70 vs. 1.57 ± 0.40 L O_2 min^{-1}). Part of this difference might be attributable to differences in dive duration. The average dive durations during the conditioned dives were significantly longer than during spontaneous dives (2.28 ± 1.53 vs. 0.97 ± 0.83 min). However, DMR for spontaneous dives decreased exponentially with increasing dive duration. For dives longer than 1 min, DMR for spontaneous dives was lower than that for conditioned dives and, as previously noted, reached levels ~8 % lower than MRs.

Given the hypothesis that increasing levels of O_2 debt are incurred during dive bouts, this result also suggests that sea lions might alter their rate of oxygen consumption based upon their physiological state (i.e., remaining levels of oxygen stores). This contention is supported by the observation that the first dive of a series of spontaneous dives was longest and had the lowest apparent $\dot{V}O_2$, while the last dive, which was followed by a long recovery period, had the highest $\dot{V}O_2$. These results indicate that the sea lions developed an O_2 debt during the first dive, which was not restored until the sea lion spent considerable time at the surface at the end of the bout. This also demonstrates why DMR cannot be accurately estimated for each separate dive during a bout.

Effect of activity on diving metabolism

One suggested explanation for the measured hypometabolism in both the Steller sea lions in our first diving study (Hastie et al. 2007) and in a similar study using California sea lions (Hurley and Costa 2001) was that the animals were trained to remain stationary at depth. Given the assumption that active swimming is more metabolically expensive than remaining at depth (see “Diving behaviour”), this would suggest that the observed hypometabolism was facilitated by a lack of energy expenditure due to movement. However, a later study that examined the relationship between activity and diving metabolism extrapolated that—for the same level of activity—the metabolic rate during diving may be as much as 29 % lower than when at the surface between dives (Fahlman et al. 2013).

The effect of activity on metabolism while submerged was specifically examined in the previously mentioned study that first incorporated more realistic bouts of five dives. The results indicated that DMR was affected by both dive depth and type of activity during the dive (Hastie et al. 2006a). The fact that both factors had a significant effect on metabolic rate may seem obvious given the presumed cost of active swimming and the fact that total travel time and distance (ascent and descent) change inherently with dive depth and the number of individual dives in a bout; but the actual results were surprising. As predicted, DMR increased curvilinearly with increasing total swimming distance, which ranged from 10 to 300 m during a bout. However, DMR also decreased curvilinearly with maximum dive depth once travel distance was accounted for, although the physiological cause for this response is unclear (possibly triggered by pressure increases?; Andersen 1966).

Overall, distance travelled and dive depth appeared to have significant, but opposing effects on DMR. To put these mathematical relationships in perspective, for dive bouts that consisted of a total of 600 m of transit distance, DMR (averaged over all dives in the dive bout) was predicted to be 3.37 L O_2 min^{-1} for dives to 10 m and 2.44 L O_2 min^{-1} for 50-m dives. Additionally, extrapolation of these results suggests that DMR during more realistic, deep dive bouts was up to 68 % greater than when resting at the surface. These results provided the first indication that the behaviour of the animals while diving greatly affects the calculated costs of diving.

Differences in dive behaviour might also partly explain why the overall metabolic rate was significantly lower for conditioned dives than spontaneous dives over the entire dive bout in the later study (Fahlman et al. 2008b). On average, maximum dive depth was shallower during the spontaneous dive trials (11.5 ± 6.3 m) than during the conditioned ones (20.1 ± 14.3 m). As underwater activity is generally higher during shallow dives (as a proportion of total dive time; Fahlman et al. 2013), particularly in the relative amount of higher cost transiting behaviour (Goundie et al. 2015b; discussed later; Fahlman et al. 2008c), the slightly higher average metabolic rate for spontaneous dives might be partly due to differences in the costs associated with activity.

Cardiac responses and activity levels

The results of our earlier diving studies highlight that estimating “the” cost of diving is complicated by various interconnecting characteristics of the dive: activity level, dive depth, single dive vs. dive bout, etc. Additionally, the relationships are made more complex by the fact that marine mammals have the ability to make a number of physiological adjustments during diving (reviewed in a number of sources, including Kooyman 2002; Davis 2014; Butler and Jones 1997). To begin to clarify the role of internal physiological adjustments on changes in the cost of diving, we measured $\dot{V}O_2$ in tandem with direct measures of both the level of physical activity and a quantified metric of the extent of the dive response (Hindle et al. 2010b). This facilitated understanding the effect of these variables on total costs, and also enabled us to examine the temporal pattern of the onset of the dive response.

Specifically, the dive response study compared the extent of bradycardia (decrease in heart rate, *f*H) during shallow and deep dives, and its relationship to $\dot{V}O_2$ and level of activity (Hindle et al. 2010b). In terrestrial mammals, *f*H increases with exercise, as a means of delivering oxygen to highly active locomotor muscles. Hence, there is a reasonable relationship between physical activity, *f*H, and $\dot{V}O_2$. However, *f*H is predicted to be disassociated with energy expenditure and activity in marine mammals (Fedak 1988). As noted previously, bradycardia and vasoconstriction serve to limit blood flow to locomotor muscles, partly to curtail blood oxygen depletion and partly to assist the release of oxygen from myoglobin stores (Davis 2014). However, it is unclear how *f*H changes during the course of different types of dives, or how maximum bradycardia relates to dive characteristics (depth, duration) or energy expenditure (despite suggestions that maximum bradycardia is unrelated to maximum dive duration across pinniped species; Mottishaw et al. 1999). The relationship between *f*H and $\dot{V}O_2$ is also likely complicated by the fact that *f*H in marine mammals is at least partly under voluntary control.

Hindle et al. (2010b) monitored *f*H in diving sea lions via two subcutaneous electrodes while simultaneously measuring acceleration in three dimensions via a data logger. The latter could be converted into a measure of total body movement, known as overall dynamic body acceleration (ODBA; Wilson et al. 2006), which is used as a proxy of physical activity (see a more detailed discussion in "Predicting rates of oxygen consumption"). Similar to the previous studies, three sea lions undertook single short dives, single long dives, or bouts of four dives to either 10 or 40 m. To better mimic natural diving, a pair of feeding stations (with alternating timing of fish delivery) was positioned about 6 m apart to promote horizontal movement at depth. The sea lions controlled both the inter-dive surface intervals and the dive durations; longer dive times were encouraged during the single dives by increased food delivery rates.

Based on decreases in DMR with increasing dive duration reported in the previous studies, the dive response (i.e., degree of bradycardia) was expected to be stronger during extended dives—particularly when diving to deeper depths and for longer durations. Minimum *f*H (our primary measure of bradycardia) was lower during dive bouts than single dives at either depth. Similarly, dive duration correlated negatively with minimum instantaneous *f*H at both trial depths, but only for dive bouts (a similar trend was observed in single dives, but this was not statistically significant). In other words, minimum *f*H was lower for longer dive bouts at both 10 and 40 m. This result highlights the flexibility in the dive response within individual animals.

