Studying Diving Energetics of Trained Steller Sea Lions in the Open Ocean

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Abstract

The costs associated with diving are a central component of a sea lion's energy budget. Accurate estimates of diving costs are needed to assess energetic and physiological constraints on foraging behavior, including the potential effects of changes in prey distribution or density. However, information on sea lion diving physiology is limited to relatively few species of pinnipeds, and there is currently no information for Steller sea lions. Information on diving energetics of pinnipeds has traditionally been gathered using either wild or captive animals. Studies with wild animals are logistically challenging and are limited by the opportunistic nature of data collection, while studies in captivity have been constrained by the physical restrictions of the holding facility. To circumvent some of these limitations, we combined the best aspects of both techniques by conducting diving metabolism studies with trained Steller sea lions in an open ocean environment. Two captive-reared Steller sea lions were housed in a holding pen and transported by boat to a diving trial area. The animals were trained to dive to predetermined depths for controlled periods of time using an underwater light targeting system and a video system to monitor behavior. At the end of each dive the sea lions returned to a respirometry dome on the surface where oxygen consumption was measured to estimate diving metabolism. This paper describes the experimental setup used to evaluate diving metabolism, discusses the logistical challenges of the study and the advantages of using such an approach to carry out physiological experiments with sea lions, and provides preliminary data on the diving energetics of Steller sea lions.

Introduction

Accurate information on the energetic consequences of foraging is required to assess the energetic requirements and physiological constraints of foraging in sea lions (Winship et al. 2002). Such information is integral to constructing predictive bioenergetic models for wild sea lions, and for assessing the impacts of changes in prey distributions or types (Winship et al. 2002). It is also central to understanding the physiological constraints that limit diving behavior (e.g., aerobic dive limits). However, there is only limited information on the energetic costs of locomotion in Steller sea lions (Rosen and Trites 2002), and no data on the energetic costs of diving.

Information on foraging energetics has traditionally been gathered by studying animals in the wild or held in captivity. Early studies of diving metabolism consisted of forced submersions with restrained laboratory harbor seals (e.g., Scholander 1940), which showed that submerged animals dramatically reduced their metabolism and heart rate (by up to 90%) during the submersion period. More recently, a limited number of studies on wild animals (e.g., Kooyman et al. 1973, 1980, 1983; Castellini et al. 1992), and with freely diving animals in captivity (e.g., Gallivan 1981, Reed et al. 1994, Hurley and Costa 2001, Sparling and Fedak 2004) have provided a greater understanding of physiological responses during dives.

Each of these approaches (wild and captive) has inherent limitations. While direct, controlled experiments can be carried out in captivity, studies are restricted by the physical restraints of a confined environment. For example, during measurements of diving metabolic rates, dives are limited to the relatively shallow depths of holding pools (Hurley and Costa 2001), and measures of swimming physiology can be limited by the flow speed of flumes (Rosen and Trites 2002), and rarely account for the biomechanical influence of swimming in an enclosed space. Conversely, although data from wild animals gives a direct measure of foraging energetics in the wild, such studies are generally limited to measurements of average field metabolic rate (e.g., Costa and Gales 2003) and are logistically challenging and often opportunistic in nature.

A unique series of studies in the wild have greatly furthered our understanding of diving and foraging energetics in Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica (e.g., Kooyman et al. 1980, Castellini et al. 1992, Williams et al. 2004). In these previous studies, the diving metabolism of seals was measured using open circuit respirometry on a dive-by-dive basis when the seals returned to breathe at the surface in discrete holes in the ice. However, it is clear that measuring oxygen consumption of wild marine mammals using respirometry techniques can only be used where the surface location is predictable (e.g., in a hole in the ice), making it unsuitable for most other species. One potential solution to overcoming these limitations is to combine the best aspects of both wild and captive techniques, and use trained sea lions to run experimental trials in the open ocean (e.g., Ponganis et al. 1997). Such an approach provides the logistical and experimental advantages of using trained animals without the restrictions of a captive environment. Specifically, by using trained sea lions in the open ocean, we could evaluate the energetic and behavioral mechanisms during dives to realistic foraging depths, and examine potential physiological or biomechanical changes concurrent with factors such as pressure changes at depth.

