QUANTIFYING THE COSTS OF DIVE BEHAVIOURS AND FORAGING STRATEGIES IN STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

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Abstract

Air-breathing divers, such as marine mammals, should adjust their diving behaviours in relation to the depth and density of their prey to minimize the energetic costs and maximize the benefits of foraging. However, there is little experimental data to test these predictions or to develop models to predict the responses of marine mammals to changes in prey availability. The objectives of my study were to 1) determine how changes in prey availability affect dive behaviour and foraging efficiency in Steller sea lions (*Eumetopias jubatus*) and 2) develop models with data from free-diving captive Steller sea lions to estimate foraging costs in wild animals and evaluate energetic trade-offs between different foraging strategies. I measured the diving metabolic rate, dive durations, and food intake of 4 trained sea lions diving in the open ocean on simulated prey patches of high- or low-densities at 10 m and 40 m. I also measured diving metabolic rates of sea lions performing 4 controlled dive types that allowed me to estimate the separate costs of different dive components (i.e., surface time, bottom time, and transiting to and from depth). I found that animals diving on prey patches with low prey density altered their dive behaviours and spent proportionally less time actively foraging, which ultimately decreased their foraging efficiency. I also found that making single, longer dives were less energetically costly than making multiple shorter dives in a bout, but that the sea lions replenished oxygen stores more efficiently when making a bout of dives. Finally, I determined the metabolic cost of transiting to and from depth (20.5±13.0 ml O_2 min^{-1} kg^{-1}) was greater than the cost of foraging during the bottom portion of a dive (13.5±4.1 ml O_2 min^{-1} kg^{-1}). With these values, I generated a predictive equation to estimate the diving costs of free-ranging animals. Overall, my results indicate that Steller sea lions do alter their dive behaviour in relation to prey availability and that different foraging strategies have different energetic costs. These results can be used to understand how changes in prey availability affect the overall energy balance and health of Steller sea lions.

Preface

I was the primary designer of all experiments described in this thesis and received suggestions and support from my co-supervisors David Rosen and Andrew Trites. I preformed all data collection and analysis, and prepared all manuscripts. Chapters 2 and 3 were written as manuscripts for which co-authors David Rosen and Andrew Trites provided edits and comments. A version of Chapter 2 has been published in the Journal of Experimental Marine Biology and Ecology as: Goundie, E.T., Rosen, D.A.S. and Trites, A.W. 2015. Low prey abundance leads to less efficient foraging behavior in Steller sea lions. J. Exp. Mar. Biol. Ecol. 470, 70-77.

All experimental protocols were approved by Animal Care Committees of the University of British Columbia and the Vancouver Aquarium. Experiments were conducted under UBC Animal Care Permit # A11-0397. I completed the ethics training requirements of the Canadian Council on Animal Care (CCAC) / National Institutional Animal User Training (NIAUT) Program, certificate #: 5679 – 12.

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List of Abbreviations

ADL	Aerobic dive limit
cADL	Calculated aerobic dive limit
MR_S	Pre-dive surface metabolic rate
AMR	Average metabolic rate calculated over the dive cycle (dives + all surface time)
DMR	Diving metabolic rate calculated over the submerged portion of dives only

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Chapter 1: Introduction

1.1 Steller Sea Lions and Changes in Prey

Steller sea lions (*Eumetopias jubatus*) range from the west coast of North America through the Aleutian Islands and the Bering Sea, into Russia and Japan (Loughlin et al., 1992). There are two genetically distinct populations of Steller sea lions within their range — the Eastern Distinct Population Segment (EDPS), which occurs east of 144°W in the Gulf of Alaska, and the Western Distinct Population Segment (WDPS) which is found to the west (O'Corry-Crowe et al., 2006). Steller sea lion populations have drastically declined since the 1970's, with the majority of the decline experienced by the WDPS. Abundance estimates suggest a 70-80% decrease, from approximately 282,000 animals in 1976 (Trites and Larkin, 1996) to an estimated 46,000-58,000 animals at the turn of the century (Pitcher et al., 2007). The dramatic decline of Steller sea lions seen in the WDPS has prompted an extensive research effort focused on gaining a better understanding of their ecology and physiology in an attempt to explain the causes for their decline and lack of recovery.

Nutritional stress has been proposed as a contributing factor to the observed population declines of Steller sea lions. This hypothesis suggests that changes in prey quality, quantity, and diversity may be affecting the health of Steller sea lion populations, as well as several other top marine predator species (Trites and Donnelly, 2003). Steller sea lions feed on a large variety of prey species that vary in both energy content and distribution (e.g., depth and schooling densities). Changes in prey quantity and quality may limit a sea lion's ability to consume sufficient prey to meet their daily energetic demands. Changes in prey density and distribution may lead to alterations in foraging patterns and, thus, foraging costs, that may lead to energetic imbalances if foraging strategies become less efficient.

Several studies have examined the physiological effects of changes in prey quality and quantity on Steller sea lions (Atkinson et al., 2008; Gerlinsky et al., 2014; Jeanniard du Dot et al., 2009; Rosen et al., 2000; Rosen and Trites, 2004, 2000). However, little is known about how much energy sea lions spend while foraging, how these costs may vary with changes in foraging conditions, and ultimately how they may alter foraging strategies.

1.2 Diving Ability and Foraging Behaviour

Foraging is an essential behaviour that requires dedicated expenditure of both time and energy, and natural selection should favor those animals that forage in the most optimal way (Krebs, 1978). Diving air-breathing animals, such as Steller sea lions, forage at depth but, as obligate air-breathers, must always return to the surface. Furthermore, they forage in an environment with patchily distributed food sources of varying quality. These physiological and resource limitations are likely to affect foraging behaviour, costs, and ultimately optimality.

The main factor that limits a marine mammal's ability to forage is the amount of oxygen stored in their bodies (Butler and Jones, 1997). As a result, marine mammals use a number of physiological adaptations to conserve oxygen while diving (the mammalian dive response) that include bradycardia, decreased blood flow, vaso-constriction in the extremities and specific organs and tissues, and ultimately an overall decrease in metabolic rate (Scholander, 1940). Steller sea lions use these same techniques while diving, but are not known to be deep or long divers. Instead, they generally dive for less than two minutes—and 90% of their dives are shallower than 50 m (Loughlin et al., 1998; Merrick et al., 1994; Merrick and Loughlin, 1997).

The time an animal can remain submerged while relying solely on their available oxygen stores is known as their aerobic dive limit (ADL) (Kooyman, 1989). The ADL and, as a consequence, the foraging ability of marine mammals depend not only on total body oxygen stores, but also on rates of oxygen consumption while diving. Steller sea lions have relatively low total body oxygen stores and high diving metabolic rates that result in a calculated ADL of only ~3 minutes (Gerlinsky et al., 2013). This short time that Steller sea lions can spend diving aerobically poses an added challenge to optimizing the foraging efficiency of Steller sea lions.

Marine mammals can dive beyond their ADL by using anaerobic metabolism (Carbone and Houston, 1996). This will increase the amount of time they can spend foraging, but diving anaerobically causes a build-up of lactic acid and carbon dioxide that will require an animal to spend more time at the surface clearing these metabolic byproducts (Houston and Carbone, 1992). The decision to dive beyond the ADL has been hypothesized to depend on the availability (depth and density) of prey. Therefore, foraging decisions should be made based on an animal's physiological ability to remain submerged, the distance between the food source and the surface, and the quality of the prey patch on which they are foraging (Thompson and Fedak, 2001). These factors impact both the time and energy spent foraging, as well as the potential energetic gains.

1.3 Research Goals

The main objective of my research was to understand how foraging ability is affected by changes in prey availability. I also wanted to explore the energetic basis and consequences of foraging decisions. Specifically, I sought to determine what foraging strategies are "optimal" in terms of time and energy, given specific conditions of prey density and distribution. I also aimed to find a way of measuring foraging costs that could be used to determine the efficiencies of observed foraging strategies, understand the costs and benefits associated with these strategies, and provide a tool for determining the foraging costs in wild Steller sea lions.

There are several models to predict how diving animals should forage in order to have the highest foraging efficiency (greatest rate of gain per unit of energy expended) (Carbone and Houston, 1996; Houston and Carbone, 1992; Kramer, 1988; Thompson and Fedak, 2001). Breath-hold divers face the unique challenge of being severely limited by the time they have to forage. Therefore, efficiency becomes an extra important factor. Optimal foraging models must be based not only on the proximity and quality of the prey patch (in this case, depth and density), but also the diving capacity of the animal. When the depletion of oxygen stores is the only factor considered, foraging models predict that animals should dive just to or slightly above their ADL (Carbone and Houston, 1996; Houston and Carbone, 1992; Kramer, 1988). This strategy maximizes the proportion of time an animal can spend foraging. However, foraging models change when the quality of a prey patch is also taken into consideration. For example, one model that included depth and density suggests that an animal would benefit from terminating a dive before reaching their ADL when feeding on shallow, low-density prey patches (Thompson and Fedak, 2001). However, it becomes less beneficial to abandon a dive early as depth and density of prey increases.

Both controlled experiments (Cornick and Horning, 2003; Sparling et al., 2007) and wild observations (Costa et al., 1989; Doniol-Valcroze et al., 2011; Mori and Boyd, 2004; Nolet et al., 1993; Thums et al., 2013) have examined dive behaviour in the context of these models. However, no studies have measured the energetic efficiency of these behaviours. My first research goal was therefore to test optimal foraging models in a controlled, but realistic setting where foraging efficiency could be measured in terms of the rate of energetic gain and expenditure (Chapter 2).

Marine mammals exhibit a variety of dive behaviours and foraging strategies (Schreer et al., 2001; Thums et al., 2008). However, accurately predicting foraging costs of free-ranging marine mammals is quite challenging. There are currently very limited ways, with mixed results, to estimate activity-specific cost of various dive behaviours (Dalton et al., 2014; Fahlman et al., 2013; Fahlman et al., 2008c; Halsey, 2011; Halsey et al., 2011; Hindle et al., 2010; Williams et al., 2004; Young et al., 2011). Therefore, my second research goal was to examine the costs and benefits of different foraging strategies, and provide activity-specific costs of diving in Steller sea lions (Chapter 3).

My thesis includes two chapters, which were written as separate manuscripts to be submitted for publications in peer-reviewed journals. Hence, there is some repetition of information between the chapters. The first data chapter (Chapter 2) focuses on changes in foraging strategies and efficiency in response to altered prey availability, and provides tests of optimal foraging models for breath-hold divers under these differing foraging conditions (i.e., changes in prey depth and density). The second data chapter (Chapter 3) focuses on determining metabolic costs of various phases of dives that can be applied to estimating the diving costs of free-ranging animals (including archived historical data), and understanding the underlying costs and benefits of different diving strategies.

As foraging is such an essential activity, understanding how foraging ability is affected by changing environments may play a key role in Steller sea lion conservation. I am hopeful that this research will provide a useful tool to assess the health of declining Steller sea lion populations and implementing recovery strategies.

Chapter 2: Low prey abundance leads to less efficient foraging behaviour in Steller sea lions

2.1 Summary

Breath-hold divers should adjust their dive behaviours to maximize the benefits and minimize the costs of foraging on prey patches of different densities at different depths. However, few studies have quantified how animals respond to changes in prey availability (depth and density), and how this affects their foraging efficiency. I tested the effects of changes in prey availability on the foraging behaviour and efficiency of Steller sea lions by measuring diving metabolic rate, dive durations, and food intake of 4 trained sea lions diving in the open ocean on controlled prey patches of different densities at different depths. Sea lions completed bouts of 5 consecutive dives on high- or low-density prey patches at two depths (10 m and 40 m). I found that the rate of energy expenditure did not change under any of the imposed foraging conditions (mean±SD: 0.22±0.02 kJ min^{-1} kg^{-1}), but that the proportion of time spent consuming prey increased with prey patch density due to changes in diving patterns. At both depths, sea lions spent a greater proportion of the dive bout foraging on prey patches with high prey density, which led to high rates of energy gain (4.3±0.96 kJ min^{-1} kg^{-1}) and high foraging efficiency (cost:benefit was 1:20). In contrast, the sea lions spent a smaller proportion of their dive bout actively feeding on prey patches with low prey density, and consequently had a lower energetic gain (0.91±0.29 kJ min^{-1} kg^{-1}) and foraging efficiency (1:4). The 5-fold differences in foraging efficiency between the two types of prey patches were greater than the 3-fold differences that I expected based on differences in food availability. My results suggest that sea lions faced with reduced prey availability forage less efficiently and therefore would have greater difficulty obtaining their daily energy requirements.

2.2 Introduction

Animals should forage optimally such that they maximize net energy gain relative to the time and energy spent foraging (Charnov, 1976; MacArthur and Pianka, 1966; McNamara, 1982). This means that foraging animals should alter their behaviour to balance the energy they spend to catch prey against the energy they acquire through feeding to meet their daily energetic requirements (i.e., minimizing costs while maximizing benefits). Time spent foraging is also an important consideration, given that minimizing the time needed to acquire sufficient energy minimizes overhead costs and predation vulnerability and maximizes time available for other behaviours.

Breath-hold divers feed at depth, but must return to the surface to breathe and exchange gases. Their foraging decisions are thus constrained by their physiological ability to remain submerged, the distance between the surface and the food source, and the quality of the prey patch on which they forage. These factors impact both the time and energy spent foraging, as well as the potential energetic gains. Several long-standing models have been developed to predict how dive duration and behaviour might vary in relation to the depth and abundance of prey, taking into account aspects of prey distribution and predator physiology (Carbone and Houston, 1996; Houston and Carbone, 1992; Kooyman, 1989; Kramer, 1988; Thompson and Fedak, 2001). However, none of these models have been tested experimentally.

Optimal foraging models for breath-hold divers predict that dive durations should all be close to or even slightly above the animal's aerobic dive limit (ADL—the time spent submerged while relying solely on their available oxygen stores) (Carbone and Houston, 1996; Houston and Carbone, 1992; Kooyman, 1989; Kramer, 1988). This strategy maximizes the proportion of time spent foraging while minimizing the proportion of time transiting to and from depth, and reducing the time needed to replenish oxygen stores at the surface. This theory is based on the premise that foraging decisions (i.e., when to terminate a dive) are made solely in relation to the depletion of an animal's oxygen stores. However, foraging decisions regarding how long to remain on a prey patch and whether or not to extend dive times past the aerobic dive limit, may also be influenced by the depth and the density of that patch.

It is predicted that animals diving on shallow, low density prey patches will be better off energetically by abandoning a dive well before approaching their aerobic dive limit instead of diving close to or beyond it (Thompson and Fedak, 2001). However, the same model also predicts that the benefits of terminating a dive early decrease as dive depth and thus travel time increase. As a result, an animal should remain longer in patches that contain high prey densities compared with those containing low prey densities—but should also remain longer feeding on low prey density patches that are at deeper depths compared to similar prey densities as shallower depths.

Understanding how differences in prey distribution and abundance affects individuals is important for determining the larger-scale impacts these factors may have on the health of entire populations. Steller sea lions (*Eumetopias jubatus*), as well as several other marine mammal and bird species in the Gulf of Alaska and Bering Sea, have experienced significant population declines that may be related to reduced prey availability (Trites and Donnelly, 2003). Several studies have tested how changes in the quality or quantity of prey affect the physiology of individual sea lions (Atkinson et al., 2008; Gerlinsky et al., 2014; Jeanniard du Dot et al., 2009; Rosen et al., 2000; Rosen and Trites, 2004, 2000). However, only a few studies have investigated how such changes in prey may also impact foraging behaviour and efficiency, and how they relate to the predictions of foraging models.

Tests of foraging models on marine mammals include studies where dive behaviour of wild animals have been compared to model predictions (Costa et al., 1989; Doniol-Valcroze et al., 2011; Mori and Boyd, 2004; Nolet et al., 1993; Thums et al., 2013) and controlled experiments with captive animals swimming in pools in simulated foraging conditions of varying quality (Cornick and Horning, 2003; Sparling et al., 2007). Both types of studies have examined aspects of foraging behaviour, but no studies have evaluated the role that foraging energetics, including foraging efficiency, plays in formulating these observed patterns. Specifically, no studies have yet measured both the costs and benefits of a particular foraging strategy for Steller sea lions foraging at realistic depths.