Another notable result of the Hindle et al. (2010b) study was that minimum *f*H appeared to be a more accurate measure for quantifying the extent of bradycardia than mean *f*H. For example, mean *f*H only showed a non-significant trend in differences between single dives and dive bouts, and demonstrated no relationship to dive duration. Minimum *f*H may be a stronger indicator of the extent of the dive response than mean *f*H because it not only (by definition) indicates maximum bradycardia, but is unaffected by the fact that *f*H is not constant during a dive cycle. Mean values can be greatly affected by the rate of onset and release of bradycardia and by changes in *f*H during the dive, such as pre-surface tachycardia (increase in heart rate). For example, instantaneous *f*H dropped an average of 64 % from pre-dive baseline within the first few seconds of the 10-m dives, reaching a minimum about 29 s post-submergence, and remained consistently reduced during these dives. As a result, mean *f*H decreased with increasing dive duration. In contrast, the onset of bradycardia was much more gradual during the deeper, longer 40-m dives, reaching a minimum after 45 s. Part of the difference in bradycardia onset time may be attributable to the differences in the time it takes to reach depths of 10 or 40 m (~9 vs. 30 s). As a result, mean *f*H during deeper dives was actually higher than during 10-m dives. In addition, transient increases in *f*H were observed periodically throughout submergence at 40 m, effectively increasing mean *f*H but not affecting minimum values. Furthermore, ascent tachycardia (a term describing the release of bradycardia which occurs prior to surfacing) occurred for both 10- and 40-m dives, but the deeper (longer) dives had a longer period of ascent tachycardia, which increased mean *f*H.

While the Hindle et al. (2010b) study demonstrated a relationship between the extent of bradycardia and dive duration, it is not the same as saying that there is a relationship between cardiovascular function and physical activity (Fedak 1988). If locomotor muscle remains at least partially perfused during diving, a correlation should occur between underwater locomotion and heart rate during diving (see further discussion in Davis 2014). In contrast, measures of exercise output (e.g., flipper stroke frequency) and *f*H should be independent over the dive period for species in which there is likely minimal blood flow to muscle during diving (e.g., emperor penguins, *Aptenodytes forsteri*, Meir et al. 2008). As an added complication, periods of elevated activity may alter peripheral reperfusion of muscles (Williams et al. 2015), resulting in the intermittent periods of increased blood flow during activity.

Hindle et al. (2010b) found that changes in *f*H during the dive and the differences in bradycardia patterns observed between different types of dives were not reflected in the apparent levels of physical activity, as measured by the ODBA accelerometry values. Activity was high in the first 2 s of diving, reflecting initial orientation and thrust to depth (see Fahlman et al. 2008a), followed by a pronounced decline of ~85 % for dives at both depths. This decline was prolonged in the 40-m dives (reflecting a longer transit time to depth), and was followed by a considerable rise ~20 s later corresponding to the start of the dive's bottom phase. Activity then fluctuated throughout the remaining underwater time; a similar pattern was observed over the majority of the time course of 10-m dives.

Contrary to the temporal pattern of *f*H, and aside from a minor elevation in the final 3 s before surfacing, there was no clear elevation in ODBA during the ascent (although see Fahlman et al. 2008c). The overall result was a significant positive linear relationship between ODBA and mean diving *f*H for dives to 10 m, but not for dives to 40 m. Furthermore, for both diving scenarios, surface *f*H correlated with dive activity, suggesting that some underwater locomotor costs were deferred to the post-dive surface interval. This further supports the speculation that locomotor muscles of Steller sea lions become hypoxic during diving, regardless of dive depth. The likely mechanism for this is a limitation of perfusion to muscle vascular beds, presumably occurring to a lesser degree in shallow dives.

Overall, the results of the Hindle et al. (2010b) study confirm that the processes of physical activity, oxygen utilization, and cardiac output are more independent in exercising diving mammals than their terrestrial counterparts. The predictive power of the relationship between *f*H and oxygen consumption over an entire dive is discussed later (see "Predicting rates of oxygen consumption").

Physiological constraints to diving

The presumed goal of the dive response is to maximize time spent being active while submerged. The results from the previous experiments confirm the ability of Steller sea lions to use physiological adjustments to maximize both foraging activity and time at depth. While marine mammals can and do also rely on anaerobic metabolism to extend submergence time, an additional assumption is that an animal which manages to fulfill its energetic demands through aerobic metabolism will be more "efficient" than one that relies on anaerobic metabolism. This is related to the additional costs associated with the production of metabolic by-products, and the time required for their post-dive clearance (Kooyman and Ponganis 1998). Hence, the aerobic dive limit (ADL) has become a standard comparative metric of diving capacity among marine mammals (Costa et al. 2001). This attribute is rarely determined directly (via appearance of blood lactate), and so researchers rely upon the calculated aerobic dive limit (cADL) to approximate the actual ADL. The cADL is quantified from total body oxygen stores (TBO; the oxygen reserve) and diving metabolic rate (i.e., the rate at which the reserves are consumed) (Butler 2006).

In the wild, adult female Steller sea lions largely exhibit a pattern of relatively brief (averaging 1.9–2.4 min), shallow (averaging 21–53 m), and frequent dives (Merrick et al. 1994; Loughlin et al. 1998). In fact, 92 % of dives in winter and 98 % of dives in summer made by adult females are <4 min (Merrick and Loughlin 1997). An important question is how much of this diving pattern represents responses to extrinsic factors (e.g., fish distribution, water depth) and how much is due to intrinsic factors (e.g., physiological constraints).

Surprisingly, the cADL of otariids has rarely been estimated, primarily because of the difficulties associated with obtaining measures of DMR. The previously described natural variation in diving metabolic rate under diverse diving regimes, in combination with differences in the method of calculating metabolic expenditure, serves to make estimates of cADL less clear than standard definitions might indicate.

We estimated the cADL in four Steller sea lions by combining estimates of total body oxygen (TBO) stores with measures of DMR while diving to 10 or 40 m (Gerlinsky et al. 2013). We started by calculating TBO from direct measures of blood oxygen stores and lean tissue mass, and estimates of lung volume and myoglobin concentrations—and found that our estimated TBO (35.9 ml O_2 kg^{-1}) was slightly lower than previously reported for young Steller sea lions and other otariids (Lenfant et al. 1970; Richmond et al. 2006). As with the previous studies, pre-dive metabolism (1.78 L O_2 min^{-1} for animals averaging 193 kg) was lower than metabolic rate during a dive. Mean DMR for single dives was 2.88 L O_2 min^{-1} but also depended significantly on dive duration. A "minimum" DMR was estimated as 2.68 L O_2 min^{-1} for dives >4.5 min, as DMR for these dives was no longer dependant on dive duration. Mean AMR was 2.24 L O_2 min^{-1} for single dives and 2.44 L O_2 min^{-1} for a bout of four consecutive dives. It should be noted that these values are significantly higher than those reported for earlier studies (1.20–1.74 L O2 min^{-1}, Fahlman et al. 2008b; Hastie et al. 2006a) and, therefore, will result in a proportionally lower cADL. The source of these differences is unclear; while the animals were larger on average than in the previous studies, some of the difference was likely due to a higher level of bottom foraging activity from the use of dual feeding stations and may, therefore, more accurately reflect the estimates of ADL in free-ranging sea lions.