Trained marine mammals in the open ocean have been successfully employed in the past to study the diving physiology of a limited number of species, including bottlenose dolphins (*Tursiops truncatus*) (Ridgway et al. 1969, Ridgway and Howard 1979), beluga whales (*Delphinapterus leucas*) (Ridgway et al. 1984, Shaffer et al. 1997), and California sea lions (*Zalophus californianus*) (Hurley 1996, Ponganis et al. 1997). These studies have been integral to understanding the diving physiology of marine mammals and their adaptations to foraging at depth. However, this approach has not been used with Steller sea lions (*Eumetopias jubatus*) and no information on their diving physiology is currently available.

The paucity of data on diving physiology of Steller sea lions led to the development of a research program that uses trained Steller sea lions diving in an open ocean environment to investigate the energetics associated with foraging behavior. The following describes the experimental setup used to measure the diving metabolism of trained Steller sea lions, and provides details concerning the logistics associated with taking trained animals into the open ocean. We also discuss the advantages and challenges of using such an approach to carry out physiological experiments on sea lions, and provide preliminary data on the diving energetics of Steller sea lions

Open ocean research station

To provide a mobile base for open ocean research, we developed a research station that consisted of a floating laboratory and a specially designed floating pen to house the sea lions. It was designed to allow us to carry out all aspects of the research, from training of sea lions to data collection and analyses. The floating lab was fully equipped to carry out all aspects of animal husbandry (e.g., health maintenance and food preparation) for the sea lions and provided a base for scientists to work from. The research station was based at a working marina in an inlet close to Vancouver, British Columbia. The design of the research station and holding pen permitted the project to be fully mobile, allowing us to base ourselves in areas appropriate for the needs of particular research projects. However, the use of a vessel as a floating laboratory imposed the logistical challenges of boat work more commonly associated with studies in the wild. These included adverse weather conditions, fouling from marine organisms, power fluctuations, and saltwater corrosion.

Two female sea lions formerly held at the Vancouver Aquarium Marine Science Centre were housed at the research station in a floating animal pen specially designed and built for the project. It allowed the sea lions access to seawater and provided a base for open ocean training. This consisted of a 6.7 m long × 4 m wide × 4 m deep stainless steel mesh pen that allowed seawater to flow through, surrounded by a 2 m wide floating concrete walkway. The sea lions had continuous access to a 2 m × 4 m haul-out area. An 8 m × 4 m shed that adjoins the pen provided equipment storage and an indoor area for training or research. The mesh pen could be fully raised to allow for maintenance and cleaning (and emergency animal access). This was carried out using two large flotation tanks on the base of the pen that could be filled with air from a compressor at the surface. These provided the buoyancy to allow it to be raised (with relative ease) using hand winches at the surface. Due to significant marine growth in the area, cleaning operations were undertaken at least once every two weeks.

Although the design of the holding pen allowed a constant flow of clean seawater through the pen, this occasionally allowed unwanted items such as floating debris and jellyfish to also enter the pen. While the sea lions frequently ingested jellyfish during their initial acclimatization period, this rapidly decreased in frequency. But the occasional ingestion of other man-made and marine debris remained a problem.

Working in the open ocean

Sea lions were transported by truck and boat to the research station at the start of June 2003. After a relatively short period of acclimatization in the holding pen (around a month), initial training in the open water was carried out in the waters immediately surrounding the research station. During this period, the distance that the sea lions could swim from the area was controlled using a tether line attached to a body harness. After approximately one month of tethered work, the restraint was removed and all further work was carried out off tether. Training in the open ocean was generally carried out during three to four sessions during the day, usually during the morning or early afternoon. During training and experimental trials, each sea lion wore a webbing body harness with a VHF tag attached to ensure that it could be located if out of visual contact. A colored, reflective strip on the harness allowed the sea lion to be visible to researchers and trainers while the sea lion was underwater.