My study tested how prey depth and abundance affect dive behaviour and foraging efficiency by measuring diving metabolic rate, dive behaviour, and food intake of 4 trained Steller sea lions diving in the open ocean on simulated prey patches of different densities at different depths. I thus empirically tested optimal foraging models for breath-hold divers by measuring energy gain and expenditure for animals diving in realistic conditions. My results provide insights into the foraging success and bioenergetic consequences of Steller sea lions in the wild faced with changes in prey availability, as well as the implications this may have for population recovery.

2.3 Materials and Methods

2.3.1 Data Collection

I measured changes in dive behaviour, metabolic expenditure, and energy intake in 4 adult female Steller sea lions diving in simulated prey patches of varying quality. Data were collected between June and August 2013. Two sea lions were 13 years old and two were 16 years old and weighed between 163-239 kg at the time of the trials. All animals were collected from rookeries as pups, and were raised at the Vancouver Aquarium (Vancouver, BC, Canada). The sea lions were subsequently housed at the University of British Columbia's Open Water Research Station (Port Moody, BC, Canada) for 4-8 years, where they regularly dove in the open ocean for research purposes. The sea lions were previously trained to be familiar with the experimental equipment and protocols and all trials were performed voluntarily under trainer control. Experiments were conducted under UBC Animal Care Permit #A11-0397.

2.3.2 Diving Metabolic Rate

I measured diving metabolic rate via flow-through gas respirometry with the sea lions diving in a variety of imposed foraging conditions (see below). Metabolic rate was measured in a 100 L clear Plexiglas dome floating on the surface of the water. Air was drawn through the dome at a rate of 475 L min^{-1}. The excurrent air was continuously sub-sampled and scrubbed of water vapor via $CaSO_4$. Concentrations of oxygen and carbon dioxide were measured using Sable System FC-1B and CA-1B analyzers, coupled to a 500H mass flow generator and controller (Sable Systems, Las Vegas, NV, USA). Oxygen and carbon dioxide concentrations were recorded every 0.5 seconds (Sable Data Acquisition system, Sable Systems Inc.). Metabolic data was analyzed using LabAnalyst X (Warthog Systems, Mark Chappell, University of California) and oxygen consumption rates were calculated from changes in gas concentrations from baseline levels (using eq. 3b, Withers, 1977). Baseline gas concentrations were set using ambient air at the start and end of the trial to correct for drift during trials. The entire system was periodically calibrated with gases of known concentrations.

Pre-dive metabolic rate (MR_S) was measured for animals resting calmly at the surface in the metabolic dome before each dive trial. MR_S was calculated as the average rate of oxygen consumption during the last 2 minutes of a 5-10 minute period, during which oxygen concentrations were stable. Post-dive rates of oxygen consumption were measured to calculate oxygen consumed during the dive and to determine the amount of time it took to return to within 5% of MR_S (recovery time).

Average metabolic rate during the dive (AMR) was calculated as the total volume of oxygen consumed during a dive cycle, divided by the total dive cycle duration. A dive cycle was defined to begin with the first dive and end with the completion of the post-dive recovery, and includes all dives, inter-dive surface intervals in a bout, and the full post-dive recovery period. Thus, AMR accounts for all of the time and energy associated with a complete foraging bout, including the time spent at the surface as well as diving.

2.3.3 Trial Protocol

The sea lions were trained to voluntarily dive between the metabolic dome at the surface and the end of two feeding tubes at depth, set either at 10 or 40 m. These depths were representative of dive depths observed in wild Steller sea lions (Merrick and Loughlin, 1997). During dives, 20 g pieces of Pacific herring (*Clupea pallasii*) were delivered to the sea lions at depth via the feeding tubes. Fish were alternately pumped out of each feeding tube to encourage movement between the tubes. Sea lions swam continually back and forth between the feeding tubes and consumed the fish pieces immediately as they came out of the tubes. Feeding was continuous and constant until after the animal chose to leave the bottom and resurface. This was monitored via a camera mounted on the feed tube. The rate of fish delivery was altered between trial types to simulate prey patches of different densities; prey delivery rates of 12 fish pieces per minute were used as the "high-density patches" and 4 fish pieces per minute as the "low-density patches". Each animal completed three trials of each prey rate and dive depth combination, for a total of 48 dive trials under 4 different foraging conditions.

Animals were fasted overnight before trials and transported to the dive site by boat. During transport and measurements of pre-dive surface metabolic rates they received minimal food reinforcement (<0.8 kg) to reduce the potential impact of digestion on metabolic rate (Rosen and Trites, 1997). Sea lions performed bouts of 5 consecutive dives, wherein they chose both dive duration and inter-dive surface intervals. The sea lions were fed <0.2 kg during each surface interval to reinforce surfacing in the dome while minimizing the influence of the food at the surface on dive behaviour. Each animal was outfitted with a tight-fitting harness holding a time depth recorder (ReefNet, Inc., Mississauga, ON, Canada) to record dive behaviour. Total dive durations were measured as the time from when the animal left the metabolic dome to when the animal returned to the surface. Surface times were measured as the time spent in the metabolic dome between dives. Bottom and transit durations were extracted from the data on the time depth recorders.

2.3.4 Foraging Efficiency

I calculated foraging efficiency in each of the four imposed foraging conditions using the equation from Weathers and Sullivan (1991):

$$\text{Mean Gross Foraging Efficiency} = \frac{\text{Energy Intake}}{\text{Energy Expended}}$$

Foraging efficiency thus represents the amount of energy gained, in kilojoules (kJ), for every kilojoule expended. Assuming that all fish delivered to depth were eaten by the sea lions (validated with previous video-taped evidence), fish mass intake was calculated as the bottom duration (recorded on the time depth recorder) multiplied by the prey delivery rate, multiplied by the average mass per fish piece (20 g per piece). Energy intake was estimated by multiplying ingested fish mass by the energetic content of the herring, which was 7.72 kJ g^{-1}, as determined by a commercial laboratory (SGS International). Total energy intake could be recalculated as the rate of energy intake by dividing total kilojoules gained by the dive cycle duration. Rate of energy expenditure was determined by converting AMR to kilojoules (1 L O_2 = 20.1 kJ, (Rosen and Trites, 2000).

2.3.5 Statistical Analysis

All data were analyzed using R software (R Core Team, 2014). Linear mixed-effects models (lme) from the nmle package (Pinheiro et al., 2015) were used. Significance was set as $\alpha = 0.05$.

Animal ID was included as a random effect to account for repeated measures for each animal. Fixed effects were prey rate and trial depth. Models were run using the maximum likelihood method. Nested models (full and reduced) were compared using a log likelihood ratio test (LRT) to determine the effect of each factor individually and the best overall model to fit the data (Pinheiro and Bates, 2000). Full models included both fixed factors while reduced models had the factor of interest removed. A significant result indicated that the full model was a better fit to the data and that the factor removed in the reduced model had a significant effect. When both fixed factors were significant, Bonferroni *post hoc* analyses were also run to compare the differences between all 4 simulated foraging conditions with prey rate and depth combined. For single model ANOVA's F and P values were reported. Values were reported for slopes only, as all intercepts were significantly different from zero. Energetics data were tested as both absolute and mass-specific values (i.e., per kg). Results did not differ between methods, so mass-specific data were reported to facilitate comparison to other studies. All values are reported as means ± SD.

2.4 Results

2.4.1 Dive Energetics

Average diving metabolic rate (AMR) for all trials ranged from 8.9 to 13.4 ml O_2 min^{-1} kg^{-1} (Table 2.1). The rate of energy expenditure (calculated from AMR) was 0.22±0.02 kJ min^{-1} kg^{-1} and did not vary among each of the four foraging conditions.

Table 2.1 Mass (mean±SD) of four adult female Steller sea lions during experimental trials from June to August 2013. Mass corrected pre-dive surface metabolic rates (MR_S) and average metabolic rates (AMR) during a dive bout are included for each animal. There was no statistical difference in metabolic rates (MR_S or AMR) between experimental conditions, so all trials are averaged for each animal (12 trials per animal).

Animal ID	Mass (kg)	MR_S (ml O_2 min^{-1} kg^{-1})	AMR (ml O_2 min^{-1} kg^{-1})
F97SI	234±7.8	7.7±0.90	10.6±1.2
F00YA	221±2.6	7.1±0.44	10.5±1.0
F97HA	178±3.4	9.2±0.69	11.3±0.93
F00BO	165±1.6	7.2±0.55	10.7±0.81

2.4.2 Dive Behaviour

A variety of dive characteristics were measured to test for differences in diving behaviour among the four foraging conditions (Table 2.2). Each complete dive cycle could be partitioned into total dive time and total surface time. Total dive time could be further divided into its constituent parts: transit time (ascent and descent times combined) and bottom time. Total surface time could be broken down into surface interval (total of all 4 inter-dive surface intervals) and post-dive recovery.

Total dive cycle duration (i.e., sum of dives, inter-dive surface intervals and post-dive recovery) increased with both prey density (LRT = 48.66, $P < 0.0001$) and depth (LRT = 45.13, $P < 0.0001$). Hence, the longest total dive cycles occurred in high-density prey patches at 40 m (20.3±2.7 minutes) and the shortest cycles were in low-density patches at 10 m (10.0±1.1 minutes). Low-density patches at 40 m and high-density prey patches at 10 m had similar intermediate dive cycle durations (combined mean = 14.7±2.2 minutes).

Total dive duration (sum of 5 dives in a dive cycle) followed the same trend as dive cycle duration, where duration increased with prey density (LRT = 42.59, $P < 0.0001$) and depth (LRT = 42.03, $P < 0.0001$). The longest total dive durations were in high-density prey patches at 40 m (12.9±2.6 minutes) and the shortest were in low-density prey patches at 10 m (4.2±1.0 minutes). In fact, the increase in dive cycle duration was primarily due to these increases in total dive duration (Fig. 2.1)

Table 2.2 Dive characteristics of Steller sea lions diving to 10 m and 40 m to either low-density (4 fish min^{-1}) or high-density (12 fish min^{-1}) prey patches. All data are for bouts of 5 consecutive dives. Dive cycle durations include the subsurface dive time, inter-dive surface intervals and post-dive recovery period summed over the entire bout. Total dive durations are the sum of all bottom times and transit times. Surface interval times are the sum of all 4 inter-dive surface intervals and post-dive recovery times are the amount of time the animals spent at the surface after a dive bout before their rates of oxygen consumption returned to pre-dive levels. Proportions of the dive bout spent foraging, at the surface, and transiting are also included. Values are mean±SD of 4 animals with 3 dive trials for each experimental condition.

		Duration (minutes)							Proportion of Bout		
Prey Rate (fish min^{-1})	Depth (m)	Dive Cycle	Total Dive	Bottom Time	Transit	Total Surface	Surface Interval	Post-Dive Recovery	Foraging	Surface	Transiting
4	10	10.0±1.1	4.2±1.0	3.1±1.0	1.13±0.06	5.8±1.0	0.7±0.2	5.2±1.1	0.30±0.08	0.58±0.08	0.11±0.02
4	40	14.6±1.7	8.3±1.6	4.0±1.4	4.25±0.42	6.3±0.7	1.5±0.4	4.8±0.5	0.27±0.07	0.43±0.05	0.20±0.03
12	10	14.9±2.7	8.3±2.4	7.2±2.4	1.15±0.07	6.6±1.0	0.8±0.2	5.8±0.9	0.47±0.08	0.45±0.07	0.08±0.02
12	40	20.3±2.7	12.9±2.6	8.9±2.4	4.05±0.39	7.4±0.8	2.0±0.6	5.3±0.9	0.43±0.06	0.37±0.05	0.29±0.02

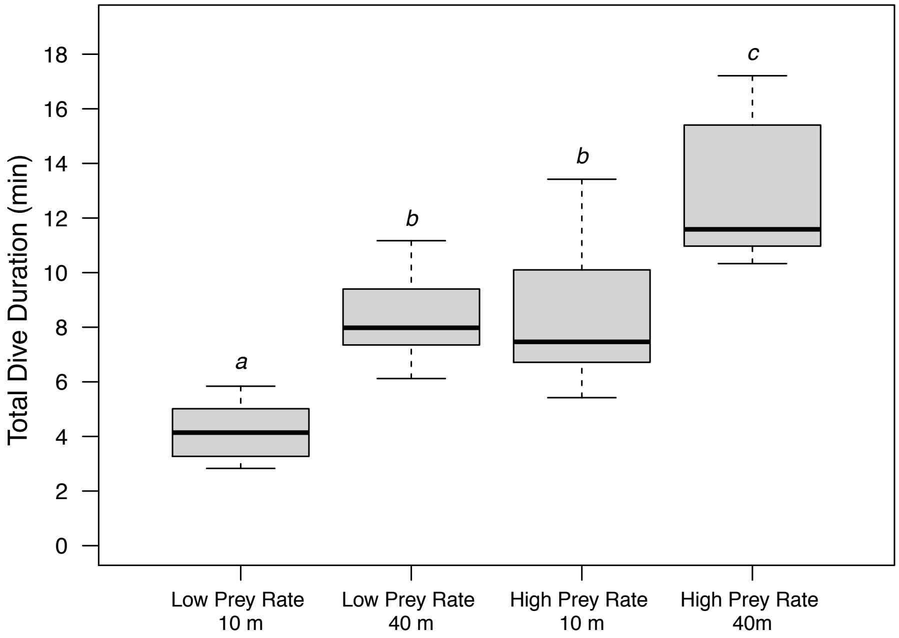

Figure 2.1 Total dive durations for Steller sea lions diving to 10 and 40 m to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches. Dive durations are the sum of the five dives in a dive cycle. Each box represents 3 dive trials from each of the 4 animals for a total of 12 trials in each foraging condition. Letters that differ indicate significant differences between foraging conditions.

The observed increase in total dive time with depth and prey density could be due to increases in transit time and/or bottom time. Total transit time (sum of descent and ascent times for all 5 dives in a bout) was 1.1±0.1 minutes for 10 m dive bouts and 4.2±0.4 minutes for 40 m dive bouts and was not affected by prey density. In contrast, bottom duration (total dive duration with transit times removed) was mainly affected by prey patch density. Sea lions remained at high-density patches longer, regardless of the depth at which they were foraging (high-density patches: 8.0±2.5 minutes, low-density patches: 3.6±1.3 minutes; LRT = 46.71, $P < 0.0001$). Depth had only a marginal effect on bottom duration in high-density prey patches, where sea lions spent slightly more time at the bottom at 40 m compared to 10 m (40 m: 8.9±2.4 minutes, 10m: 7.2±2.4 minutes; LRT = 4.16, P = 0.04). There was no effect of depth on bottom duration in low-density prey patches (LRT = 3.81, P = 0.05). The longest bottom times were in high-density patches at 40 m and the shortest bottom times were in both low-density prey patches (Fig. 2.2).

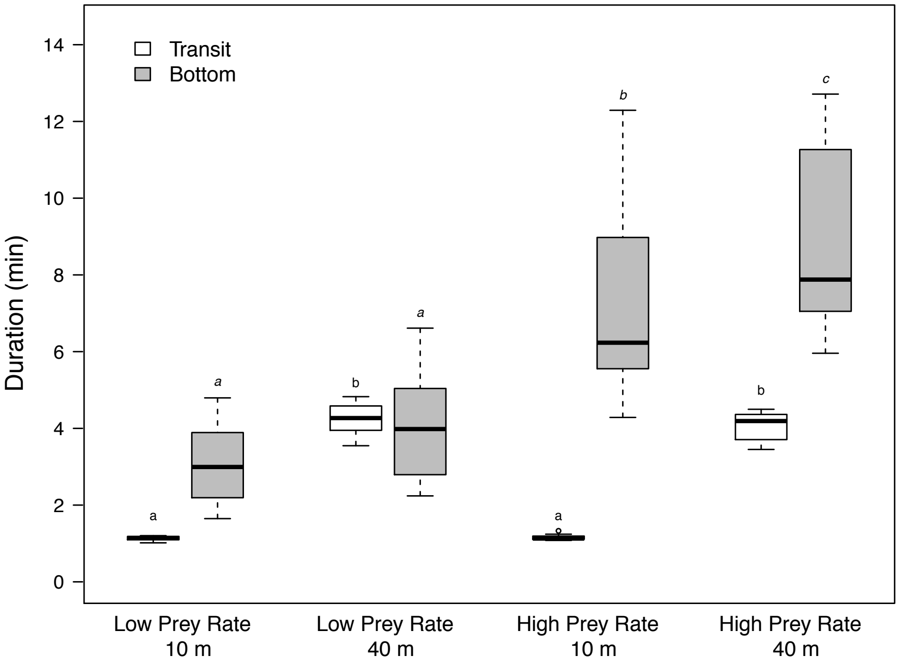

Figure 2.2 Differences in transit and bottom durations for Steller sea lions diving to 10 and 40 m to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches. Transit durations (in white) include the sum of descent and ascent times for all five dives in a dive cycle. Bottom durations (in grey) are the portion of the dive spent foraging at depth summed over the five dives in a dive cycle. Each box represents 3 dive trials from each of the 4 animals for a total of 12 trials in each foraging condition. Letters that differ indicate significant differences between foraging conditions.