The cADL for a single dive was 3.0 min based on the observed AMR and 2.5 min based on the calculated minimal DMR. Actual dive durations for single dives were conspicuously longer (4.4 min on average) than the cADL. However, the dive durations of the sea lions when performing consecutive dives in a bout became progressively shorter and were, on average, ~2.2 min each—slightly less than their cADL, and more similar to the behaviour of wild animals. Undertaking shortened dives during bouts may reflect the incurred oxygen debt maintained by sea lions during such diving (Fahlman et al. 2008b). Our sea lions spent short (average 18 s) surface intervals between their dives, which was likely insufficient to fully replenish their oxygen stores—indicating a delayed payoff of oxygen debt. Hence, a consecutive bout of diving (akin to what animals typically perform in the wild) may be more constrained by aerobic limits than a single dive, and the average duration of dives in a bout may correspond more closely to the ADL. In other words, if there is no immediate need to fully balance oxygen stores or process accumulated lactate, single dives may be "uncoupled" from aerobic limits (Horning 2012).

The importance traditionally placed on ADL as an ecological and physiological meaningful measure of diving capacity is a bit misleading. In most mammals, high partial pressures of blood carbon dioxide (PCO_2) rather than low blood oxygen pressures (PO_2) play a central role in the control of ventilation (Phillipson et al. 1981; Schagatay 2010). There is no reason to expect that the same general mechanism does not control diving in marine mammals, with high PCO_2 ultimately driving a return to the surface to breathe. However, it would seem advantageous for marine mammals to defer surfacing for gas exchange as long as possible (although see discussion in "Foraging strategies" on the effect of increased recovery times). Hence, apnea is generally considered to be one of the critical characteristics of the classical dive response. At first glance, listing the need for a mammal to not breathe while submerged may seem needlessly obvious. However, in the case of diving mammals, the apneic adaptation refers to a dampening of the breathing response in conditions that would induce respiratory drive in most mammals.

The blood PO_2 of marine mammals can reach levels below that typically exhibited by terrestrial counterparts (Meir et al. 2009). At the same time, the blood of marine mammals can carry more CO_2 as carboxyhemoglobin than terrestrial mammals (Tift et al. 2014), and they may be more tolerant of higher PCO_2 levels and better able to buffer its effects (Castellini 1991; Lenfant et al. 1970). While a number of studies conducted in tanks suggest that breath-hold duration of marine mammals is affected by high blood PCO_2 levels (hypercapnia) (Pasche 1976; Gallivan 1980), no work had been conducted on animals diving freely to realistic depths. While there is some evidence that surface interval durations are managed to allow adequate removal of CO_2 (Boutilier et al. 2001; Fahlman et al. 2008b), it is unclear what role PO_2 plays in regulating dive duration, particularly during dive bouts.

To assess the influence of PCO_2 and PO_2 on the physiological control of dive behaviour, we tested how increasing levels of inspired CO_2 (hypercarbia) and decreasing inspired O_2 (hypoxia) affected the diving metabolic rate, submergence times, and dive recovery times (time to replenish O_2 stores and eliminate CO_2) in our freely diving Steller sea lions by altering the gas composition within the respirometry dome (Gerlinsky et al. 2014a). While hypercarbia (starting as low as 2 % CO_2) increased breathing frequency, it did not affect metabolic rate, or the duration of dives or surface intervals (tested up to 3 % CO_2). Changes in breathing rates indicated that respiratory drive was altered by hypercarbia at rest, but also suggested that blood CO_2 levels remained below the threshold that would alter normal dive behaviour.

Regardless of the inspired air conditions (whether breathing ambient air, hypercarbia, or hypoxia), it took the sea lions longer to remove accumulated CO_2 than it did for them to replenish their O_2 stores following dives (as seen in other mammals). This difference between O_2 and CO_2 recovery times grew with increasing dive durations, increasing hypercarbia, and was greater for bout dives, suggesting that there could be a build-up of CO_2 load with repeated dives (despite any compensatory changes in ventilation rate). Although we saw no evidence of CO_2 limiting dive behaviour within our testing conditions, the longer time required to remove CO_2 may eventually exhibit control over the overall time which they can spend in apnea and thus regulate overall foraging duration.

Foraging strategies: interacting effects of physiology, prey, and nutritional status

Of course, sea lions are not slaves to their physiology; motivation and cost-benefit considerations are important in shaping behaviour. This is the basis of an entire area of study—optimal foraging theory—which has its own subset of theories regarding how a breath-hold diver should optimize its subsurface foraging behaviour based on prey patch characteristics and physiological limits (see Thompson and Fedak 2001; Carbone and Houston 1996). To address these theories, we conducted a study to quantify how sea lions respond to changes in prey availability, and how this affects their foraging efficiency by measuring DMR, dive durations, and food intake of animals diving on prey patches at varying depths (10 and 40 m) and densities (delivered at 4 and 12 fish min^{-1}) (Goundie et al. 2015a).

The rate of energy expenditure of the four sea lions did not change while diving in any of the simulated foraging conditions, but the proportion of time spent consuming prey increased with prey patch density due to alterations in diving patterns. While it may seem an obvious choice to prolong dive duration to remain longer on a higher quality forage patch, there is a consequence to this strategy in the form of extended post-dive recovery times. However, for the sea lions, the increased time at depth more than offset the subsequent increases in surface recovery time. At both depths, sea lions spent a greater proportion of the dive bout foraging in the high-density prey patches (45 vs. 28 %), leading to higher rates of energy gain and foraging efficiency (cost:benefit ratio). Conversely, in low-density prey patches, the animals spent a smaller proportion of the dive bout actively feeding and, consequently, had lower rates of energy gain and foraging efficiency. In other words, by extending the dive duration in a high-density patch, the increase in overall foraging efficiency (considering the increased recovery times) was still significantly greater (~5:1) than that due to differences in prey availability alone

(3:1). Conversely, our results indicate that sea lions foraging in areas with reduced prey availability forage less efficiently and, therefore, would have greater difficulty fulfilling their daily energy requirements than might be predicted from estimates of prey density alone.

Understanding the interactions between foraging behaviour and aerobic capacity is further complicated by the fact that neither the physiology (e.g., metabolism) nor the oxygen stores of sea lions remains constant, resulting in variable diving abilities. For example, total oxygen stores were only slightly higher during the winter than the summer or spring in Steller sea lions. However, given the seasonal differences in body mass, this meant that mass-specific blood volume of Steller sea lions was significantly higher in the winter than in summer (Gerlinsky et al. 2013). Of course, any form of mass-scaling is fraught with difficulties and differences of opinion. However, in this case, the differences are physiologically relevant for their effect on cADL, given that DMR also changes with body mass.

The findings of Gerlinsky et al. (2013) highlight that sea lion physiology is markedly seasonal; their net aerobic diving capacity is the product of simultaneous changes in blood volume, body mass (including muscle oxygen stores), and resting metabolism (which may itself affect DMR). These changes are even greater during periods of nutritional stress, which are characterized by rapid changes in body mass (with a seasonally varying portion from core tissues; Rosen 2009) and either increases or decreases in resting and diving metabolism (depending on season and type of nutritional challenge; Rosen and Trites 2002; Svärd et al. 2009).