The sea lions were transported to dive trial areas, located in Burrard Inlet (49°17'25"N, 122°54'55"W) and Indian Arm (49°19'30"N, 122°55'30"W) near Vancouver, during training and experimental sessions in a specially designed transport boat. This 6.7 m vessel had a front-loading ramp that

Figure 1. A sea lion being trained to undertake diving experiments in the open ocean.

could be lowered to allow the sea lion access to the water (Fig. 1). The sea lions were trained to board the vessel from the holding pen, and enter the water using the loading ramp. Research equipment and staff were housed in a small research vessel that operated independently of the transport vessel. For animal safety, both vessels were generally stationary when sea lions were in the water, and each was fitted with propeller guards to ensure that the sea lions were not injured if boat maneuvers were necessary.

From the outset of the open ocean work, the sea lions were usually comfortable working in the ocean. However, novel visual and acoustic stimuli frequently provided challenges. For example, although routine vessel noise was not problematic, encountering loud impulsive underwater sounds within the hearing range of Steller sea lions such as recreational or commercial boat–based active sonar systems (~30 kHz @ ~210 dB) frequently resulted in adverse behavioral reactions such as refusal to swim in the open ocean. On such occasions, the sea lion's behavioral response was usually to terminate the task being carried out and immediately return to the cage on the transport vessel. Large vessels maneuvering in the immediate vicinity of the transport vessel would often elicit a similar response.

The presence of other marine mammals was not generally a problem during work in the open ocean. The only other species found regularly around the research station were harbor seals (*Phoca vitulina*) and, although interactions were observed, these were short and non-aggressive. The presence of harbor seals did lead to the potential for disease or parasite transmission between species. In response, we developed a strict quarantine protocol for both animals and staff at the research station that minimized the potential for transmission to sea lions housed at the aquarium. In addition, daily health checks were carried out on the sea lions, and regular blood tests were done to monitor health status.

Prior to the start of the project, it was anticipated that the presence of wild fish in the open ocean might be problematic, both from a training (i.e., self-reinforcement) and an experimental (i.e., uncontrolled diet profile) perspective. Although prey captures were occasionally observed, these did not generally lead to significant training problems, and were obvious enough that they could be accounted for during experimental trials.

Diving metabolism experiments

The first set of experiments in this project was designed to evaluate the metabolism of sea lions during dives to depth. Sea lions were conveyed in the transport vessel from their holding pen to dive trial areas where they carried out dives to an underwater target light system at depth and returned to a respiratory chamber at the surface. The sea lions freely chose to cooperate with all data collection and were never restrained or confined during any of the experimental trials. To maintain cooperation during the trials, sea lions were occasionally fed small amounts of fish (maximum of 0.5 kg of herring). Due to the short duration of trials (~20 min) and the small amount of food, this was unlikely to have affected the metabolic rate measurements due to the heat increment of feeding (Rosen and Trites 1997). Although it was not possible to completely discount the possibility of capture of wild fish during the descent and ascent phases of dives, observed prey captures were usually extremely overt and it appeared that the sea lions were swimming directly and quickly between the surface and target at depth during experimental trials.

The respiratory chamber consisted of a 190 liter Plexiglas dome attached to a 1.5 m × 1.5 m floating base. A 0.7 m wide "skirt" made of plastic-coated fabric mesh was draped over the outside edges of the flotation base creating a box effect, thus reducing the likelihood that the sea lion would leave the chamber before the end of the trial. Metabolism at the surface in the respiratory chamber was estimated using open circuit gas respirometry (Kaufmann et al. 1989). Air was drawn through the dome at a constant rate of 200 to 250 liters per minute using a Sable Systems Flow Kit 500H (Sable Systems International, Las Vegas, Nevada). Oxygen

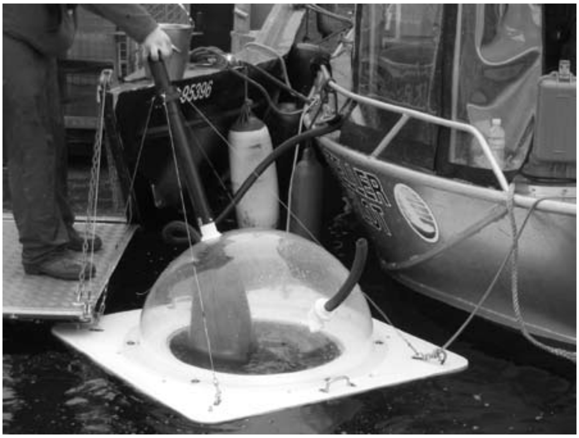

Figure 2. Sea lion in the respiratory dome at the water surface between the transport and research vessels.