Total surface duration (sum of 4 inter-dive surface intervals and post-dive recovery period) increased directly with total dive duration (ANOVA, $F_{1,43} = 12.04$, $P = 0.0012$; Fig. 2.3). As a result, sea lions spent the most time at the surface when foraging in high-density prey patches at 40 m where dive durations were the longest, and the least amount of time at the surface when foraging in low-density prey patches at 10 m where dive durations were the shortest.

Surface interval duration (sum of the 4 inter-dive surface intervals in a dive cycle) followed the same overall trend as total surface duration, increasing significantly with dive duration (ANOVA, $F_{1,43} = 77.04$, $P < 0.0001$; Fig. 2.4a). In contrast, dive duration had no effect on post-dive recovery time (ANOVA, $F_{1,43} = 0.19$, $P = 0.67$; Fig. 2.4b). This means that the observed increase in total surface time with increased dive duration was due to increases in the inter-dive surface intervals and not the post-dive recovery period.

Independent of dive duration, dives to 40 m had longer surface intervals than dives to 10 m (LRT = 51.23, P < 0.0001; Fig. 2.4a), while post-dive recovery time was longer for dives to high-density prey patches than for dives to low-density prey patches (LRT = 5.40, P = 0.02; Fig. 2.4b). The shortest total surface durations (5.8±1.0 minutes), which were when animals were foraging in low-density prey patches at 10 m, were characterized by both short surface interval durations and recovery times. The longest total surface times (7.4±0.8 minutes), seen with dives to high-density prey patches at 40 m, are due to both long surface interval durations and recovery times.

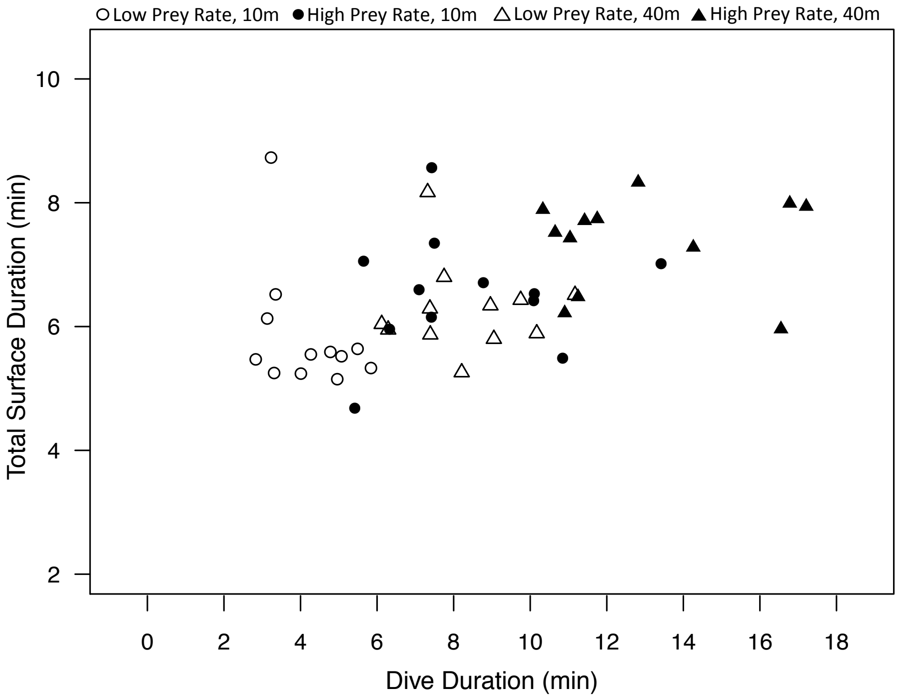

Figure 2.3 Total surface duration (inter-dive surface intervals and post-dive recovery period) for 48 dive trials by 4 Steller sea lions as a function of dive duration (sum of 5 dives in a bout). Each point represents a single dive trial. Filled symbols are dives in high-density prey patches (12 fish pieces min^{-1}) and open symbols are dives in low-density prey patches (4 fish pieces min^{-1}). Circles represent dives to 10 m and triangles represent dives to 40 m. Each of the 4 Steller sea lions performed 3 dive trials in all 4 foraging conditions.

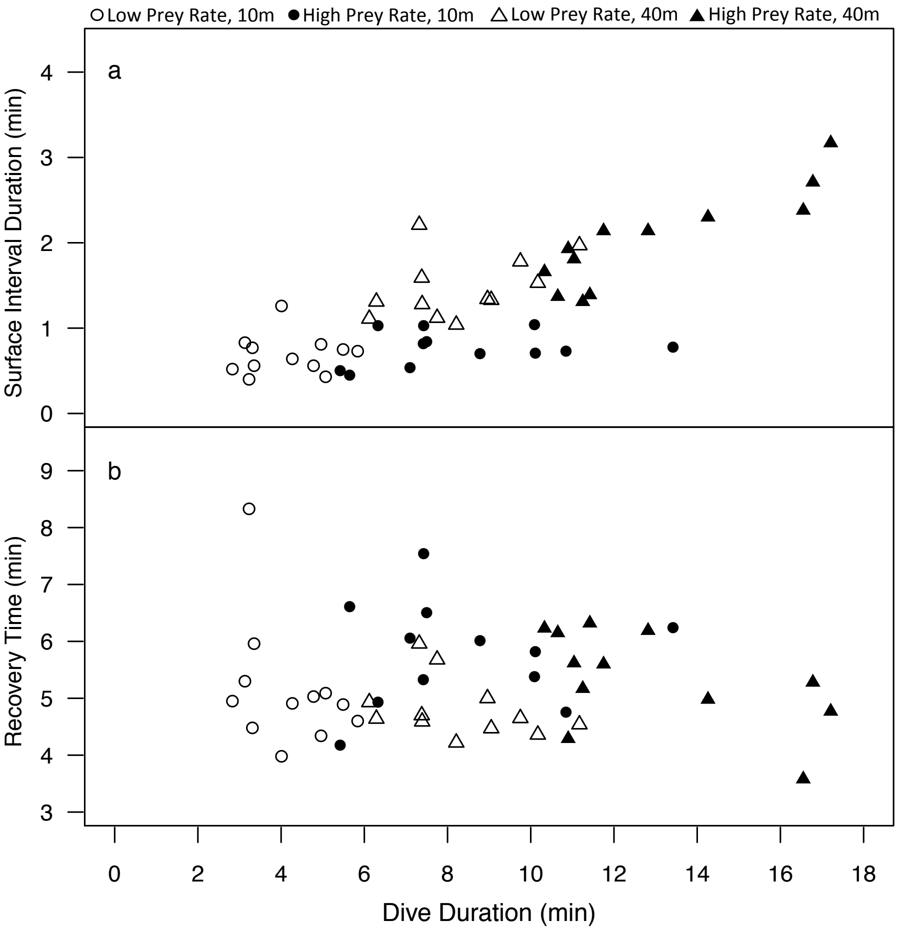

Figure 2.4 (a) Inter-dive surface interval duration and (b) post-dive recovery time for 48 dive trials by 4 Steller sea lions as a function of total dive duration (sum of 5 dives in a bout). Each point represents a single dive trial. Filled symbols are dives in high-density prey patches (12 fish pieces min^{-1}) and open symbols are dives in low-density prey patches (4 fish pieces min^{-1}). Circles represent dives to 10 m and triangles represent dives to 40 m. Each of the 4 Steller sea lions performed 3 dive trials in all 4 foraging conditions.

Changes in dive characteristics combine to result in differences in the proportion of the total dive cycle spent foraging under the different foraging conditions (Fig. 2.5). The proportion of the dive cycle spent as bottom time is the only time when the sea lions are actively consuming fish. Conversely, the proportion of the dive cycle made up of all other portions of the dive cycle (transit, surface intervals and recovery) represents time not acquiring prey. In high-density prey patches, the proportion of time spent foraging (bottom time) was significantly greater than when diving to low-density prey patches (high-density: 0.45±0.07; low-density: 0.28±0.08), while the proportion of time spent not foraging in high-density patches was significantly lower (LRT = 41.64, $P < 0.0001$). Depth had no effect on either proportion (LRT = 3.14, P = 0.08). Transit time comprised a very small proportion of the dive cycle, and so the aforementioned differences in proportions were mainly due to changes in total dive durations and surface durations. Dive duration changed more dramatically between high- and low-density prey patches, while surface durations were less affected. While both dive and surface durations were longer in high-density prey patches, the proportion of time spent at the surface was lower because the increase in dive duration was much greater than the associated increase in surface duration.

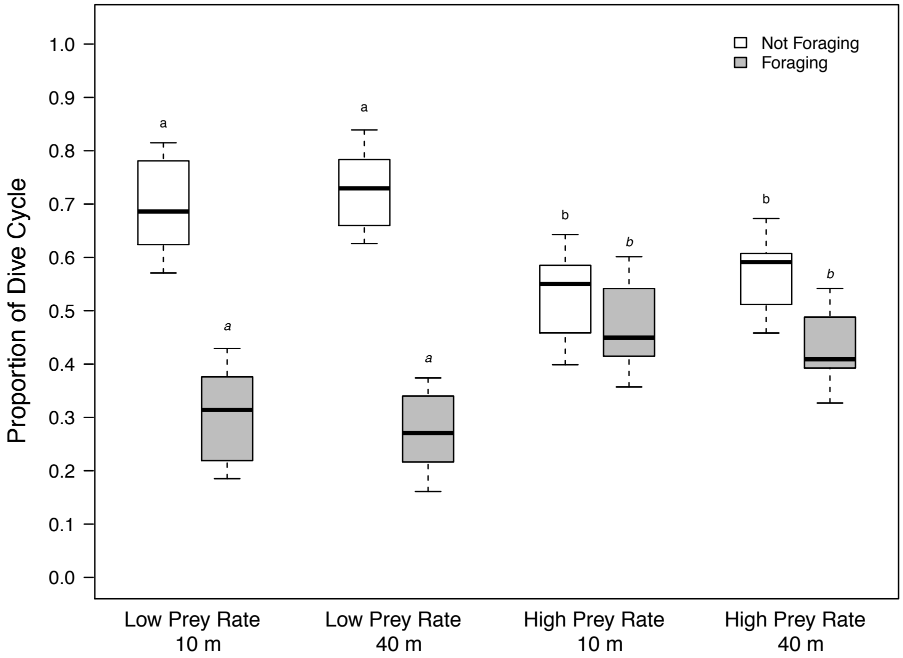

Figure 2.5 Differences in the proportion of a dive cycle spent foraging (grey) and not foraging (white) for Steller sea lions diving to 10 and 40 m in low-density (4 fish pieces min^{-1}) and high-density (12 fish pieces min^{-1}) prey patches. "Foraging" includes only the total time spent at depth consuming fish (bottom time) and "not foraging" includes all time spent at the surface and transiting to and from depth. Each box represents 3 dive trials from each of the 4 animals for a total of 12 trials in each foraging condition. Letters that differ indicate significant differences between foraging conditions.

2.4.3 Foraging Efficiency

Foraging efficiency is the outcome of the rate of energy intake and energy expenditure (Table 2.3). As previously noted, the rate of energy expenditure was independent of dive cycle duration (ANOVA, $F_{1,43} = 2.33$, $P = 0.13$) and was constant across all experimental conditions (Fig. 2.6a). Therefore, any differences in foraging efficiency between experimental conditions were the result of changes in the rate of energy intake.

Table 2.3 Diving energetics and characteristics used to calculate foraging efficiency for Steller sea lions diving to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches at 10 m and 40 m. Average diving metabolic rate (AMR) was measured via flow-through respirometry and converted to a rate of energy expenditure (1 L O_2 = 20.1 kJ). The mass of fish consumed was calculated as the prey rate multiplied by the bottom time and the average mass of each piece (20 g). The fish consumed (kg) was multiplied by the energetic content (7.72 kJ g^{-1}) and divided by dive cycle duration to determine the rate of energy intake. Foraging efficiency was calculated as energy intake divided by energy expenditure and represents the energy gained for every kJ spent.

Prey Rate (fish min^{-1})	Depth (m)	DMR (ml O_2 min^{-1} kg^{-1})	Energy Expenditure (kJ min^{-1} kg^{-1})	Bottom Duration (min)	Fish Consumed (kg)	Dive Cycle Duration (min)	Energy Intake (kJ min^{-1} kg^{-1})	Foraging Efficiency
4	10	10.3±1.4	0.21±0.03	3.1±1.0	0.24±0.08	10.0±1.1	0.94±0.3	4.7±1.7
4	40	11.0±0.8	0.22±0.02	4.0±1.4	0.32±0.1	14.6±1.7	0.87±0.3	4.0±1.4
12	10	10.6±0.8	0.21±0.02	7.2±2.4	1.7±0.6	14.9±2.7	4.4±0.9	20.7±3.9
12	40	11.3±0.8	0.23±0.02	8.9±2.4	2.1±0.6	20.3±2.7	4.1±1.1	18.6±5.2

The rate of energy intake is a product of bottom time, prey ingestion rate, and prey energy content. Prey delivery rates in high-density prey patches were 3 times that of low-density prey patches. Therefore, all other factors being equal, rates of energy intake should be 3 times higher under these conditions. However, changes in dive behaviour meant that the proportion of total dive time spent actively ingesting prey (i.e., % total dive cycle composed of bottom time) changed in each test condition. Energy intake was averaged over the entire dive cycle, so when an animal spent a greater proportion of a dive cycle foraging and a smaller proportion at the surface, the average rate of energy intake increased. Hence, prey intake rates were significantly higher in high-density prey patches (LRT = 108.50, $P < 0.0001$). Energy intake was 4.3±0.96 kJ min^{-1} kg^{-1} in high-density patches, and 0.91±0.29 kJ min^{-1} kg^{-1} in low-density patches. As a result, the rate of energy intake was 4.7 times higher in high density prey patches, exceeding what was expected due to the difference in food density alone, due to the greater proportion of time spent foraging in these patches (Fig. 2.6b).

The proportion of the dive cycle spent foraging was independent of dive cycle duration within each prey patch density (high-density patches, ANOVA, $F_{1,19} = 0.58$, $P = 0.46$; low-density patches, ANOVA, $F_{1,19} = 0.18$, $P = 0.68$). Hence, rate of energy intake was also independent of dive cycle duration within each prey patch density (high-density patches, ANOVA, $F_{1,19} = 0.91$, $P = 0.35$; low-density patches, ANOVA, $F_{1,19} = 0.64$, $P = 0.43$). Depth also had no effect on the proportion of the dive cycle spent foraging and, therefore, did not affect the rate of energy intake (LRT = 1.22, $P = 0.27$).