Given the aforementioned considerations, we conducted a set of studies to specifically examine whether episodes of nutritional stress affect the sea lions' capacity to successfully forage. Animals under some level of nutritional challenge often exhibit depressed resting metabolic rates in air (Guppy and Withers 1999). Studies with non-diving Steller sea lions have demonstrated that this response is contingent upon the type of nutritional challenge and season (Rosen and Trites 2002). If altered metabolic rate at rest parallels changes during diving, this would result in proportional (but inverse) alterations in ADL. At the same time, decreasing core body mass due to energy deficits would theoretically decrease both metabolic requirements and myoglobin oxygen stores, each with opposite effects on ADL. In addition, reductions in the subcutaneous blubber layer could increase thermoregulatory costs during diving (Fahlman et al. 2005; Rosen et al. 2007). In theory, any increase in diving metabolism or decrease in oxygen stores would reduce ADL and impede foraging capacity; however, the actual net effect of episodes of nutritional stress on diving sea lions is difficult to predict.

To address the potential effects of nutritional status and body condition on diving abilities, we first examined the effect of an acute period of nutritional stress on diving behaviour and costs (Svärd et al. 2009). Specifically, we measured changes in metabolism while resting at the water surface and while diving, before and after three 9–10 day fasting periods; two trials were conducted in summer and one in winter. MRs was greater in the winter, both before and after the fasts, despite no seasonal differences in the initial body mass. Over the course of the fasts, mass-corrected MRs decreased significantly during both seasons, but more during the summer fasts (−16.4 ± 4.7 %) than the winter ones (−8.0 ± 9.0 %). Perhaps as a result of these metabolic differences, the sea lions experienced a slightly greater degree of mass loss during the winter fasts than the summer episodes (−10.6 ± 0.8 % vs. −9.5 ± 0.03 %). In contrast to MRs, mass-corrected DMR (over single dives) increased significantly following the winter fasts (13.5 ± 8.1 %), but did not change during summer trials (−1.1 ± 3.2 %). As a result, the ratio between diving and surface metabolism was significantly higher in winter. We hypothesized that the increased DMR during the winter fasts (both as an absolute cost and relative to MRs) was attributable to an increased thermal challenge via convective heat loss while diving. This suggests that Steller sea lions are more sensitive to changes in body condition due to acute food shortages in the winter compared with the summer.

Interestingly, the metabolism of the sea lions at the surface in between individual dives in a bout was constant prior to the food restriction period, but increased significantly after the first dive in a bout when sea lions were fasted, regardless of season (Svärd et al. 2009). If this was an effect of the heat increment of feeding (HIF), it implies that the immediate processing of ingested energy was of higher priority than optimizing diving ability (which is adversely affected by increases in metabolism due to digestion) in nutritionally challenged sea lions. The inhibition of digestion until completion of foraging dives under "nutritionally normal" conditions has been seen in other diving vertebrates and may be a crucial mechanism to conserve food or alter diving ability (Sparling et al. 2007a; Rosen et al. 2015), as discussed below and in Rosen et al. (2007).

While Svärd et al. (2009) examined changes in diving metabolism in response to an acute period of nutritional stress, sea lions in the wild may be more typically exposed to longer periods of partial under-nutrition. In addition, changes in TBO stores that accompany mass loss must also be measured to fully appreciate any potential impacts of nutritional status on ADL. Resulting changes in ADL will directly affect overall diving behaviour, costs, and foraging capacity.

We addressed this issue by examining the effects of nutritional status on both sides of the ADL equation (Gerlinsky et al. 2014b). We measured DMR, blood O_2 stores, body composition, and dive behaviour prior to and during a period of restricted food intake (resulting in a 10 % decrease in body mass over 3 weeks). Four sea lions completed either single long dives or bouts of four dives to either 10 or 40 m before and after the period of mass loss. The sea lions controlled both the dive durations and inter-dive surface intervals. We predicted that total body oxygen (TBO) stores would decrease following a nutritional stress event due to changes in core body mass (and associated decreases in myoglobin stores) with blood oxygen stores likely being proportionally reduced. We also predicted that DMR would increase, as seen in the previous study (Svärd et al. 2009), rather than mirror the metabolic depression exhibited by fasting sea lions on land (Rosen and Trites 2002). In combination, these proposed changes should lead to a dramatic decrease in ADL, with a resulting decrease in average dive durations.

What we found was quite different from what we had expected. While sea lion lean body mass declined 6 % as a direct result of the nutritional stress event, TBO stores actually increased 32 %. This increase was due to increased blood oxygen stores, driven by a 23 % increase in absolute blood volume coupled with an 8 % increase in red blood cell counts. While mass-specific DMR did increase, this was primarily due to decreases in mass rather than changes in absolute metabolism. More importantly, this increase in DMR was less than the concurrent increase in TBO stores. As a result, the cADL increased by 10 % in nutritionally stressed sea lions.

Nutritionally stressed sea lions also increased the duration of their single long dives (from 4.6 to 5.2 min), with an associated increase in post-dive recovery times (from 5.6 to 6.1 min). While this increase in dive duration is thought to have been the result of the longer ADL, the role of increased motivation for food in nutritionally stressed sea lions cannot be discounted. As demonstrated in earlier studies, longer dive durations in this study also resulted in lower DMR. However, mass-specific DMR was still higher for a given dive duration in nutritionally stressed sea lions.

As with single dive cycle duration, the total duration of a bout dive cycle also increased with nutritional stress. However, the overall increase in duration for a complete dive bout was not due to an increase in submergence time, but rather the proportion of time the sea lions spent at the surface during a cycle of four dives (due to both increased inter-dive surface intervals and post-dive recovery periods). This is consistent with the proposition that the sea lions were consuming O_2 (and producing CO_2) at a higher rate when nutritionally stressed for a given dive duration and, therefore, had to spend more time (relative to unstressed animals) replenishing oxygen stores and offloading CO_2 while at the surface.

Physiologically-induced changes in diving behaviours likewise affect sea lion foraging efficiencies. The increased time spent at the surface for a given subsurface time affects the proportion of their dive cycle spent actively foraging/ingesting prey. For single dives, the nutritionally stressed animals consumed more fish per minute of a dive cycle (dive and post-dive recovery duration) and had slightly higher foraging efficiency (~7 % higher), despite having higher mass-specific DMRs. However, for dive bouts, the amount of fish consumed per minute of dive cycle by the nutritionally stressed sea lions was lower and their mass-specific DMR was higher, which combined to reduce their foraging efficiency by ~20 %.

Past foraging success can also affect the cost of diving through the effects of HIF, the increase in metabolism associated with the processing of a meal. An increase in DMR caused by HIF would effectively decrease the ADL (which, as previously noted, may have explained the results of Svärd et al. 2009). Conversely, if digestion is suspended while foraging due to vasoconstriction that limits blood flow to the stomach or intestine during diving (Zapol et al. 1979), neither $\dot{V}O_2$ nor ADL will be affected by successful foraging. In addition to serving to maintain foraging efficiency by maintaining the ADL, this could also lead to a temporal separation of diving and digestion (as proposed in phocid seals; Sparling et al. 2007a; Crocker et al. 1997) that would result in the post-foraging surface intervals being extended, as is often observed in wild pinnipeds.