concentrations were continuously subsampled using a Sable Systems FC-1B Oxygen Analyzer. A data acquisition system recorded an average gas concentration from the analyzers every second. Flow rate was corrected to standard temperature and pressure (STPD) through automatic concurrent barometric pressure and temperature readings at the flow meter, and gas levels were calibrated daily according to manufacturer instructions. The subsample of air was drawn through two columns of Drierite (W.A. Hammond Drierite Co. Ltd., Xenia, Ohio) and two columns of soda lime to absorb CO_2 from the air sample. Changes in oxygen concentration were converted to oxygen consumption rates using equation 4b from Withers (1977).

All tests were performed in the morning, at least 16 hours postprandial. The respiratory chamber was deployed at the water surface from the research vessel (Fig. 2) and the target light system was positioned beneath the chamber at a predetermined depth (Fig. 3). The target light system consisted of three components: (1) a small white sphere that each sea lion was trained to target on; (2) an underwater light (Multi-Sea Lite P/N 710-040-601, Deep Sea Power and Light Inc., San Diego, California) with a diffuser filter over the front; and (3) an underwater camera (P/N 740-048-601; Deep Sea Power and Light Inc.) that allowed us to monitor the attendance and behavior of the sea lion at the target (Fig. 3).

Each sea lion was trained to remain calm and stationary with its head in the respiratory chamber for a period of 6 minutes to obtain a standard measure of oxygen consumption at the surface. The sea lion then swam to

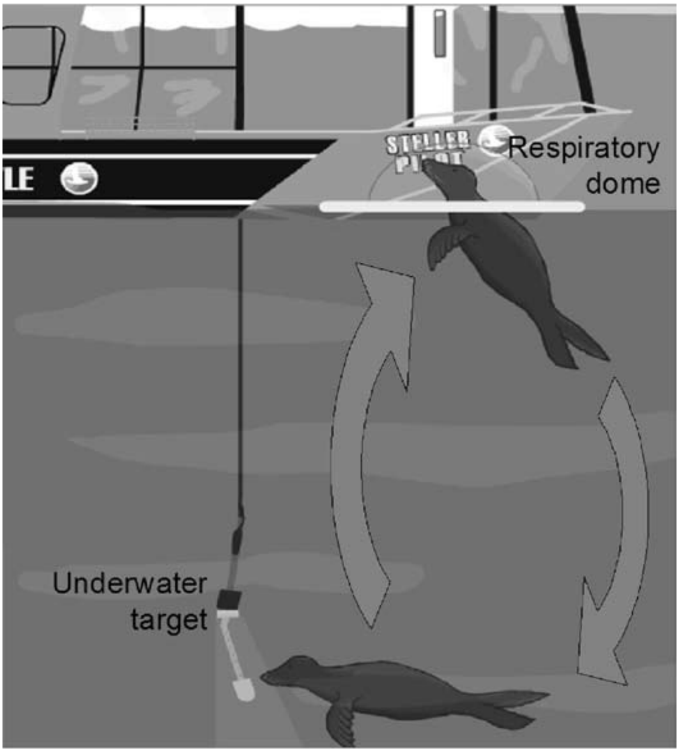

Figure 3. Sea lions are trained to dive from a respiratory dome at the surface to variable depths using an underwater light targeting system and a video system to monitor behavior.

depth on command and remained stationary at the target light for a predetermined duration (between 1 minute and 3 minutes). The sea lion was trained so that when the light was switched off, it returned to the respiratory chamber at the surface where an estimate of post-dive metabolism was made for 10 minutes. Around 3 months of training was required to carry out the dive element of this study, and we attempted to maintain sea lions at each duration for around a week prior to data collection.