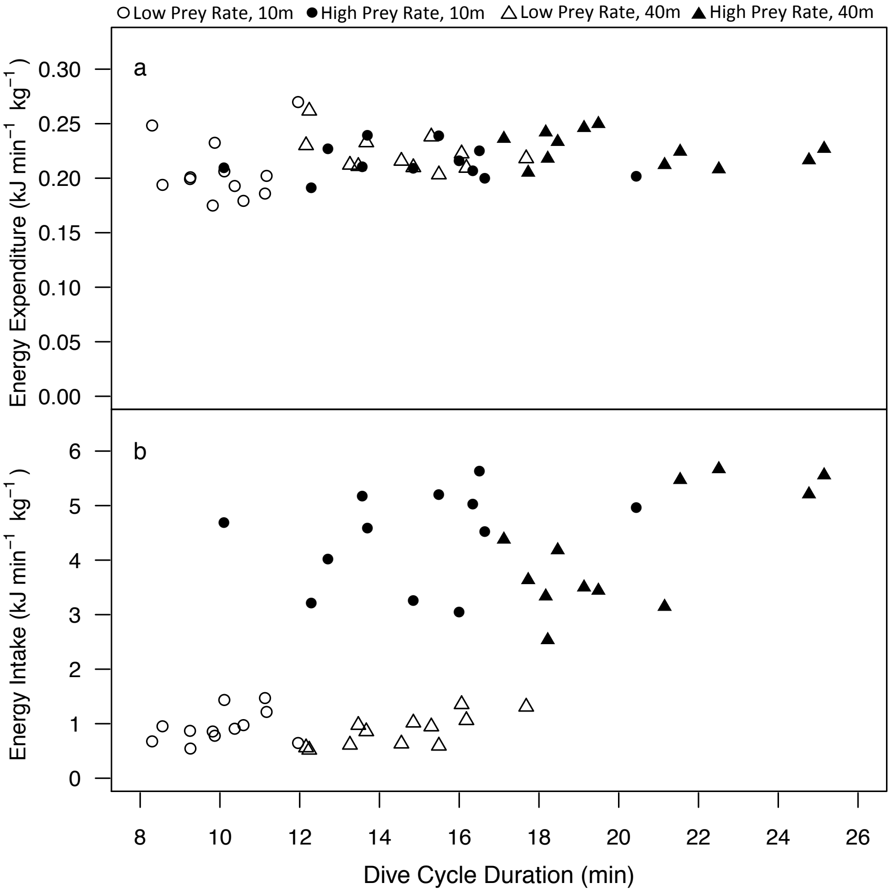

Figure 2.6 Rate of (a) energy expenditure and (b) energy intake for 48 dive cycles as a function of cycle duration for 4 Steller sea lions. Each point represents a single dive cycle. Filled symbols are dives in high-density prey patches (12 fish pieces min^{-1}) and open symbols are dives in low-density prey patches (4 fish pieces min^{-1}). Circles represent dives to 10 m and triangles represent dives to 40 m. Each of the 4 Steller sea lions performed 3 dive trials in all 4 foraging conditions. Note the differences in the scales of the y-axis.

In high-density prey patches, the greater rate of energy intake with no concomitant increase in the rate of energy expenditure led to significantly higher foraging efficiencies than in low-density prey patches (LRT = 96.37, $P < 0.0001$). Foraging efficiency was 19.6±4.6 in high-density prey patches and 4.3±1.6 in low-density prey patches, meaning that for every 1 kJ spent, sea lions gained 19.6 kJ in high-density prey patches and 4.3 kJ in low-density patches (Fig. 2.7). Similar to the differences seen in rates of energy intake, this 4.6 times difference in foraging efficiency between high- and low-density patches is due to the greater proportion of time spent foraging combined with the increased food availability in high-density prey patches.

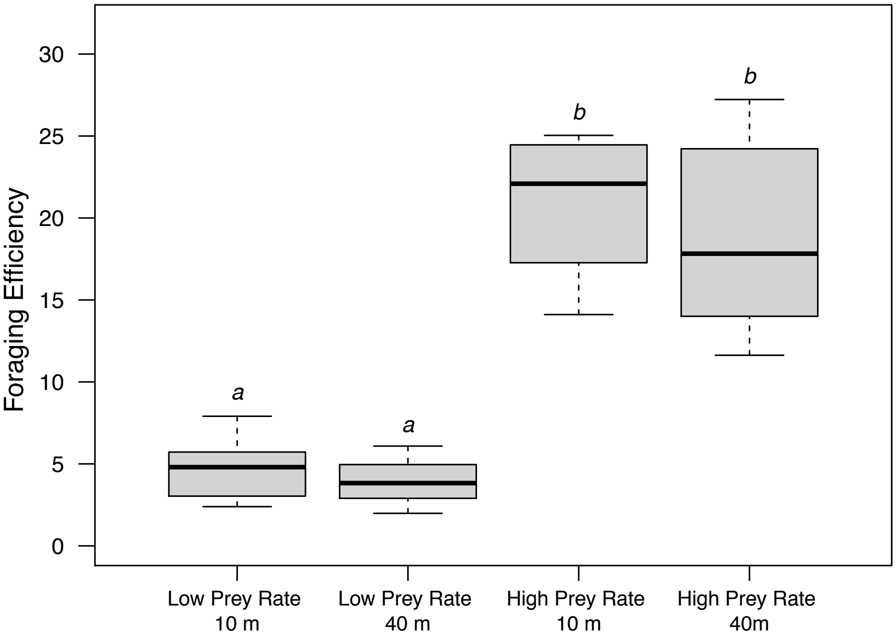

Figure 2.7 Foraging efficiency for Steller sea lions diving to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches at 10 and 40 m. Foraging efficiency was calculated as energy intake divided by energy expenditure and represents the amount of energy gained for each kJ spent. Each box represents 3 dive trials from each of the 4 animals for a total of 12 trials in each foraging condition. Letters that differ indicate significant differences between foraging conditions.

2.5 Discussion

Mathematical models have largely been the basis for current understanding of the effects that prey depth, prey density, and aerobic dive limits have on the foraging behaviours of air-breathing predators (Carbone and Houston, 1996; Houston and Carbone, 1992; Kramer, 1988; Thompson and Fedak, 2001). These models have yielded a number of predictions, but few empirical tests have ever been undertaken with diving vertebrates (e.g., Carbone and Houston, 1994; Cornick and Horning, 2003; Sparling et al., 2007), and none have quantitatively tested both the behavioural and energetic effects that changes in prey can have on the foraging efficiencies of air-breathing diving predators.

Consistent with the predictions of behavioural foraging models, I found that the sea lions increased the duration of their dives in response to increases in prey depth and patch density. The duration of the deeper dives on higher prey densities were often close to or beyond the animals' aerobic dive limits (ADL) and sea lions feeding on the low-density prey patches in shallower water abandoned their dives earlier, well before reaching their aerobic dive limits. However, counter to model predictions, there was a marked decrease in foraging efficiency when animals abandoned dives earlier in low prey densities.

2.5.1 Effects of Depth on Dive Behaviour

Houston and Carbone's (1992; 1996) model predicted changes in foraging behaviour for breath-hold divers based solely on the depth of the prey and an animal's ADL, the temporal limit to an animal's reliance on aerobic metabolism. Their model suggested that, for deeper dives, it is beneficial to increase the time spent foraging (i.e., bottom time) to compensate for the longer travel time and minimize the number of trips needed to the prey patch. Their models also predicted that an animal should dive just to the point of switching to anaerobic metabolism, or even slightly longer. This was based on the assumption that diving beyond the ADL necessitates proportionally longer recovery times at the surface to remove metabolic end-products of anaerobic metabolism (Butler, 1988; Carbone and Houston, 1996; Houston and Carbone, 1992). Hence, diving for durations close to the ADL creates the largest proportion of time forging and ensures maximal rates of oxygen uptake at the surface due to the larger oxygen partial pressure gradient between the air and the animals' blood.

While two previous studies have also observed the same effects of travel distance on dive duration (Carbone and Houston, 1994; Sparling et al., 2007), they were conducted in a pool and only examined shallow depths and horizontal swimming distance. In contrast, my study tested this prediction on animals diving to realistic depths in the open ocean, similar to what is seen in wild animals. This is an important distinction given that depth not only directly affects transit time, but also affects an animal's physiology.

Individual dive durations averaged 1.3 minutes at 10 m depths and 2.1 minutes at 40 m. In comparison, the calculated ADL (cADL) of these same Steller sea lions is 3 minutes (Gerlinsky et al., 2013). Although dive durations were longer at 40 m, they were still on average below their cADL at both depths, which does not quite agree with Houston and Carbone's (1992; 1996) predictions that an animal should dive close to their ADL. However, the dive times I measured to 40 m correspond to measurements on wild Steller sea lions, where dive durations to depths of

20-50 m averaged 1.9-2.4 minutes, also well below the cADL (Loughlin et al., 1998; Merrick et al., 1994). This indicates that the sea lions in my study were making similar foraging decisions to those of their wild counterparts. It is possible that the sea lions were not diving close to their cADL because they were making bout dives where they were not fully recovered between each dive. This is also consistent with wild dive behaviour where animals make frequent, short consecutive dives (Loughlin et al., 1998; Merrick et al., 1994).

Dives within a dive bout are not thought to be physiologically independent events. Rather, the first dive in a bout tends to be the longest, and incurs the highest apparent depletion of oxygen reserves (Fahlman et al., 2008b; Kooyman et al., 1973). During subsequent inter-dive surface intervals, these oxygen reserves are thought to be only partially replenished, given the decreasing efficiency of re-oxygenation with increasing surface durations. As a result, subsequent dives are shorter, because the sea lions start with smaller oxygen reserves. Thus, average duration of subsequent dives would appear to be less than the ADL despite the fact that, physiologically, the animals finish their dives with similarly depleted oxygen stores.

2.5.2 Effects of Patch Quality on Dive Behaviour

A model by Thompson and Fedak (2001) predicted that diving behaviour is not only based on a an animal's ADL and the distance to the prey patch, but also on how productive the animal perceives the patch to be. For example, if an animal does not find prey within a set amount of time (i.e., prey rate of 0), they should perceive that patch as poor quality and abandon the dive well before reaching their ADL. Presumably, although not explicitly stated, an animal's dive duration should increase with increasing prey patch quality.

Consistent with Thompson and Fedak's (2001) model predictions, the sea lions in my study diving in high-density prey patches dove longer than in low-density prey patches. Due to the logistics of having animals reliably dive, my study did not use 0 prey rates (as described in Thompson and Fedak, 2001). However, given the sea lions abandoned their dives earlier in low-density patches, the results of my study indicate that the sea lions could make foraging decisions based on the quality of prey patches beyond simply "presence" or "absence" of prey. This is consistent with the results of two previous experimental studies on pinnipeds that found that dive duration increased in higher density prey patches (Cornick and Horning, 2003; Sparling et al., 2007), although one previous study on diving birds found that prey density had no effect on dive duration (Carbone and Houston, 1994). However, as previously noted, all of these studies were conducted under highly artificial, physically limited conditions.

Changes in behaviour related to differences in prey patch density were more dramatic than changes related to depth. This indicates that, although depth is an important factor for determining foraging behaviour, decisions are mainly driven by the amount of prey available in a given prey patch. Increases in dive duration with increases in prey were primarily due to an increase in time spent at depth on the bottom. Transit times did not differ between prey densities, and the differences in transit time required to get to different depths were small compared to the differences in bottom times associated with changes in prey density.

Prey patch density also affected other aspects of the dive behaviour. As a result of the longer dive times at deeper, high-density prey patches, total surface durations also increased reflecting a need to spend more time recovering from these longer dives. As the cADL of the animals used in this study was 3 minutes (Gerlinsky et al., 2013), the sea lions were assumedly using anaerobic metabolism for dives beyond this threshold. The foraging conditions associated with longer surface durations correspond to the conditions where a greater proportion of the dives were over the cADL (Fig. 2.8).

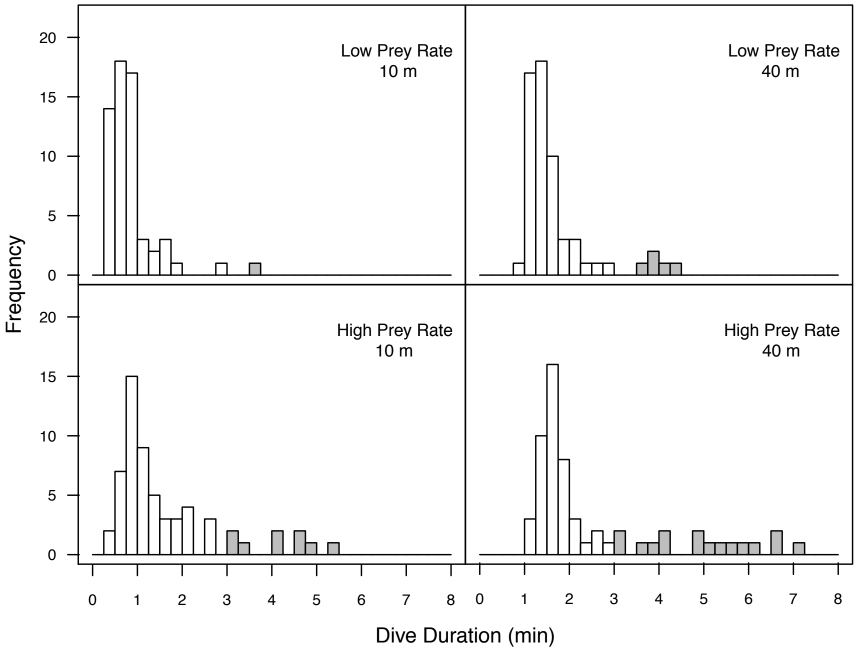

Figure 2.8 Frequency distribution of individual dive durations for Steller sea lions diving to 10 and 40 m in low-density (4 fish pieces min^{-1}) and high-density (12 fish pieces min^{-1}) prey patches. Data is for 60 individual dives in each condition (bouts of 5 dives for each of the 12 trials). Grey bars indicate dives greater than the 3 minute calculated aerobic dive limit for Steller sea lions.

Anaerobic metabolism leads to a build up of lactate in the blood, which needs to be metabolized at the surface before an animal is fully recovered and capable of making another anaerobic dive (Butler and Jones, 1997; Kooyman, 1989; Scholander, 1940). Hence, recovery from dives beyond an animal's ADL require a proportionally greater surface time than dives within their ADL. The longer total time the sea lions spent at the surface was due to longer inter-dive surface intervals and was not the result of longer post-dive recovery times. This suggests that the sea lions chose to spend more time at the surface between dives when dive durations were longer, rather than accumulate a greater oxygen debt with increased dive durations that would need to be paid back at the end of the dive bout with increased recovery times.

Animals diving in deep, high-density prey patches had the highest proportion of dives longer than the cADL (27%), while animals in shallow, low-density prey patches had the least (2%). By diving beyond their ADL, the sea lions were able to acquire more energy on a given dive (due to longer times at depth), but then needed to spend more time recovering at the surface. It therefore makes sense that the sea lions would dive more frequently above their ADL when in the high-density prey patches. However, taking advantage of the abundant prey ultimately affected their foraging efficiency in unexpected ways.

2.5.3 Foraging Efficiency

Foraging efficiency may be the most inclusive measure of the impacts of changes in prey availability, as it incorporates changes in behaviour and physiology. Ultimately, foraging models are designed to predict foraging strategies that should maximize foraging efficiency. In previous studies examining the effects of prey availability on foraging behaviour of marine mammals, no measures of energy expenditure were made and foraging efficiency was either not discussed (Carbone and Houston, 1994; Sparling et al., 2007) or simply expressed as catch per time spent foraging (Cornick and Horning, 2003). In my study, I quantified foraging efficiency in relation to the behaviours observed as well as the predictions made by foraging models by measuring both the energy expenditure and gain of sea lions foraging in realistic conditions.

Since the cost of diving did not change in any of my foraging conditions, differences in foraging efficiency were solely the result of changes in overall rate of energy intake. In my trials, energy intake rates, and therefore foraging efficiency, were almost exclusively affected by prey density and not dive depth, as reflected by changes in the proportion of the dive bout spent foraging in each condition.

On first consideration, an animal’s foraging efficiency might be predicted to remain constant with changing bottom times if the recovery time is also assumed to be proportional to the dive time. However, my results demonstrate that this was not the case. The shorter surface durations were not brief enough proportionally to compensate for the shorter bottom times, leading to a smaller proportion of time spent foraging in low-density prey patches.

At higher prey densities, the animals stayed at the prey patch longer, often beyond their cADL. This greater reliance on anaerobic metabolism required longer surface recovery times, but the overall proportion of a dive cycle spent actively ingesting prey was still greater than for low-density patches. As a result, there was a surprisingly large difference in foraging efficiency observed between high- and low-density prey patches. Most notably, the sea lions were subjected to 3 times less food in low density patches and so—all other factors being equal—should have had a foraging efficiency that was 3 times less in low-density patches. In reality, however, their foraging ultimately ended up being almost 5 times less efficient.