To further examine the nature of the metabolic interactions between digestion and diving, we compared the cost of diving in fasted and pre-fed Steller sea lions foraging under controlled conditions (Rosen et al. 2015). Four sea lions completed a bout of four, 3-min dives with 1-min inter-dive surface intervals, after either fasting overnight (at least 18 h), or 1 h after being fed a 3-kg meal of herring. Pre-dive MRs was higher in the pre-fed animals than the fasted animals, indicating an effect of digestion on metabolism. However, while DMR was also higher in the pre-fed animals, the sea lions displayed a significant reduction in the apparent additive effect of digestion during diving. The increase in rate of oxygen consumption during diving was only 54 % of the increase observed in pre-dive metabolism, suggesting the partial deferment of digestion during the active diving phase. Immediately following a dive, there was a rapid, almost complete return to pre-dive levels of metabolism, suggesting a rapid reinstatement of the digestive process.

The results of Rosen et al. (2015), in combination with the findings of Svärd et al. (2009) on the effects of nutritional state on the extent of digestion while diving, suggest that Steller sea lions diving to depth partially defer digestion while actively foraging and that the classically held view that digestion and diving are incompatible processes may be much more variable and adaptable to the specific diving conditions and behaviours than previously thought.

Thus, when nutritionally compromised, ADL may be even shorter, as sea lions may prioritize digestion as soon as prey is ingested.

Predicting rates of oxygen consumption

While measures of rates of oxygen consumption and carbon dioxide production are usually considered to represent the "gold standard" for estimating rates of energy expenditure during diving, respirometry is largely a logistically unfeasible methodology in studies of wild animals. As noted previously, a rare exception is the ability to transport seals to isolated ice holes, although this may, in itself, set up an artificial diving situation (Castellini et al. 1992). In lieu of direct measures of oxygen consumption, scientists have relied on alternate indirect measures to predict energy expenditure. All of these proxy measures require calibration experiments to produce predictive mathematic equations, and ideally to determine the accuracy and precision of these techniques. Some, such as the doubly labeled water turnover method, have been well described, but only provide a single value of energy expenditure over extended timeframes rather than the specific costs of diving and are, therefore, not discussed here (for validation studies in otariids, see Butler et al. 2004; Dalton et al. 2014). Our laboratory has been actively investigating the efficacy of three potential proxies for estimating energy expenditure during diving: heart rate, body acceleration, and behavioural budgets.

Heart rate

In terrestrial mammals, increases in $\dot{V}O_2$ from activities such as exercise induce a proportional increase in heart rate (*f*H) (Hiilloskorpi et al. 2003). Fick's Equation (Fick 1870) formulized the relationship between $\dot{V}O_2$, *f*H, stroke volume, blood oxygen content, and tissue oxygen extraction. It is not feasible to measure all of the physiological variables in Fick's Equation on freely diving animals (Ponganis et al. 1990, 1991). Consequently, the application of this method on marine mammals assumes that an increase in *f*H is the primary response to increased oxygen demand, and that the remaining parameters of Fick's Equation either vary proportionally to *f*H or remain constant (although see Miedler et al. 2015).

Given the apparent relationship between *f*H and whole-body O_2 use in air, and the fact that *f*H is relatively easy to obtain via attached telemetry devices from a free-diving animal (at least compared with other circulatory variables; Ponganis 2007), many researchers have made a case for using *f*H as an indirect measure of free-ranging energy expenditure in marine mammals (e.g., Green et al. 2009; Butler et al. 2004). In captive swimming (non-diving) California sea lions, *f*H overestimated the rates of oxygen consumption by an average of only 2.7 %, although error estimates ranged widely from −28 to +23 % (Boyd et al. 1995).

Our initial investigations with Steller sea lions also began by simultaneously monitoring $\dot{V}O_2$ and *f*H in four non-diving, juvenile animals while resting in air, resting in water, or while swimming in a 5800-L metabolic flume tank (1.8 m max depth; McPhee et al. 2003). The study was limited by several logistical constraints, particularly for the trials in the flume tank. The activity of the animals was limited by the size and depth of the tank (3.2 × 1.8 × 1.0 m), although changes in the internal water current were used to promote a range of $\dot{V}O_2$ and *f*H from the animals. In addition, due to the necessity of attaching the surface electrodes to the fur under gas anesthesia, multiple measurements (up to 18) were conducted in the same session (although the individual periods of data collection were separated to try to maintain a level of statistical independence).

Despite these limitations, the preliminary tests seemed to confirm the hypothesis that *f*H accurately predicted $\dot{V}O_2$, at least in non-diving pinnipeds. Combining all of the data obtained in both air and water environments demonstrated that *f*H could account for a large amount of the variance (~70 %) in mass-specific $\dot{V}O_2$. The resulting predictive equation was different from that of other marine mammal species, although it was most similar to other otariids (e.g., Butler et al. 1992; Boyd et al. 1995; Williams et al. 1991). While this initial study demonstrated the validity of the basic principal, it did not test the efficacy of the technique under realistic conditions for a diving marine mammal. As discussed earlier, the relationship between exercise and *f*H in diving marine mammals is different than in their terrestrial counterparts. Diving is characterized by variable periods of bradycardia and tachycardia (which were not observed in the swimming sea lions) that are temporally independent of physical work and associated aerobic metabolism (Williams et al. 2015).

A follow-up study examined the relationship between $\dot{V}O_2$ and *f*H in both diving and non-diving sea lions (Young et al. 2011b). Data from non-diving animals that were tested in either the aforementioned flume tank or while resting at the water's surface prior to diving in the open ocean provided a single predictive equation with a relatively low standard error of the estimate. Curiously, the equation predicting metabolism while resting in water (either in the flume tank or at the water's surface in the open ocean) was different than the one resulting from data gathered from post-absorptive animals resting in ambient air. Mathematically, the resulting regression equations indicated that changes in *f*H while in air were associated with much greater changes in $\dot{V}O_2$ than when in water, although the reason for this difference is unknown.

The ability of *f*H to predict $\dot{V}O_2$ in diving sea lions was less clear. When examined over the dive portion only (i.e., DMR), *f*H could not be used to predict $\dot{V}O_2$ for either single dives or dive bouts. This would be expected, given the previously discussed changes in *f*H during a dive (i.e., intermittent bradycardia and pre-surface tachycardia; Hindle et al. 2010b), as well as potential changes in stroke volume and the level of pulmonary shunting. However, *f*H could predict AMR calculated over the entire dive cycle, which is more consistent with the concept that the dive cycle (submergence and subsequent surface periods) is a distinct physiological unit (Kramer 1988; Butler and Jones 1997; Green et al. 2003).

However, when the AMR dive data were examined more closely, two statistically distinct predictive equations could be produced for single long dives and bouts of four consecutive dives. Furthermore, the equation predicting AMR from *f*H for single long dives was not statistically distinct from the regression predicting $\dot{V}O_2$ resting at the surface, and, hence, could be combined into a single predictive equation. This suggests that single extended dives were more physiologically similar (in the relationship between cardiac function and oxygen consumption) to that of animals resting at the water's surface than those undertaking a bout of multiple dives. This result may be because, unlike in dive bouts, there is no cumulative oxygen debt in between single dives, so that the relationship between *f*H and $\dot{V}O_2$ remains more similar to that observed in non-diving activities. The separate equation required to predict $\dot{V}O_2$ from *f*H during dive bouts not only had a low predictive error but was also quite robust. Specifically, the *f*H:$\dot{V}O_2$ relationship was not significantly affected by dive duration, dive depth, or water temperature (under the conditions tested).