To date, we have carried out 31 dive trials with single dives up to 30 meters depth ranging in duration from 65 seconds to 200 seconds. Although these depths and durations are well below the maximums recorded for wild Steller sea lions, they do encompass a significant proportion of their wild dives (Merrick and Loughlin 1997, Loughlin et al. 2003). This confirms that it is possible to use trained Steller sea lions to carry out experimental trials to evaluate diving metabolism, and to collect meaningful

Table 1. Summary of preliminary estimates of oxygen consumption rates at the surface and during 31 dives for two Steller sea lions. Dive durations were between 65 and 200 seconds to depths between 5 m and 30 m. All values of mass, and surface and diving oxygen consumption rates are means (±SD).

Sea lion	n	Mass (kg)	Surface oxygen consumption (ml $kg^{-1}min^{-1}$)	Diving oxygen consumption (ml $kg^{-1}min^{-1}$)
F00BO	13	117.6	11.4 (±1.5)	6.1 (±2.1)
F97SI	18	193.6	10.1 (±1.0)	5.7 (±2.1)

bioenergetic data in the open ocean. Experimental trials with multiple dives have also been carried out ranging from 3 to 5 consecutive dives of 30 seconds. This approach allows realistic simulation of foraging dives without the restraint of a captive environment. Furthermore, it allows the evaluation of diving metabolism on a dive-by-dive basis over a series of dives, and allows researchers to examine the influence of changes in dive parameters and environmental characteristics. Preliminary estimates of oxygen consumption rates at the water surface and during single dives to depth are shown in Table 1.

Overall, despite the logistical and financial investment inherent in a project of this scope, and the challenges of taking captive animals into the wild, the advantages of using trained animals to carry out bioenergetic studies in the wild are significant. A perceived inherent weakness of using trained animals to carry out energetic studies is its applicability to wild animals. For example, it is clear that the trained animals' physiological state and behavioral responses may be governed to an extent by the expectations of the trainer, or be a response to the training itself rather than a "natural" response to diving and foraging. We do not think that the sea lions exhibited an extreme metabolic adjustment based on an assumed maximum dive duration, as they were no longer naïve to the intended dive parameters once data collection began. However, behavioral patterns during dives may be influenced by the training; unlike many diving patterns in the wild (e.g., Le Boeuf et al. 1992, Crocker et al. 2001) ascent rates observed in our studies were generally significantly faster than descent rates, a potential artifact of providing the food resource at the surface rather than at depth. It is clear that an approach that allows the animals to dictate their own dive characteristics and concurrent physiological responses would be preferable in future studies of foraging energetics.

Despite these caveats, using the approach described in this study, many of the apparent shortcomings can be overcome. For example, the inherent physical limitations of a captive environment (e.g., experimental pool dimensions) are no longer an issue, allowing accurate simulation of dives in the wild, and an evaluation of the influence of pressure at depth. Furthermore, with over a year of carrying out trained dives to depth before data collection commenced, the physiological fitness of the animals is likely to be more representative of wild animals than in previous studies with captive animals.

The success of the current project has allowed us to develop a research program focused on detailed aspects of diving physiology and locomotion. These include studies of the consequences of variations in diving and swimming characteristics and the influence in changes in body condition on diving physiology. Overall, the open ocean research program allows the energetic costs of foraging in the wild to be accurately assessed, and provides a means for assessing their energetic requirements and physiological constraints, as well as determining the potential effects of changes in prey distribution or density.

We are currently evaluating whether variations in prey encounter rates at depth result in variations in behavioral patterns (Thompson and Fedak 2001, Cornick and Horning 2003) or metabolic adjustments made by diving sea lions. This will be complemented by a study of the influence that changes in body condition (through simulated changes in buoyancy) have on these processes. Furthermore, we aim to assess the biomechanical and energetic influence of telemetry devices by examining detailed changes in facets of swimming behavior and oxygen consumption while wearing telemetry packages of different shapes and sizes. In addition, our research setup allows investigators to test foraging models and assess their applicability to Steller sea lions, and provides investigators with a means of measuring other important physiological mechanisms, such as hearing sensitivity (e.g., Ridgway et al. 2001, Kastak and Schusterman 2002), and their associations with water depth.

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