Depth did not affect foraging efficiency as predicted, due perhaps to the sea lions not varying their rates of energy expenditure between depths. Metabolic rate may not have changed with depth because the sea lions were not diving deep enough to push themselves physiologically. Little effect of depth on diving metabolism has been seen for spontaneous dives less than 50 m (Hastie et al., 2006a). For this study, depth was limited to 40 m; however, in the wild Steller sea lions rarely dive beyond 50 m, making the depths used in my study relevant (Merrick and Loughlin, 1997).

Although the observed changes in diving behaviour agreed with model predictions and the majority of previous studies, these behaviours did not increase foraging efficiency as suggested. Giving up earlier in low-density prey patches appeared to result in lower foraging efficiency due to much lower rates of energy gain, while the rate of energy expenditure remained the same. It is possible that the "giving up rule" suggested by Thompson and Fedak (2001) only works if animals have a reasonable chance of finding a better prey patch. While this might be a beneficial strategy in the wild, the sea lions in my study were aware that the prey availability would remain constant within a trial.

There are several potential alternate explanations for the unexpectedly large difference in foraging efficiency I observed between prey patch conditions. It is possible that my measures of oxygen consumption during the presumed recovery period after a trial missed some added cost for such dives that went above the animals' ADL. The sea lions were considered to have recovered when oxygen consumption after the dive returned to pre-dive resting levels. However, there was no way to tell whether or not all metabolic byproducts of anaerobic respiration were cleared and the animal was actually "fully recovered". As the majority of dives above the ADL were in high-density prey patches, it is possible that I underestimated the costs associated with these longer dives associated with higher prey patch densities. This would have inflated the apparent difference between foraging efficiency in high and low-density patches.

The foraging patterns I observed could also possibly be explained by motivation of the animals. Steller sea lions are opportunistic feeders and their prey sources are unpredictable, so it is likely that they took advantage of a patch that was perceived to be productive. In the high-density prey patches, animals were more willing to push themselves to dive close to or above their ADL because the potential payoff warranted such effort. In contrast, there was still always a net gain in low-density prey patches, but the rate of gain may not have been large enough to motivate the sea lions to make longer dives.

2.5.4 Conclusions

The changes in foraging behaviour observed in the sea lions were similar to those reported in several studies of marine birds, reptiles, and mammals in the wild, where dive behaviour depended on depth and/or density of prey (Boyd and Arnbom, 1991; Dolphin, 1987; Elliott et al., 2008; Hays et al., 2004; Heath et al., 2007; Thompson et al., 1991; Wallace et al., 2015). This consistency between studies suggests that captive animals can provide meaningful insights into their wild counterparts. In the wild, it is very difficult to measure the energetic consequences of behaviours and captive studies such as this help create a more complete picture of foraging conditions and energetics in relation to the behaviours observed.

As reduced or redistributed prey has been suggested as a possible contributor to the decline of Steller sea lion populations in Alaska (Trites and Donnelly, 2003), it is important to understand how changes in prey availability affect individuals within the population. My results suggest that sea lions faced with reduced prey abundance are less efficient foragers, making it more difficult for them to reach their daily energy requirements. This has implications for population health, recovery, and monitoring, as individual sea lions will either be at a lower nutritional plane or will have to spend more time foraging—ultimately taking away time and energy for other essential activities.

Chapter 3: Dive behaviour can predict metabolic expenditure in Steller sea lions

3.1 Summary

Quantifying costs associated with foraging contributes to understanding the energetic impact that changes in prey availability have on the energy balance of an animal and the fitness of populations. However, estimating the costs of foraging is difficult for breath-hold divers such as Steller sea lions that feed underwater. I developed models parameterized with data from free-diving captive sea lions to estimate the costs incurred by wild Steller sea lions while foraging. I measured diving metabolic rate of trained Steller sea lions performing 4 types of dives to 10 and 40 m in the open ocean—and estimated the separate costs of different dive components (i.e., surface time, bottom time, and transiting to and from depth). I found that the sea lions' diving metabolic rate was higher while transiting (20.5±13.0 ml O_2 min^{-1} kg^{-1}) than while swimming at depth (13.5±4.1 ml O_2 min^{-1} kg^{-1}). My energetic model accurately predicted oxygen consumption for submergence alone (within 9.5%) and complete dive cycles (within 7.7%). Comparing the differences in the efficiency of different dive strategies revealed that single dives were energetically less costly than a continuous series of single dives (bout dives). However, the sea lions were more efficient at replenishing their oxygen stores following bout dives compared to single dives, and could therefore spend a greater portion of their time foraging while undertaking bout dives. The metabolic rates I measured for the different behavioral components of diving can be applied to time-depth recordings from wild sea lions to estimate energy expended by Steller sea lions while foraging. This can be used in turn to understand how changes in prey availability affect energy balance and the health of individuals in declining populations.

3.2 Introduction

The ability to accurately determine the costs of underwater activity for breath-hold divers is essential for understanding their diving energetics and associated foraging strategies. Foraging is one of the largest components of an animal's energy budget and has major impacts on overall energy balance. Accurate estimates of diving costs are needed to understand how physiological constraints and energetic demands may affect foraging costs and strategies in the wild under different environmental conditions.

Steller sea lion (*Eumetopias jubatus*) populations in Alaska have declined since the 1970s, potentially due to reduced prey availability (Loughlin et al., 1998; Trites and Donnelly, 2003). Optimal foraging models for breath-hold divers suggest that animals should maximize their efficiency by altering their dive behaviour in response to the depth and abundance of prey (Carbone and Houston, 1996; Houston and Carbone, 1992; Thompson and Fedak, 2001). Altered dive behaviour in response to changes in prey could impact foraging costs, and thus the animal's overall energy balance. However, to test these model predictions, energetic expenditure during diving needs to be quantified. Quantifying the costs of different diving behaviours would also permit the costs and benefits of different diving strategies to be compared.

Respirometry is the most accurate method available to measure metabolic costs of diving. It provides direct measures of O_2 consumption and CO_2 production, and works over both fine- and long-term time scales (Boyd, 2002; Fahlman et al., 2008b). However, conducting respirometry measurements is challenging when dealing with wild diving animals (Boyd, 2002), and is generally not plausible with marine mammals, except with animals that reliably resurface within ice holes (Kooyman et al., 1973).

The doubly labelled water dilution method is often used in field studies to estimate CO_2 production in relation to diving behaviour (Boyd et al., 1995b; Dalton et al., 2014; Sparling et al., 2008). However, this technique only provides an average metabolic rate over several days making it difficult to quantify the costs of different activities. Other methods have been tested as proxies for direct measurements of diving metabolic rate with mixed results. Heart rate (Hindle et al., 2010; McPhee et al., 2003; Young et al., 2011), overall dynamic body acceleration (Dalton et al., 2014; Fahlman et al., 2013; Fahlman et al., 2008c; Halsey, 2011; Halsey et al., 2011) and fluke or flipper stroke rate (Williams et al., 2004) can be used to estimate energy expenditure, but are limited under certain conditions and are often logistically difficult to obtain.

In theory, energetic expenditure during diving can be estimated through activity budgets. The proportion of time spent diving and dive characteristics are relatively easy to obtain from wild animals equipped with time-depth recorders, which have been routinely deployed for decades. However, this behavioural data needs to be coupled with estimates of activity-specific energy expenditure from captive or field studies. Unfortunately, most studies investigating energy expenditure in wild animals are only able to apply a single overall energetic cost to all diving activity (Costa et al., 1989; Winship et al., 2002), which inherently assumes an equivalent and constant cost of diving. In contrast to this assumption, pinnipeds generally perform a variety of dive behaviours related to different dive types (Schreer et al., 2001; Thums et al., 2008) that likely have different costs.

The metabolic costs of different types of diving behaviour, such as the costs of diving at different depths and with varying levels of activity, have been measured in captive Steller sea lions (Fahlman et al., 2008b; Fahlman et al., 2008c; Gerlinsky et al., 2013; Hastie et al., 2006a; Hastie et al., 2006b). However, these previous studies quantified only the total metabolic cost over the entire dive or dive series. While these experimental manipulations of dive types (i.e., depth, activity level, and submergence time) have provided insights into the effects of different diving strategies and behaviours on energetic costs, the specific contributions of different phases of the dive to total costs has been impossible to discern. This makes it difficult to estimate the energetic costs of different dives and extrapolate the results into more generalized models of diving bioenergetics and associated foraging strategies that can be applied to the wider variety of dive behaviours seen in wild animals.

My study separated and measured the costs of individual portions of dives in trained Steller sea lions diving in the open ocean. My goal was to use measurements of diving costs in free-diving captive sea lions to develop a model to estimate the diving costs of wild Steller sea lions and model the energetic impacts of different dive types. I also wanted to compare and understand the root differences in the efficiency of different dive strategies. This would allow the costs and benefits associated with various foraging strategies to be assessed, and would provide insight into how changing foraging strategies due to changes in prey availability may impact the foraging costs and overall energy balance of wild Steller sea lions.

3.3 Materials and Methods

3.3.1 Data Collection

I measured changes in the diving metabolic rates (DMR) of 4 adult female Steller sea lions performing specific dive patterns, and separated the costs associated with different parts of a dive. Specifically, I targeted the costs of resting at the surface, transiting to and from depth, as well as the effect of different levels of foraging activity at depth. Data collection occurred between February to May 2013 from two 13-year old and two 16-year old sea lions, weighing between 150-229 kg (Table 3.1). All animals were wild-born and raised at the Vancouver Aquarium (Vancouver, BC, Canada). The sea lions were housed at the University of British Columbia's Open Water Research Station (Port Moody, BC, Canada) for 4-8 years, and had been previously trained to be familiar with all experimental equipment and to perform dive trials in the open ocean voluntarily under trainer control. Experiments were conducted under UBC Animal Care Permit #A11-0397.

Table 3.1 Mass (mean±SD) of four adult female Steller sea lions during experimental trials from February to May 2013. Mass specific pre-dive surface metabolic rates (MR_S) are included for each animal. All trials are averaged for each animal (16 trials per animal).

Animal ID	Mass (kg)	MR_S (ml O_2 min^{-1} kg^{-1})
F97SI	225±1.7	8.8±1.1
F00YA	211±1.7	7.9±0.8
F97HA	170±2.3	10.4±2.0
F00BO	152±2.1	8.8±0.9

3.3.2 Metabolic Rates

I measured rates of oxygen consumption via flow-through gas respirometry (as described by Goundie et al., 2015) with the sea lions performing a variety of pre-set dive types described below. In brief, I measured metabolic rate in a 100 L Plexiglas dome floating on the surface of the water. Air was drawn through the dome at a rate of 475 L min^{-1} and was sub-sampled and scrubbed of water vapor via $CaSO_4$. Concentrations of oxygen and carbon dioxide in the incurrent and excurrent flows were measured using Sable System FC-1B and CA-1B analyzers, coupled to a 500H mass flow generator and controller (Sable Systems, Las Vegas, NV, USA). I recorded gas concentrations every 0.5 seconds (Sable Data Acquisition System, Sable Systems Inc.), and analyzed the metabolic data using LabAnalyst X (Warthog Systems, Mark Chappell, University of California) and calculated oxygen consumption rates using eq. 3b in Withers (1977).

I measured pre-dive metabolic rate (MR_S) while animals rested calmly at the surface in the metabolic dome before each dive trial. MR_S was calculated as the average rate of oxygen consumption during the last 2 minutes of a 5-10 minute period when oxygen concentrations were stable. Post-dive rates of oxygen consumption were measured to calculate oxygen consumed during the dive and to determine dive recovery time (i.e., the amount of time at the surface needed for oxygen consumption to return to within 5% of MR_S).

I calculated diving metabolic rate (DMR) as the total volume of oxygen consumed above resting levels at the surface (MR_S), divided by the dive duration. This provided an estimate of the metabolic expenditure for only the submerged portion of the dive and excluded the time and energy spent at the surface. Differences in DMR during dives with different characteristics (see below) allowed me to calculate the costs associated with individual portions of a dive.

3.3.3 Trial Protocol

The sea lions were trained to voluntarily dive between the metabolic dome at the surface and the end of either one or two feeding tubes set at depths of either 10 m or 40 m. These depths are representative of dive depths observed in wild Steller sea lions (Merrick and Loughlin, 1997). During dives, 0.02 kg pieces of Pacific herring (*Culpea pallasii*) were delivered to the sea lions at depth via the feeding tubes at a rate of 12 pieces per minute. Depending on trial protocols, fish pieces were either alternately pumped out of each feeding tube to encourage movement between the tubes or pumped out of a single tube so the animals would remain fairly stationary at depth.

Animals were fasted overnight before trials and transported to the dive site by boat. During transport and measurements of pre-dive MR_S, the sea lions received minimal food reinforcement (<0.8 kg) to reduce the potential impact of digestion on metabolic rate (Rosen and Trites, 1997; Rosen et al., 2015). The sea lions performed 4 different dive types at each depth (Fig. 3.1) and all animals completed 3 trials of each dive type and depth combination for a total of 96 dive trials.

The dive types included:

- i. Transit dives. Single dives where animals dove to depth and back to the surface with no bottom time,
- ii. Stationary dives. Single dives where animals dove to depth and remained stationary at one feeding tube for 3 minutes of bottom time,
- iii. Active dives. Single dives where animals dove to depth and travelled between the two feeding tubes for 3 minutes of bottom time, and
- iv. Active bouts. Bouts of 3 consecutive dives, each with one minute of bottom time (for a total of 3 minutes to be comparable to single, longer dives) and inter-dive surface intervals of ~20 seconds for 10 m dives and ~35 seconds for 40 m dives. Surface interval times for these bouts were chosen as the shortest time possible to ensure the sea lions did not fully recover between dives, but where animals would reliably continue diving. The sea lions received <0.2 kg during each inter-dive surface interval.

Specific bottom durations for these dive types were achieved by turning off a light at the bottom of the feeding tubes (animals were previously trained to return to the surface once the light was turned off). Each animal was outfitted with a tight-fitting harness holding a time depth recorder (ReefNet, Inc., Mississauga, ON, Canada) to record dive behaviour and confirm bottom times.

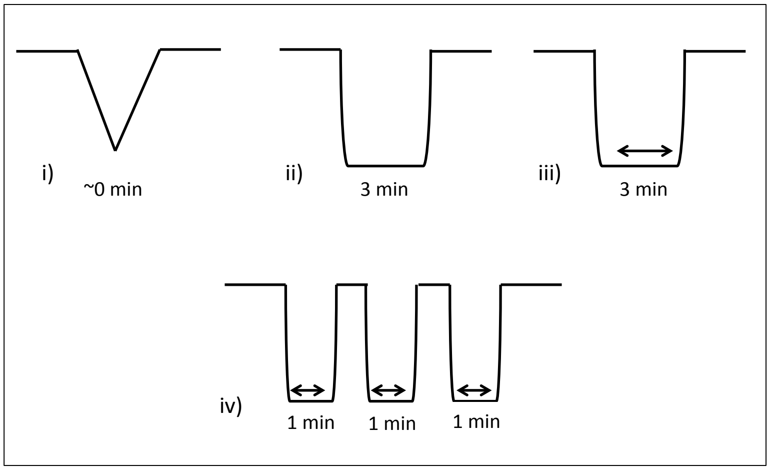

Figure 3.1 Schematic illustrating experimental dive types, showing changes in depth over time (not distance). For transit dives (i), the Steller sea lions dove to depth and immediately returned to the surface with little to no bottom time. Stationary dives (ii) included 3 minutes of non-active bottom time at one feeding tube. Active dives (iii) included 3 minutes of active bottom time swimming between 2 feeding tubes. Bout dives (iv) consisted of 3 consecutive dives with one minute of active bottom time each. Each animal completed 3 trials for each dive type at 10 m and 40 m.