The results of the Young et al. (2011b) study reinforced the concept that different types of dives are physiologically distinct. On a practical level, the results demonstrate the importance of applying the appropriate equation for the correct type of diving behaviour when predicting $\dot{V}O_2$ from *f*H. For example, incorrectly applying the predictive equation for animals resting in water to estimate $\dot{V}O_2$ of sea lions performing dive bouts would overestimate $\dot{V}O_2$ by ~25 %. Fortunately, in studies with wild sea lions, dive types (single dives vs. bouts) can be identified through the simultaneous collection of data from time-depth recorders (TDRs).

Digestion is another factor that might affect the relationship between $\dot{V}O_2$ and *f*H. As previously noted, the digestion of food causes an increase in rates of oxygen consumption and the heat increment of feeding (HIF) in Steller sea lions on land has been shown to double $\dot{V}O_2$ (Rosen and Trites 1997). Previous studies have indicated that digestion is partly suppressed during diving (Rosen et al. 2015), although HIF during diving may be more pronounced during periods of nutritional stress (Svärd et al. 2009). It is unknown whether this increase in $\dot{V}O_2$ associated with digestion is accompanied by a parallel increase in *f*H, and what effect this might have on the predictive strength of heart rate.

Preliminary investigation into this question was undertaken as part of the original *f*H:$\dot{V}O_2$ calibration study (McPhee et al. 2003). The *f*H and $\dot{V}O_2$ for one of the male sea lions were monitored for 3 h following ingestion of a bulk meal of either 6 or 12 kg of herring. As expected, $\dot{V}O_2$ increased over the measurement period, but heart rate displayed no apparent parallel increase.

A more detailed study monitored the *f*H and $\dot{V}O_2$ of four sea lions for 4–4.5 h after being fed 4- or 6-kg meals of herring in the previously described metabolic tank or dry metabolic chamber (Young et al. 2011a). The results seemed to indicate differences in the *f*H:$\dot{V}O_2$ relationship depending on whether they were tested on land or in the water. When sea lions were tested on land, the *f*H:$\dot{V}O_2$ relationship was not impacted by meal size or whether they were fed or not, enabling a single predictive equation. The picture was slightly different for sea lions tested while in water (but not diving). Although *f*H could be used to predict $\dot{V}O_2$ after consuming a 4-kg meal, the relationship was different than that for when the same animals were fasted. Furthermore, *f*H could not be used to predict $\dot{V}O_2$ when the sea lions had consumed a 6-kg meal.

It is unclear what caused the apparent collapse of the relationship after consuming the 6-kg meal. We hypothesized that the larger meal would produce a larger observed increase in $\dot{V}O_2$ that was not accompanied by a comparative increase in *f*H, but no such difference in scope of $\dot{V}O_2$ with meal size was observed (although the effect was longer). Overall, the results indicated that meal size and submergence in water changed the relationship between $\dot{V}O_2$ and *f*H. It is unclear the degree to which these differences are associated with circulatory changes that sea lions may undergo in preparation for diving that at least partly alter the course of digestion (as discussed earlier in relation to Rosen et al. 2015; Svärd et al. 2009).

Overall, the ability of heart rate to accurately predict rates of energy expenditure in wild sea lions is complicated beyond the associated technical concerns. The relationships between activity, metabolic expenditure, and heart rate during apneic exercise are made problematic by the cardiovascular adjustments associated with the dive response. Hence, while reasonable predictive equations can be formulated for sea lions on land, at the water surface, or actively diving, substantial errors can be accrued by improper application of the different equations. Furthermore, there is evidence that digestion can significantly disrupt these relationships. Collectively, this makes effective application of this technique to estimate energy expenditure in wild sea lions extremely difficult.

Physical activity

Many of the problems associated with proxies (such as heart rate or doubly labeled water) that might be used to predict rates of energy expenditure are logistical. Methods that require substantial data processing, serial timed captures of individual animals, and/or attachment of a significant mass of sensitive electronics present difficulties when dealing with wild marine mammals.

Using measures of body acceleration would, in theory, avoid some of these problems (Halsey et al. 2011b). It requires a single attachment of a relatively small, inexpensive biologger (often encapsulated into existing electronics, such as time-depth recorders) which can collect data at a high frequency that can be readily converted into a single index per unit time (e.g., per dive). Use of body acceleration as a proxy for metabolic rate is based on the Newtonian theory that an animal exerts force to achieve motion, and that the force required scales to the levels of energy expenditure (Gleiss et al. 2011). A common metric for remotely measuring activity levels is overall dynamic body acceleration (ODBA; Wilson et al. 2006). ODBA uses data from three-dimensional accelerometers to calculate dynamic movement (i.e., movement not due to gravity) in space and time, and has been found to be closely related to measures of $\dot{V}O_2$ in a number of diving vertebrates (Enstipp et al. 2011; Halsey et al. 2011a), although this success is far from universal (Dalton et al. 2014; Halsey et al. 2011b). The equation used to predict $\dot{V}O_2$ from the measures of ODBA—derived from controlled calibration studies—is an expression of the basic cost of metabolism (represented by the equation's intercept) and an incremental, linear increase in metabolism with increased work attributable to physical movement.

Initial tests suggested that ODBA worked well for predicting $\dot{V}O_2$ for diving Steller sea lions. An analysis of 141 independent dives (between 1 and 12 dives with full recovery during each trial, 1 trial per day) from three sea lions diving to depths between 10 and 50 m reported that ODBA alone was able to predict metabolic rate to within 7 % of the measured value (Fahlman et al. 2008c). While this study also suggested that the predictive relationship was not different whether the animals were diving or resting at the surface, a follow-up study, including additional data ($n = 266$), found that the relationship differed between when sea lions were actively diving and when they were resting at the surface (Fahlman et al. 2013). This study also suggested that there were no effects of a 9–10-day fasting period on the relationship between ODBA and $\dot{V}O_2$, despite a 7 % decrease in DMR.

However, a subsequent study by Volpov et al. (2015) using four sea lions undergoing a set of controlled dives was less supportive of the use of ODBA as a proxy of $\dot{V}O_2$. These trials incorporated a second feeding station at depth, longer dive durations, and more dives per bout in an effort to assess if ODBA could predict $\dot{V}O_2$ with increased levels of activity and oxygen depletion. The sea lions executed three dive types—single dives, bouts of multiple long dives with 4–6 dives per bout, or bouts of multiple short dives with 10–12 dives per bout—to depths of 40 m, resulting in a range of activity and oxygen consumption levels.

The Volpov et al. (2015) study found that there was no statistical relationship between ODBA and $\dot{V}O_2$ when sea lions were resting at the surface in contrast to the earlier studies (Fahlman et al. 2008c, 2013). Similar to these earlier studies, ODBA could predict AMR over the dive cycle when data from all dive types were combined. Interestingly, dive type (as defined above) was a significant model factor—and there were no significant linear relationships between AMR and ODBA within each dive type when data for each dive type were analyzed separately.

There is a natural temptation when disparate results are presented to try to identify which study is "correct". A more useful approach is to try to determine the possible reasons for the discrepency in results among these studies. Possible suggestions include variation in statistical approach, including different analysis time scales (see Jeanniard du Dot et al. 2016), or seasonal differences (see Dalton et al. 2014). While there have been suggestions that the non-linear movements ("twists and turns") that otariids exhibit while diving decrease the capacity for ODBA to predict $\dot{V}O_2$ (see Ware et al. 2016), this hurdle is still only theoretical. In the end, while ODBA may eventually prove to be a reasonable way to predict the cost of diving in wild, free-swimming sea lions, significant questions remain regarding its future application and interpretation.

Diving behaviour

An alternate, potentially simpler method to determine the energy expenditure of diving sea lions by using behavioural time budgets was also tested at the Open Water Station. Traditionally, time budgets have been used to estimate the energy expenditure of wild animals by employing single-value estimates of energetic costs of defined activities. For example, the amount of time "diving" would be multiplied by a single estimated rate cost, allowing no flexibility for differences in diving behaviours normally exhibited by animals. This level of estimation might be suitable for many ecological questions, but cannot be used to extrapolate the energetic consequences of differences in diving behaviours between individuals or changes across time, such as those induced by environmental changes.

As already noted, the previous work in our lab clearly indicated that changes in the behaviour and structure of a dive affected its energetic cost (e.g., Fahlman et al. 2008c; Hastie et al. 2006a). To that end, we investigated whether a foraging dive could be broken down into its major components—surface time, transiting to and from depth, and bottom time—to inform a mathematic model that could be used to predict total $\dot{V}O_2$ using these gross behavioural categories (Goundie et al. 2015b). This study measured DMR of four Steller sea lions performing four types of dives to 10 and 40 m. The dives differed in the amount of bottom time (including a V-shaped "bounce" dive) and level of bottom activity, such that estimates could be made of the separate costs of four different dive components: surface time, transiting to and from depth, resting bottom time, and active bottom time. It also allowed for comparisons to be made between the costs of single dives and dive bouts. Not surprisingly, the sea lions' DMR was higher while transiting to and from depth (20.5 ± 13.0 ml O_2 min^{-1} kg^{-1}) than while swimming and "foraging" at depth (13.5 ± 4.1 ml O_2 min^{-1} kg^{-1}), both of which were higher than when at the surface (9.2 ± 1.6 ml O_2 min^{-1} kg^{-1}). A resulting time-energy model that incorporated these individual behavioural cost estimates subsequently accurately predicted oxygen consumption for both the time that sea lions were submerged (within 9.5 %) and for complete dive cycles (submerged and subsequent surface time, within 7.7 %).

The results also explained why diving costs were higher for dive bouts than for single dives that had equal total bottom times. We found that the DMR of a single dive bout with a 3-min bottom time (14.4 ± 3.1 ml O_2 min^{-1} kg^{-1}) was significantly lower than for a bout of three dives, each with a 1-min bottom time (18.0 ± 2.8 ml O_2 min^{-1} kg^{-1}). The difference in costs directly related back to differences in the behaviour during the dive. Specifically, a higher proportion of time during a dive bout is spent performing the more energetically expensive transiting behaviour compared with an equivalent single dive.

This difference in costs between single dives and dive bouts also has several impacts on overall foraging efficiency. Assuming that bottom time scales to energy intake opportunities (foraging), then the higher costs of dive bouts would lead to a lower overall energetic efficiency compared with single dives. However, the sea lions were more efficient at replenishing their oxygen stores when undertaking bout dives compared with single dives, as determined by total time required to be at the surface before full apparent metabolic recovery (including inter-dive surface intervals for bouts). As a result, the sea lions could spend a greater portion of their total time foraging while undertaking bout dives. Therefore, although single dives were energetically less costly than dive bouts, dive bouts were more efficient in terms of long-term foraging gain.

Insight to date

To date, we have examined numerous methods for accurately measuring the energy expenditure of Steller sea lions in the wild. Some, such as heart rate, demonstrate high statistical relationships, but may be limited by logistical issues. Body acceleration has shown promise in a number of terrestrial species, but its predictive abilities for air-breathing diving vertebrates remains contested. We have also examined the use of simpler metrics, such as time-energy budgets, that seem statistically robust and are relatively simple to apply. Although no single measure has emerged as a superior method of estimating energy expenditure in wild marine mammals, our studies have made it clear that appropriate calibration trials, across a range of realistic behaviours, are essential before any such techniques can be employed in the field.

Past progress and future research

The research program with the trained Steller sea lions at the Open Water Research Station was designed to answer what we originally, naively conceived to be a simple question: "What is the diving metabolic rate of Steller sea lions?" It quickly became apparent that this question was unsophisticated. The more pertinent, and far more interesting, question became "What is the diving metabolic rate of Steller sea lions under different circumstances, and what are the energetic and ecological consequences?" This more complex view, in turn, affected the pursuit of our five broad program objectives:

1. Measure the energetic cost of diving.
2. Investigate the relationship between individual physiology and diving capacity.
3. Investigate the physiological mechanisms that underpin dive behaviour.
4. Test specific optimal foraging theories for diving mammals.
5. Develop and test proxies for energy expenditure that could be used to measure the energy expenditure of diving in wild sea lions.

Over the past decade, we made extensive progress towards these goals, as illustrated in Fig. 4. Conducting studies with trained animals under a carefully controlled set of environmental and physiological conditions allowed us