3.3.4 Calculating Separate Dive Components

The cost of transit to and from 40 m depth was measured directly as the DMR for the transit dives. However, DMR for transit dives to 10 m could not be measured directly, as they were only approximately 15 seconds long and not long enough to reliably register an increase in oxygen consumption after a dive. Hence, the rate of oxygen consumption for 10 m transit dives was extrapolated from the DMR measured for 40 m transit dives and the dive duration for the 10 m dives. This assumed similar metabolic rates for transiting to different depths. This is likely the case as previous studies have indicated that any metabolic adjustments associated with dive depth do not occur immediately, indicating that metabolic rates should be similar for the beginning portions of the dives to both depths (Hindle et al., 2010).

I calculated the cost associated with the bottom portion of a dive for the stationary and active single dives using:

$$\text{DMR}_{\text{Bottom}} = \frac{(\text{O}_2\ \text{consumed}_{\text{Total}} - \text{O}_2\ \text{consumed}_{\text{Transit}})}{\text{Bottom Time}} \qquad \text{Eq. 1}$$

This provides DMR for the specific type of bottom activity only. Separate averaged values for each animal was used for oxygen consumption due to transiting. All times for transit and the bottom portions of the dives were extracted from the TDR data.

3.3.5 Validation

To test whether the estimates of DMR that I calculated from the individual components (surface, transit, and activity-specific bottom times) could be used to predict total diving cost for other, more complex dives, I compared calculated volumes of oxygen consumption (using the DMR estimates of each dive component) to actual measurements of oxygen consumption for an independent set of dives from a previous study with the same experimental set-up and animals (Goundie et al., 2015). For these trials, rates of oxygen consumption were measured over bouts of 5 consecutive dives of varying duration, where the sea lions chose both dive duration and surface time. Predicted rates of oxygen consumption were estimated using associated TDR data that provided the transit, bottom and surface times for each dive.

Oxygen consumption was calculated separately for "submergence only" and for a complete "dive cycle". Submergence only refers to only the total oxygen consumed during the portion of the dive cycle spent underwater (i.e., actively diving). Dive cycle refers to the total oxygen consumed during all portions of entire dive event (i.e., diving, inter-dive surface interval and recovery time). While submergence only and dive cycle measurements can be made for both single dives and dive bouts, for this study I only predicted oxygen consumption for dive bouts.

For the estimates of submergence only, transit and bottom times (T) of those dives were multiplied by the calculated DMR for each respective portion of the dive. This provided separate estimates of oxygen consumed for the transit and bottom portions of the dives, which could be summed to provide an estimate of the total oxygen consumed over the entire submerged portion of the dive.

$$\mathrm{O_2\ Consumption_{Dive\ Only}} = (\mathrm{T_{Transit}} * \mathrm{DMR_{Transit}}) + (\mathrm{T_{Bottom}} * \mathrm{DMR_{Bottom}}) \quad \text{Eq. 2}$$

For dive cycles (including oxygen consumption both during dives and at the surface), I calculated the additional oxygen consumption during time spent at the surface (both inter-dive surface intervals and post-dive recovery periods) using estimates of MR_S such that:

$$O_2\ \mathrm{Consumption}_{\mathrm{Dive\ Cycle}} = (T_{\mathrm{Transit}} * DMR_{\mathrm{Transit}}) + (T_{\mathrm{Bottom}} * DMR_{\mathrm{Bottom}}) + (T_{\mathrm{Surface}} * MR_s) \quad \mathrm{Eq.}\ 3$$

I then compared both of these estimates of oxygen consumption (Eqs. 2 and 3) to the measured volume of oxygen consumption for the same dives to determine if one method was more accurate for estimating diving costs.

3.3.6 Statistical Analysis

I used R software (R Core Team, 2014), and linear mixed-effects models (lme) from the nmle package (Pinheiro et al., 2015) with significance set at α = 0.05. To account for repeated measures with each animal, models included animal ID as a random effect. Fixed effects were trial depth and either full dive type (single stationary, single active, bout) or dive component (transit, stationary bottom, active bottom). I ran my models using the maximum likelihood method, and used a log likelihood ratio test (LRT) to compare full and reduced models to test the effect of each factor individually and determine the best model to fit the data (Pinheiro and Bates, 2000). Full models included two fixed factors (depth and full dive type or depth and dive component), while the reduced models had one factor removed. A significant result indicated that the full model was a better fit to the data and that the factor removed had a significant effect. When dive or component type was a significant factor, I used Tukey *post hoc* analyses with Bonferroni adjusted p-values to determine differences between types. For single model ANOVA's F and P values were reported for slopes only, as all intercepts were significantly different from zero.

The first analysis compared the calculated costs of separate dive components. The partitioned cost of transit, stationary and active dive components were compared, with depth as an additional potential model component. Next, the total costs (DMR) of both single dive types (stationary and active) and bout dives were compared, again with depth included as a potential model factor. Similarly, the effect of dive type and depth on post-dive recovery time and cumulative recovery time (includes both post-dive recovery time and inter-dive surface interval times) was tested. The relationship between recovery times and total volumes of oxygen consumed were also tested. Transit dives were not included in these full dive comparisons, as they were designed only for calculating individual dive components.

I used a linear regression model (lm) to determine the relationship between the measured values and calculated values of oxygen consumption in the additional dive set, and the difference (%) between the measured and calculated values. A similar analysis was also undertaken using linear mixed effects models (lme). When results did not differ between these statistical methods, I used the simpler linear regression. Although lme models are better able to account for repeated measure effects, they do not yield reliable R^2 values. I estimated the mean percent difference between measured and calculated values separately for the 2 predictive equations (i.e., over the submergence portion of a dive only and over the entire dive cycle)—and subsequently incorporated these values as a correction factor to the individual metabolic rates for each component of each predictive equation. To determine if the slopes for the relationship between the measured and calculated volumes of oxygen consumed (for both original and corrected calculated values) were significantly different than 1, I used the slope.test function from the smatr package in R (Warton et al., 2012). Finally, I calculated 95% confidence intervals for the slopes. The amount of error for the final corrected values was calculated as average % residual.

Oxygen consumption data were tested as both absolute and mass-specific values (i.e., per kg). Results did not differ between methods, so I reported mass-specific data to facilitate comparison with other studies. All values are reported as means ± SD.

3.4 Results

3.4.1 Diving Energetics

Pre-dive surface metabolic rate (MR_S) for all trials ranged from 6.5 to 14.0 ml O_2 min^{-1} kg^{-1} with an average of 9.2±1.6 ml O_2 min^{-1} kg^{-1} (Table 3.1). Diving metabolic rate (DMR) was not affected by depth in any of the dive types (LRT = 0.060, P = 0.81), so depths were combined in each dive type.

Comparing the DMR of single dives (with and without bottom activity) and bout dives revealed a significant effect of dive type (single or bout) on DMR (LRT = 29.53, P < 0.0001).

Surprisingly, activity level during the bottom portion of a dive did not affect DMR (Tukey, $P = 0.35$). The average DMR was 13.8±3.8 ml O_2 min^{-1} kg^{-1} for single stationary dives and 14.9±2.9 ml O_2 min^{-1} kg^{-1} for active dives (Table 2). Bout dives had a higher DMR than single dives (Tukey, $P < 0.001$), averaging 18.0±2.8 ml O_2 min^{-1} kg^{-1} (Fig. 3.2).

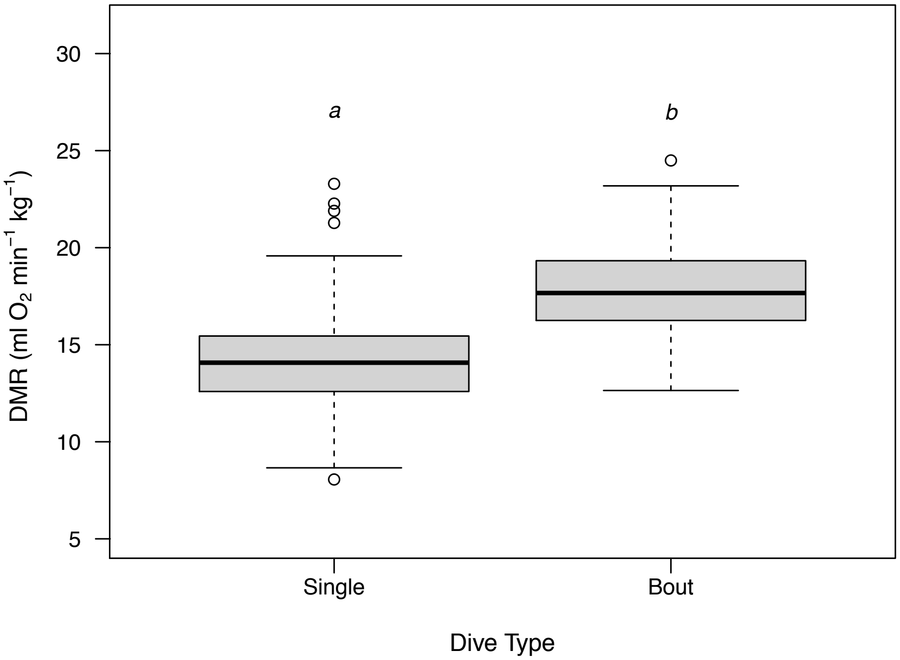

Figure 3.2 Diving metabolic rates (DMR) for Steller sea lions performing single and bout dives to 10 m and 40 m. Single dives had 3-minute bottom times and bout dives consisted of 3 consecutive dives with a 1-minute bottom time each. Stationary and active single dives were combined, as there was no statistical difference in DMR. The box for single dives represents 12 dive trials from each of the 4 animals for a total of 48 trials. The box for bout dives represents 6 dive trials for each of the 4 animals for a total of 24 trials. There were significant differences between dive types. Depths were combined because there was no statistical difference between DMR at 10 m and 40 m.

Comparing post-dive recovery times following single and bout dives revealed no effect of depth ($LRT = 1.62$, $P = 0.20$), dive type ($LRT = 2.57$, $P = 0.28$) or total oxygen consumption (ANOVA, $F_{1,67} = 3.47$, $P = 0.07$) on recovery. Recovery times were 6.3±1.5 minutes for stationary dives, 6.0±1.0 minutes for active single dives and 5.8±1.2 minutes for bout dives. In other words, even though bout dives were more costly, recovery time did not increase. This was likely due to the sea lions replenishing some oxygen at the surface between dives, instead of only during the post-dive recovery period.

Cumulative recovery time (calculated to include both surface intervals and post-dive recovery times—and account for the oxygen replenished during inter-dive surface intervals during bout dives) was also not affected by depth (LRT = 3.48, P = 0.062) or dive type (LRT = 4.71, P = 0.095), due to the large overlap in duration between types. However cumulative recovery time was significantly related to the total volume of oxygen consumed (ANOVA, $F_{1,67} = 28.77$, $P < 0.0001$; Fig. 3.3).

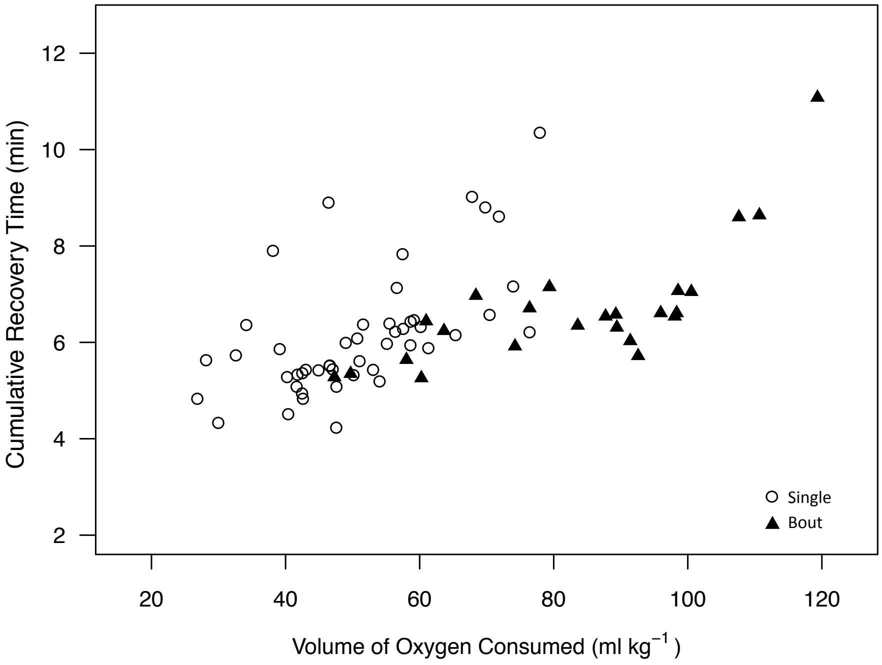

Figure 3.3 Cumulative recovery time of Steller sea lions as a function of the volume of oxygen consumed during single and bout dives. Cumulative recovery time includes all inter-dive surface intervals and post-dive recovery times. Each point represents a single dive or single dive bout. Open circles represent single dives and filled triangles represent bout dives. Depths were combined, as were stationary and active single dives. Data are from four Steller sea lions, each of which performed 12 single dives and 6 dive bouts for a total of 72 trials.

Despite the higher DMR and generally higher volumes of oxygen consumption during bout dives, recovery time was still not significantly greater than single dives, even when time at the surface between dives was included. Calculating a "recovery efficiency" ratio (as the volume of oxygen consumed divided by the cumulative recovery time) determined the amount of oxygen replenished per minute at the surface—and showed a significant effect of dive type on recovery efficiency (LRT = 60.97, P < 0.0001). Recovery efficiency was the same between both single dive types (8.4±1.6 ml O_2 kg^{-1} min^{-1}; Tukey, $P = 0.060$), while bout dives had higher recovery efficiency than single dives (12.5±2.1 ml O_2 kg^{-1} $min^{-}1$; Tukey, $P < 0.0001$; Fig. 3.4). This suggests that occasional surface intervals during dive bouts conveyed an advantage for gas exchange compared to single dives.

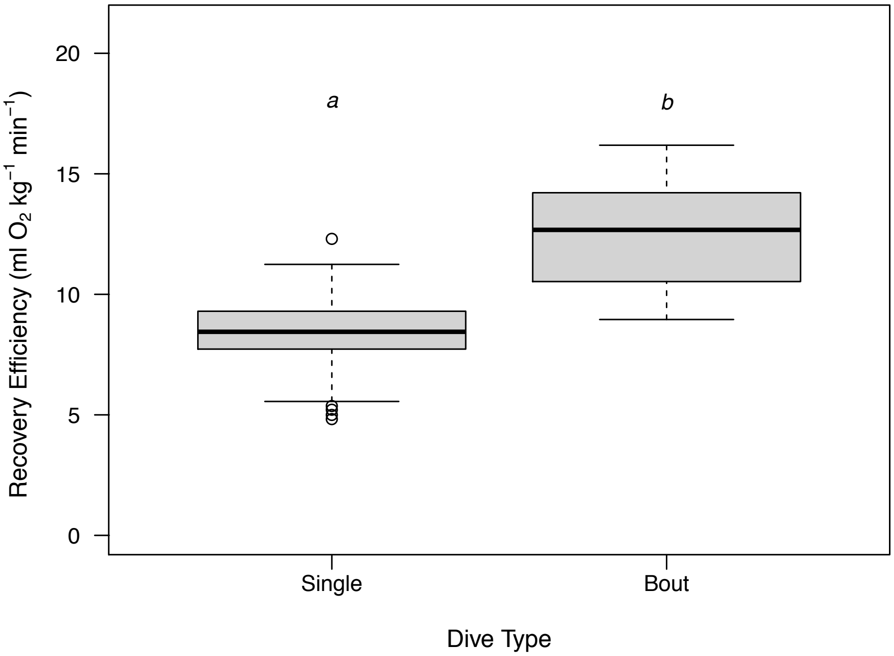

Figure 3.4 Recovery efficiency for Steller sea lions performing single and bout dives. Single dives had 3-minute bottom times and bout dives consisted of 3 consecutive dives with a 1-minute bottom time each. Stationary and active single dives were combined because there was no statistical difference in recovery efficiency. Recovery efficiency was calculated as the volume of oxygen replenished per minute spent at the surface. There were significant differences between dive types. The data for single dives are from 12 dive trials from each of the 4 animals for a total of 48 trials. The data for bout dives derives from 6 dive trials for each of the 4 animals for a total of 24 trials.