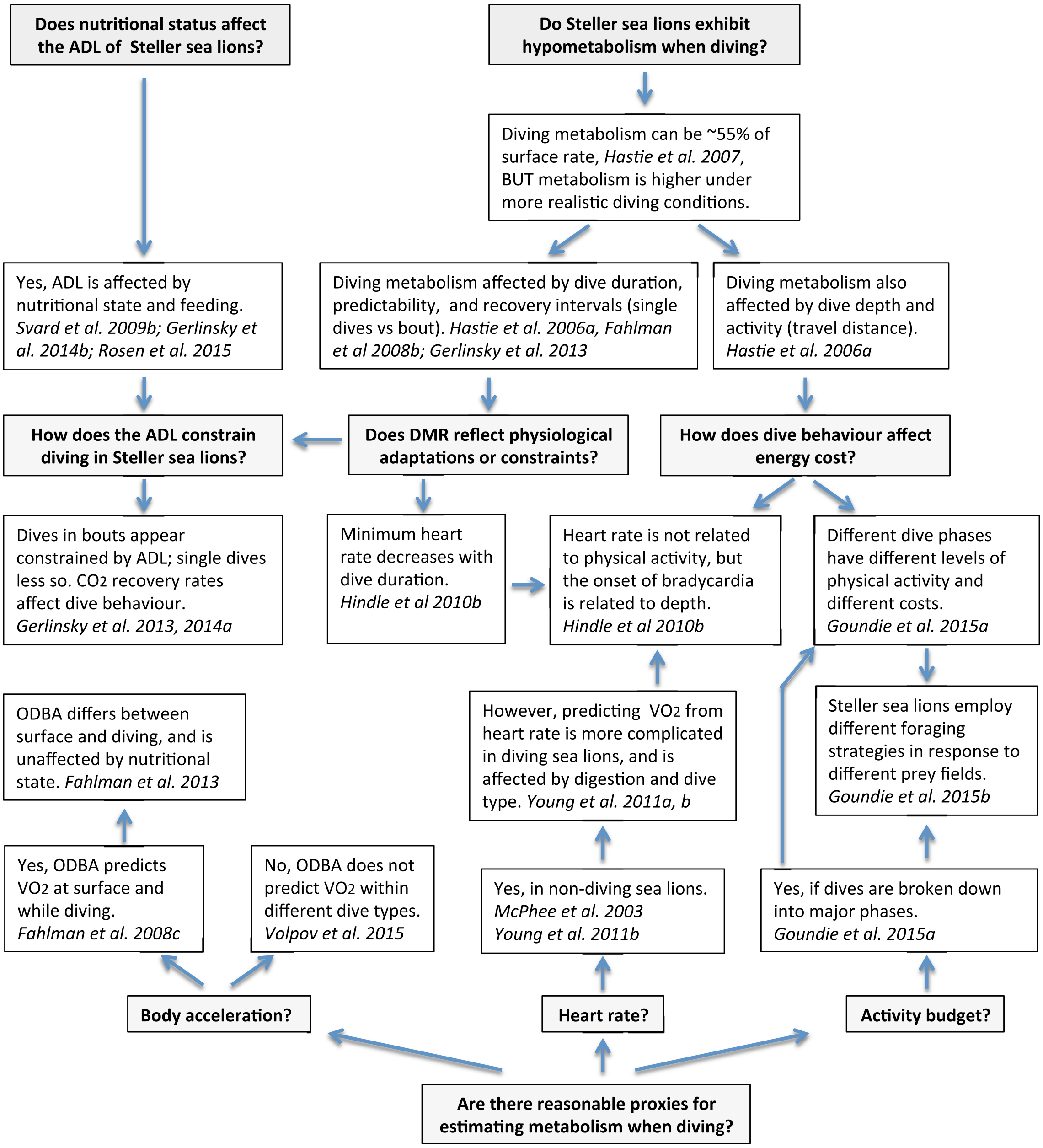

Fig. 4 Schematic outlining major study questions and results arising from the Steller sea lion Open Water research program

to quantify the effect of specific, known changes on dive behaviour and energetics.

We have realized that there is not a single "cost to diving", but rather that it varies with a number of behavioural (i.e., activity level, dive profile) and physiological (i.e., dive response, nutritional status) parameters. Although metabolic rate while diving *may* be lower than that at the surface under a set of specific conditions, these do not reflect natural circumstances. When undertaking more natural diving behaviour, the cost of diving and foraging is affected by the type of diving (dive bouts or single dives), the level of underwater activity, the dive duration and depth, and the nutritional status and physical condition of the animal. These factors also affect the aerobic diving capacity of individual animals, although behavioural motivation (perhaps tied to nutritional status and season) may blunt the influence (although not the physiological consequences) of the aerobic dive limit on actual dive behaviour.

Of course, the usual motivation for diving is to undertake foraging. Our studies have quantified the trade-offs that sea lions must make when balancing their time at depth acquiring prey and at the surface acquiring oxygen (and, perhaps, more importantly, offloading CO_2 and other metabolic by-products). These have also demonstrated the potential energetic effects of changes in their environment, such as changes in the distribution (depth) or abundance of their prey.

Through such controlled manipulations, we have been able to test specific hypotheses, such as those modelling the optimal foraging and diving of pinnipeds and other marine mammals. Obviously, we have not tested all possible variables. However, our research program has revealed a consistent theme—that dive behaviour and physiology can vary considerably. While variability between individuals has often been discussed, these data reveal the wide extent of within-individual variability. Taken together, they provide the first comprehensive look at both physiological and behavioural plasticity in a foraging marine mammal. As the complexity and interconnectedness of physiology and behaviour become better understood, these insights will be critical for understanding individual limits and the ability of species to cope with changing habitat and altered environmental conditions.

The breakthroughs we achieved were made possible by eliminating the physical constraints usually associated with working with trained marine mammals. Our experimental set-up allows our trained Steller sea lions to mimic the diving behaviour of their wild counterparts. That is not to say that the range of environmental conditions the trained sea lions are exposed to is identical to that experienced by animals in the wild. However, this is one of the strengths of the experimental paradigm. By controlling which aspects of the sea lion's biotic or abiotic environment are varied or held constant, it is easier to define their effect. In addition, such experimental manipulations can shed light on how tightly specific aspects of behaviour and physiology are ingrained, or the scope of their potential expression. Such investigations can further inform future studies about what might be important factors to consider (such as the effect of disturbance on diving behaviour and physiology).

In addition to understanding the effects of biotic and abiotic changes on sea lion foraging behaviours, our studies also tested a number of theories that examine the motivations and consequences to an animal for extending dives beyond their aerobic dive limit. These have primarily taken the form of measuring the energetic and behavioural consequences of increased dive duration. A limit to all of these studies, however, has been an inability to actually determine ADL, instead having to rely upon the comparison of observed rates of oxygen consumption with estimated body oxygen reserves (e.g., Gerlinsky et al. 2013, 2014b). The next obvious step is to integrate the measures of blood PO_2 during dives and post-dive blood lactate levels to directly measure ADL. Such measures have only been obtained for a single Otariid species to date (California sea lion; Ponganis et al. 1997). Similar experiments with our Steller sea lions would provide valuable insight into their physiological capacity.

While this review has focussed on our studies of sea lion diving energetics and physiology, this unique experimental set-up can be used to conduct other avenues of scientific inquiry. For example, we have conducted studies examining the ways that sea lions compensate for changes in buoyancy (Fahlman et al. 2008a), and shown the significant effects of ocean currents and swimming depth on surface swimming costs and behaviour in Steller sea lions (Hindle et al. 2010a). We have also conducted studies exploring the possible use of blood microparticles in diving sea lions as a biomarker for decompression sickness in marine mammals, such as that hypothesized to result from sudden changes in diving behaviour induced by anthropogenic sound exposure (Fahlman et al. 2016).

Our ability to control and monitor the behaviour, energetics, and environment of the sea lions has also provided opportunities to develop, test, and calibrate methods and technologies to study wild sea lions. For example, in addition to the previously described studies of the efficacy of using heart rate or accelerometry to predict energy expenditure in sea lions, we have also sought to develop new devices and methods to predict energy expenditure (Ware et al. 2016). We have also conducted studies testing a satellite-linked fluorometer mounted on sea lions to monitor zooplankton (Lander et al. 2015), thereby turning sea lions into oceanographic platforms of opportunity.

Ultimately, understanding the physiology, energetics, and behaviour of diving in sea lions is not just important for matters of comparative physiology or testing optimal foraging theories. This information is also central to aspects of conservation ecology. The interaction between marine mammals and their prey base is becoming of increasing importance, as potential conflicts between human activities (fishing, climate change) and populations become central in the discussions of resource partitioning and species conservation. The cost of diving and foraging has a major effect on the total prey required by marine mammal populations, and the potential impact which those populations have on prey resources. Conversely, the behavioural and energetic consequences of changes in an individual sea lion's biotic and abiotic environment are ultimately constrained by their physiological capacity. Understanding the interactions between these process will not only inform how a sea lion might respond to environmental changes, but also their capacity for compensation and the consequences for failing to adjust to their new conditions.

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