3.4.2 Dive Components

Depth did not affect DMR of separated components (LRT = 0.20, $P = 0.66$), so data from all depths were combined. However, oxygen consumption rates did differ between components (LRT = 11.44, $P = 0.0033$; Table 3.2). The transit portion of a dive had a significantly higher DMR than the bottom portion of a dive (Tukey, $P < 0.01$). Activity level (stationary or active) during the bottom portion had no effect on DMR (Tukey, $P = 1.0$), so data from stationary and active bottom portions could be combined (Fig. 3.5). The cost for transiting to and from depth was 20.5±13.0 ml O_2 min^{-1} kg^{-1}, and the average cost for the bottom portion of a dive (regardless of activity) was calculated as 13.5±4.1 ml O_2 min^{-1} kg^{-1}.

Table 3.2 Diving energetics and durations used to calculate the metabolic costs of separate dive components for Steller sea lions performing 3 different dive types to 10 m and 40 m. Dive types included transit dives with no bottom time, stationary dives with 3 minutes of non-active bottom time and active dives with 3 minutes of active bottom time (Fig. 1). Volume of oxygen consumed and the diving metabolic rate (DMR) of the separate components were calculated from the total volume of oxygen consumed and the complete dive durations, transit times, and bottom times. The DMR of transit to 40 m was measured directly from the transit dives, and the transit costs for 10 m dives were extrapolated from dive times. The DMR of the bottom portion of the dive was calculated by subtracting to volume of oxygen consumed during a transit dive from the total volume consumed during the stationary or active dive types. This was then divided by the bottom time of the dive to get the DMR of the bottom portion of the dive. DMR of full dives are also included for comparison to components only.

	Vol. O$_2$ Full Dive (ml kg^{-1})		DMR Full Dive (ml O$_2$ min^{-1} kg^{-1})		Dive Duration (min)		Transit Time (min)		Bottom Time (min)		Vol. O$_2$ Component (ml kg^{-1})		DMR Component (ml O$_2$ min^{-1} kg^{-1})	
	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m	10 m	40 m
Transit	4.7±0.3	17.1±11.5	20.5±13.4	20.5±13.4	0.2±0.0	0.9±0.1	0.2±0.0	0.8±0.1	0.0±0.0	0.0±0.0	4.7±0.3	17.1±11.5	20.4±13.2	20.5±13.4
Stationary	43.1±15.7	55.4±11.1	13.3±4.8	14.4±2.6	3.3±0.1	3.8±0.1	0.3±0.0	0.9±0.1	3.0±0.1	2.9±0.1	38.4±15.8	38.2±12.0	12.8±5.1	13.1±4.0
Active	51.6±11.8	54.6±7.6	15.6±3.6	14.3±1.9	3.3±0.1	3.8±0.1	0.3±0.1	0.8±0.1	3.1±0.1	3.0±0.1	46.8±12.1	37.6±8.0	15.4±4.1	12.5±2.4

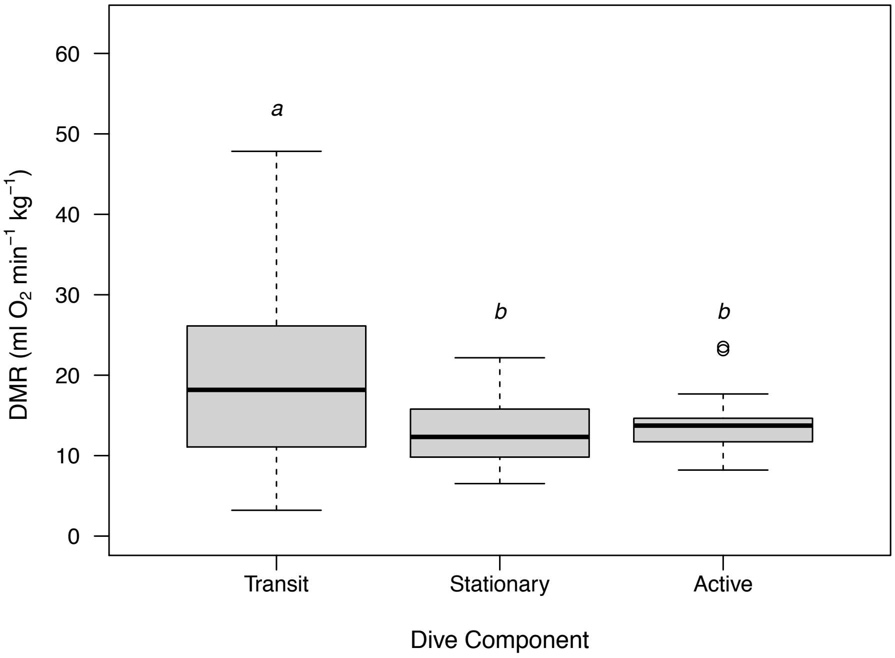

Figure 3.5 Diving metabolic rates (DMR) of separate dive components calculated from the diving costs for Steller sea lions performing 3 dive types to 10 m and 40 m. Dive types were: transit dives with no bottom time, dives with 3 minutes of non-active bottom time and dives with 3 minutes of active bottom time. Dive components include “Transit” (the cost of diving to and from depth), “Stationary” (the cost of being at depth with little to no activity) and “Active” (the cost of actively swimming at depth). Each box represents the calculated dive component for 6 dive trials from each of the 4 animals for a total of 24 trials for each dive component. Transit dives were significantly more costly than Stationary or Active components. Depths were combined because there was no statistical difference between 10 m and 40 m.

3.4.3 Validation

With the calculated costs of the separate dive components for transit, bottom, and surface times I was able to predict oxygen consumption (both for submergence only and dive cycles) for a set of independent dive bouts from a previous study (Goundie et al., 2015). There was a strong linear relationship between the calculated and measured volumes of oxygen consumed for submergence only (ANOVA, $F_{1,43} = 551.27$, $P < 0.0001$; Slope = 1.13, $R^2 = 0.92$; Fig. 3.6a), with a slope that was significantly different than 1 ($P = 0.01$; 95% CI [1.03, 1.23]). On average, oxygen consumption was overestimated by ~5.9% (Fig. 3.6b). Comparing calculated and measured values for complete dive cycles also resulted in a strong linear relationship (ANOVA, $F_{1,43} = 453.47$, $P < 0.0001$; Slope = 1.17, $R^2 = 0.91$; Fig. 3.7a) that also had a slope significantly different than 1 ($P = 0.004$; 95% CI [1.07, 1.28]) and overestimated oxygen consumption by ~21.8% (Fig. 3.7b).

The difference (%) between measured and calculated values for predictions of both submergence only and dive cycles was not affected by volume of oxygen consumption or, by extension, dive duration (dive, ANOVA, $F_{1,43} = 0.53$, $P = 0.47$; cycle, ANOVA, $F_{1,43} = 0.28$, $P = 0.60$). These overestimates (5.9% for submergence only and 21.8% for dive cycles) were applied as correction factors to the activity-specific metabolic rates for the appropriate predictive equations (Table 3.3).

With these correction factors applied, the predictive equations changed slightly for both the submergence portion only (Fig. 3.6c) and the complete dive cycle (Fig. 3.7c). The corrected slope was no longer significantly different from 1 for submergence only ($P = 0.17$; 95% CI [0.97, 1.15]) and was only marginally different from 1 for the dive cycles ($P = 0.05$; 95% CI [0.83, 1.0]). The error, calculated as average % residual, was 9.5% for submergence only and 7.7% for dive cycles.

Table 3.3 Corrected metabolic rates of separate dive components (DMR) and surface time (MR_S) for Steller sea lions. A correction factor of -5.9% was applied to each component for the submergence portion of a dive only, and a correction factor of -21.8% was applied to each component for dive cycles.

	Metabolic Rate (ml O_2 min^{-1} kg^{-1})	
	Submergence Only	Dive Cycle
Transit	19.2	16.0
Bottom	12.7	10.6
Surface	--	7.2

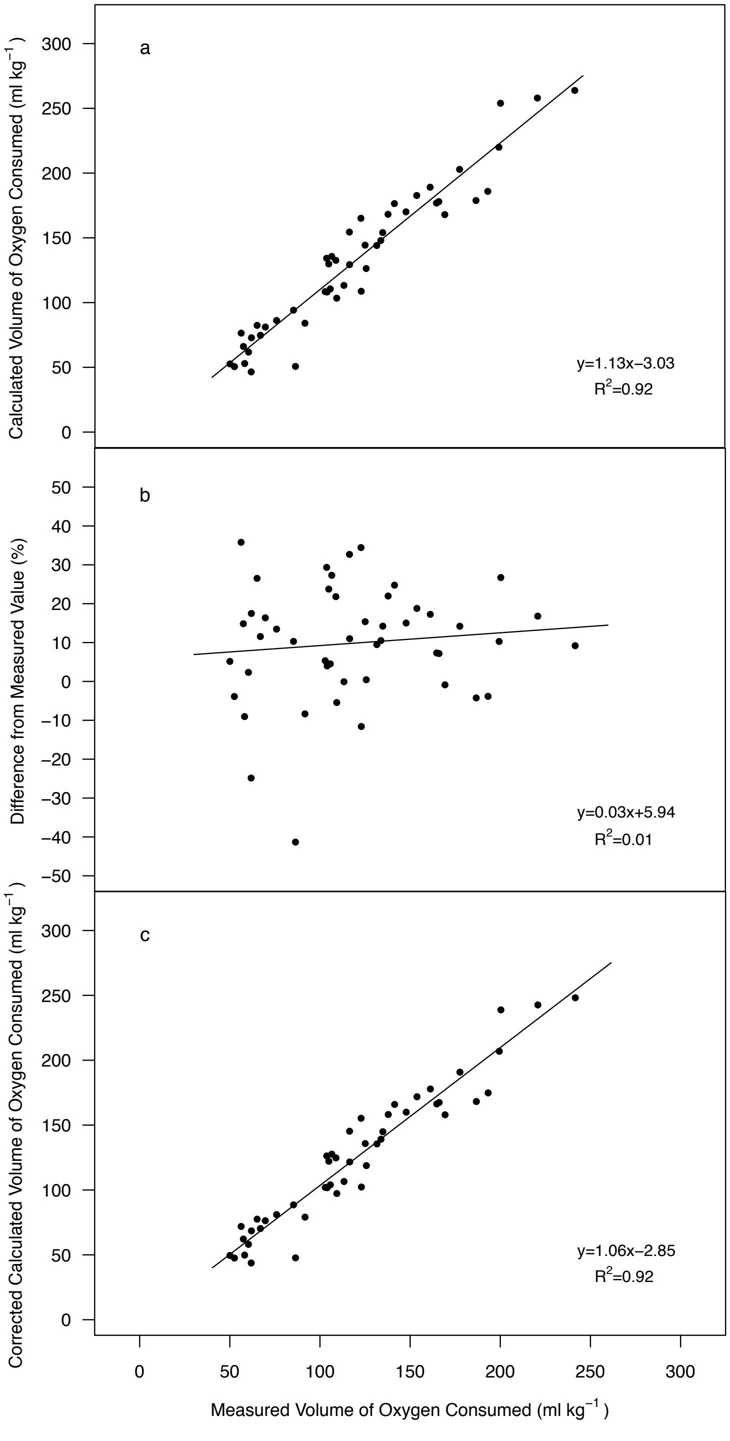

Figure 3.6 (a) Volume of oxygen consumed by 4 Steller sea lions during the submergence portion of dives calculated from the estimated DMR of the transit and bottom components of a dive, (b) percent difference between measured and calculated values, and (c) calculated values with -5.9% correction factor applied as a function of the measured volume of oxygen consumption for the same dives. This includes only the volume of oxygen consumed above resting metabolic rate during diving. Each point represents a single dive bout. Data are from four Steller sea lions, each of which performed 12 dive bouts for a total of 48 trials. Linear equations and R^2 values are included.

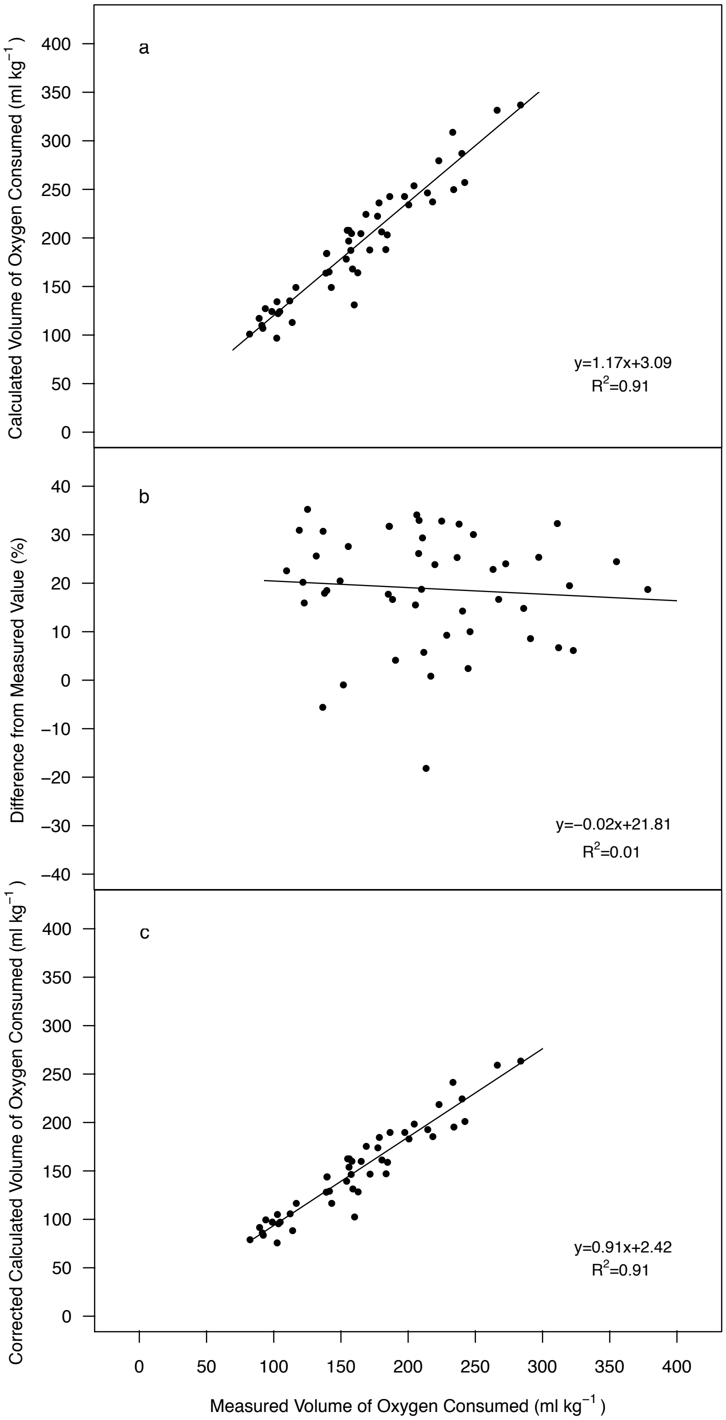

Figure 3.7 (a) Volume of oxygen consumed by 4 Steller sea lions during dive cycles calculated from the surface metabolic rate (MRs) and the estimated DMR of the transit and bottom components of a dive, (b) percent difference between measured and calculated values and, (c) calculated values with -21.8% correction factor applied as a function of the measured volume of oxygen consumption for the same dive cycles. Dive cycles include the volume of oxygen consumed during dives and at the surface. Each point represents a single dive bout. Data are from four Steller sea lions, each of which performed 12 dive bouts for a total of 48 trials. Linear equations and R^2 values are included.

3.5 Discussion

Foraging behaviour for diving animals is plastic, changing with the physiological capabilities of the animal and the conditions under which they forage. Accurate activity-specific estimates of energy expenditure are needed to understand the costs and benefits associated with different strategies. My study quantified the costs of different portions of a dive in Steller sea lions to provide a means of estimating the costs of diving and evaluating the energetic consequences of changes in diving behaviour in response to environmental changes.

I found that transiting to and from depth was more costly than time spent at the bottom, and that there were no differences in cost between the depths and activity levels I tested. This explained why longer single dives were less energetically expensive than multiple shorter dives. However, shorter dives were more time efficient, as oxygen was replenished more effectively when animals made multiple short dives. Results from my study can be used to estimate diving costs of wild animals, as well as interpret aspects of foraging models and wild diving patterns.

3.5.1 Metabolic Costs of Dive Components

As expected, the transiting portion of a dive was more costly than the bottom portion. This likely reflects a strategy of increased transit speeds to get to depth quickly (Boyd et al., 1995a). Not surprisingly, higher levels of activity, such as increases in the number, speed or magnitude of flipper strokes, are directly related to higher costs of diving (Davis and Williams, 2012; Williams et al., 2004). Similarly, pinnipeds have also been observed to decrease swimming speeds and activity levels during the bottom portion of the dive to conserve energy (Hassrick et al., 2007). The differences in costs between transiting and bottom time indicate that the sea lions likely employed a strategy of getting to depth quickly and then reduced swimming speed at depth to maximize bottom time.

However, fast transit times and slow bottom times is not the only strategy for allocating time and energy that diving animals can employ to optimize foraging (Thompson et al., 1993). An alternate strategy is for animals to conserve energy while transiting, either by slowing swimming speeds or by using passive gliding to get to and from depth (Gallon et al., 2007; Williams et al., 2000). These strategies maximize time spent foraging by minimizing oxygen consumption and thereby increasing overall aerobic dive time. Such strategies that minimize costs arriving to depth would optimize foraging efficiency if this resulted in spending a greater proportion of the dive cycle engaged in active foraging.

Using passive gliding to get to and from depth has been observed in several species of diving animals. This strategy helps conserve energy and can be used to increase speeds without adding a large extra cost by using changes in buoyancy to accelerate without increasing stroke rate (Crocker et al., 2001; Davis et al., 2001; Hassrick et al., 2007; Hindell and Lea, 1998; Williams et al., 2000). However, this behaviour is typically seen only with deep dives (>80 m) where changes in buoyancy are more pronounced (Williams et al., 2000). Similarly, animals that exhibit reduced swimming speed on the transit portion of a dive (Gallon et al., 2007) are generally those with longer aerobic dive limits (ADL) that are also making long, deep dives.

As Steller sea lions are generally short, shallow divers (Loughlin et al., 1998; Merrick et al., 1994; Merrick and Loughlin, 1997) with short aerobic dive limits (Gerlinsky et al., 2013), and the animals in the study had maximum dive depths of 40 m, it is not surprising that they used the strategy of expending more energy to rapidly get to their foraging depth. This strategy optimizes energy gain and maximizes potential prey intake through increased foraging time. This strategy has also been observed in another Otariid species (Boyd et al., 1995a). For shallow diving animals with relatively short ADLs the benefits gained by using reduced swim speeds during transit (i.e., marginally increased ADL), would be less than the benefits associated with shorter transit times due to increased swim speed.

Some of the differences in costs observed between the transiting and bottom portions of a dive could be attributable to the duration of the dives. The physiological changes associated with the classic diving response, including metabolic depression and bradycardia, do not occur immediately upon submersion, but rather transpire gradually over the course of the dive (Fahlman et al., 2008b; Hindle et al., 2010; Kooyman, 1985; McDonald and Ponganis, 2014). Therefore, during the experimental transit dives, there was likely not enough time for full metabolic adjustments to occur as they would during the dives with extended bottom times. The metabolic costs of the experimental transit dives would accurately reflect the descent portion of natural dives — but the ascent portions that, in realistic dives, occur later may, on first consideration, be assumed to have a lower metabolic rate. However, the ascent portion of natural dives are also associated with increased metabolic activity, such as surfacing tachycardia, as part of general tissue reperfusion in preparation for clearing metabolic byproducts and replenishing oxygen stores (McDonald and Ponganis, 2014; Thompson et al., 1993). As a result, my estimate for transiting to and from depth likely closely reflects the actual costs during extended, realistic dives.

Surprisingly, activity level during the bottom portion of dives (inactive vs. active) had no effect on DMR. This is possibly because there was not enough difference between the two activity types in my study. Although sea lions remained fairly stationary at the single feeding tube for inactive bottom time trials, the animals sometimes made tight circles around the tube to remain properly aligned with where the fish were delivered. This may have been energetically indistinguishable from the minimal efforts required to swim between the two tubes during "active" bottom time trials. Also, the animals may have been slightly negatively buoyant at both depths used in my study (Fahlman et al., 2008a). Hence, the energy required to remain stationary at the level of the feeding tube may have obscured any energetic differences due to differences in the level of active swimming. Although I was not able to measure different levels of activity during the bottom portion of the dives, there is evidence from wild pinnipeds to suggest that there is little variation in swimming speed once animals are foraging at depth (Hassrick et al., 2007).

Dive depth did not alter the cost of any dive component. I did not expect to see increased metabolic suppression in my study, as a previous study on diving Steller sea lions predicted that metabolism should not decrease for dives shallower than 50 m (Hastie et al., 2006a). For my study, depth was limited at 40 m due to the location of the dive set-up. However, wild data on Steller sea lion dive patterns indicate that approximately 90% of dives are shallower than 50 m (Merrick and Loughlin, 1997), making the depths used in my study relevant to the majority of dives seen in the wild. Furthermore, previous work with trained sea lions has demonstrated that the degree of their dive response appears to depend upon dive time and not depth (Hastie et al., 2006a; Hindle et al., 2010; Hurley and Costa, 2001). As such, a greater dive response would be associated with the longer time required to travel to deeper depths (Castellini et al., 1992; Williams et al., 2004), and the tendency to remain longer at deeper depths. Therefore, my estimates are most applicable to dives of similar durations to those used during this study.

3.5.2 Applications of Results

One of the goals of my study was to determine whether the total cost of a dive could be reasonably estimated from a simple bioenergetic model of its component behaviours. Such a model would not only allow the energetic consequences of observed foraging behaviours to be quantified, but would also allow a retrospective analysis of a wealth of archived dive data to better understand historical changes in foraging behaviour that may have occurred in response to changes in the sea lion's environment.

Results of my validation demonstrated a very tight correlation between measured and calculated diving costs, both when calculated for submergence only and for complete dive cycles. The precision of my estimates was similarly high for both estimates. However, the accuracy of my estimates differed in that my model over-estimated the total volume of oxygen consumed above resting levels during submergence by 5.9%, but over-estimated the costs for an entire dive cycle by 21.8%. This was unexpected given that most proxies for estimating oxygen consumption are more accurate when applied over an entire dive cycle (Fahlman et al., 2008c; Young et al., 2011), presumably because it represents a complete physiological event (Kooyman, 1985).

For both submergence only and dive cycles, my calculated values for oxygen consumption overestimate measured costs. The fact that overestimates were higher when calculated over the entire dive cycles compared to submergence only suggests that the difference may lie in my estimates of surface metabolism. In my calculations, I used estimates of pre-dive surface metabolism (MRs) to calculate both inter-dive and post-dive surface metabolism. The inter-dive and post-dive rates of oxygen consumption were assumed to be a simple additive component to the cost of diving, with no physiological interaction. If this assumption is incorrect, my estimates of metabolism during the inter-dive surface intervals and the post-dive recovery period could be inflated, and the effect would be greater for estimates calculated over the entire dive cycle.

Unfortunately, my data do not provide a means to separate and measure actual surface costs between dives.

Despite the potential bias of surface costs, the correlation between the calculated and measured costs was very tight, indicating that my model can be used to provide activity-specific estimates of energy expenditure for wild animals. The average over-estimate remained constant across different dive types, providing further evidence that this method, combined with a suitable correction factor, can accurately estimate the costs of submergence only or dive cycles of wild animals (Table 3.3). Although there was variability in the individual differences between measured and calculated values, this would, in theory, average out with an increasing sample size and more dives. Including the correction factor results in an estimate of error (9.5% for submergence only and 7.7% for dive cycles) that is similar to the error seen when using other techniques to estimate oxygen consumption. For the same animals used in this study, there was a 7% error when using overall dynamic body acceleration to estimate oxygen consumption (Fahlman et al., 2008c) and a 9-17% error when using heart rate to estimate oxygen consumption (Young et al., 2011). However, it is important to note that error is often calculated in different ways between studies, and direct comparisons should be made with caution.

3.5.3 Effects of Dive Strategies

The difference observed in the total costs of full dives was consistent with the results from the calculated costs of the separate dive components. Bouts of dives were more costly due to the larger proportion of time spent transiting, which was the portion of a dive with the highest metabolic cost. This confirms that the added transit involved in multiple shorter dives increases the overall cost of the dive, and that it is more energetically efficient to make fewer longer dives.

Although dive bouts had a higher rate of oxygen consumption than single dives, they did not have longer post-dive recovery times for similar total submergence times. In fact, it was marginally shorter than for single dives. This is partly because the sea lions were able to partly replenish oxygen stores during inter-dive surface intervals. Although cumulative surface time was not related to dive type, it was related to the more physiologically relevant measure of total oxygen consumption. In fact, animals making multiple shorter dives may be able to replenish their oxygen more efficiently than animals making longer single dives because the rate of gas exchange would be greatest during the brief surface intervals when differences in blood/atmosphere partial pressures are greatest (Fahlman et al., 2008b; Kooyman et al., 1973). This was confirmed by my measures of recovery efficiency where bout dives indeed had higher efficiency than single dives. Hence, by making multiple shorter dives, animals can partially replenish oxygen during the short surface intervals more efficiently than when they made a longer single dive and have to fully replenish oxygen supplies at the end of the dive.

As with most strategies, there are offsetting costs and benefits to both extended single dives and dive bouts with equal bottom times. The most obvious differences between single dives and dive bouts are in the comparisons of time and energetic cost. My study confirmed that making multiple shorter dives (dive bouts) was more energetically costly than making equitable single dives. However, there is a benefit to using the dive bout strategy due to its shorter total recovery time, resulting in proportionally less time needed at the surface to replenish oxygen. Thus, while longer single dives appear to be a more efficient use of energy, several shorter dives may be a more efficient use of time, as animals need to spend proportionally less time at the surface. Decreased time at the surface can not only increase chances of finding prey, but also possibly decrease vulnerability to predators (Heithaus and Frid, 2003).

3.5.4 Foraging Models and Wild Dive Patterns

The results from my study can be used to evaluate different models of diving strategies for foraging vertebrate divers. Various foraging models for breath-hold divers predict that animals should dive close to or just beyond their aerobic dive limit (ADL) (Carbone and Houston, 1996; Houston and Carbone, 1992; Kooyman, 1989; Kramer, 1988). This strategy maximizes foraging time without the added cost of using anaerobic metabolism. The near-complete depletion of oxygen stores also maximizes oxygen uptake at the surface due to the large partial pressure difference between the animals' lungs and the air. The calculated aerobic dive limit (cADL) of Steller sea lions is approximately 3 minutes (calculated for the same animals used in this study; Gerlinsky et al., 2013), which is similar to single dive times used in my study.

My results, in combination with model predictions, suggest that the most efficient dive types should be multiple dives, close to the animals' ADL, with short surface intervals in between. This would minimize diving costs by keeping the proportion of time transiting as low as possible without using anaerobic metabolism, while allowing the greatest amount of time for foraging. Recovery efficiency would also be maximized with this diving strategy by having the greatest possible partial pressure difference at the beginning of each short surface interval.

Prey availability must also be considered when modeling optimal dive behaviour and interpreting dives in the wild. Foraging models of diving mammals suggest that animals should abandon a dive earlier when fewer prey are available (Thompson and Fedak, 2001). This would increase the cost of diving, as more time would be spent transiting; however it would also increase the chances of finding food in another location.

Wild Steller sea lions show similar dive patterns to what my experimental results predict to be the most efficient strategy. Animals in the wild make multiple consecutive dives to depths of 20-50 m that are on average 1.9-2.4 minutes long (Loughlin et al., 1998; Merrick et al., 1994). Although these observed dive durations were below the animals' cADL, it is unlikely that they were fully recovering between dives, which would effectivly lower the amount of time they could rely on aerobic metabolism alone for each subsequent dive.

3.5.5 Conclusions

Understanding the costs associated with foraging for Steller sea lions has become increasingly important. As changes in prey are a potential factor contributing to their decline (Trites and Donnelly, 2003), it has become necessary to understand how foraging strategies, and the associated costs and benefits, may vary in response to these changes. My results provide activity-specific estimates of diving costs to contribute to more accurate bioenergetic models for Steller sea lions—as well as quantitative tests to help better interpret foraging models and diving strategies. This has possible applications for future studies on dive behaviours of wild sea lions, including the potential for historical analysis of archived dive data, and can help to understand how shifts in prey affect overall energy balance and the health of individuals in declining populations.

Chapter 4: Conclusions

The goal of my study was to determine how changes in prey abundance and distribution affect the foraging ability of Steller sea lions. To do so, I tested foraging behaviour and efficiency in response to changes in prey depth and density by measuring metabolic rate, dive behaviour, and food intake of captive sea lions that were freely diving on simulated prey patches. I also examined the costs and benefits of various foraging strategies, and generated activity-specific estimates of diving costs that can be applied to current and historical dive data, and used to parameterize bioenergetic models. To do this, I designed controlled dive types that allowed for the costs of separate components to be extracted. This allowed me to produce and test a predictive equation of dive costs, and to evaluate the root cause of the energetic differences between dive types.

Overall, my study found that Steller sea lions alter their foraging behaviour in response to changes in prey density and that these modifications in dive behaviour affect foraging efficiency and metabolic costs. In general, I found that sea lions use foraging strategies that are less energetically efficient when feeding on patches of low prey abundance. I also, found that transiting to and from depth is the most costly portion of a dive and that making multiple shorter dives is more energetically costly than making single longer dives. However, animals recover more quickly from multiple shorter dives, making them a more efficient use of their time.

4.1 Summary of Findings

In agreement with models predicting optimal foraging strategies for breath-hold divers (Carbone and Houston, 1996; Houston and Carbone, 1992; Kramer, 1988; Thompson and Fedak, 2001), the sea lions in my study generally dove for durations close to their aerobic dive limit (ADL), but abandoned dives earlier when foraging on low-density prey patches. However, contrary to model predictions, the sea lions did not increase, or even maintain foraging efficiency by giving up earlier on low-density prey patches. Instead, abandoning a prey patch earlier when density is low decreased foraging efficiency by about 5 times compared to high-density prey patches because they spent proportionally less time foraging (i.e., less time for prey intake) and lowered their efficiency more than can be accounted for simply by differences in prey density. With wild animals, the strategy of giving up early on a prey patch that is perceived to be poor quality may increase the chances of the animal finding a more productive food source elsewhere. The animals in my study did not have the option of finding a better prey source, and using this strategy left them with low energetic gain and efficiency. However, wild animals can take the chance of leaving a prey source to find something more profitable, which may pay off—but as these results indicate, could also be detrimental if nothing better is found. These results highlight the inherent risks or rewards that could be associated with alternate foraging decisions.

My results also demonstrated that transiting was more costly than time spent at the bottom. This corresponds with diving behaviours observed in wild animals (Boyd et al., 1995a; Hassrick et al., 2007) and the known physiological responses to diving (Fahlman et al., 2008b; Hindle et al., 2010; Kooyman, 1985; McDonald and Ponganis, 2014). This finding provides further insight into the costs and benefits of different foraging strategies. High metabolic costs during transiting suggest that Steller sea lions employ a strategy of getting to depth quickly, and spending more energy to do so rather than travelling to depth slowly but saving energy. This indicates that for short, shallow divers, such as Steller sea lions, the benefits gained from saving energy through longer, slower transit times (i.e., longer dive times) do not outweigh the benefits of shorter transit times (i.e., greater relative foraging time) due to faster swim speeds.

Single dives were less energetically costly due to less time spent transiting, which is consistent with my finding that transiting is more costly than time spent at the bottom. However, while bout dives were more energetically costly because of proportionally more time transiting, animals making bout dives were able to replenish their oxygen stores more efficiently. As a result, animals employing bout dives spent proportionally less time at the surface recovering between dives. This allowed them to spend a greater proportion of their time foraging. This highlights the trade-off between maximizing either time or energy through different diving strategies.

When using the separately estimated metabolic costs for transiting to and from depth, bottom time, and surface time determined from my study, I was able generate predictive equations to estimate diving costs based solely on behavioural data. Estimated diving costs were within 9.5% for the submergence portion of dives only and within 7.7% for complete dive cycles. These results are within the range of error of other methods for estimating energy expenditure (Fahlman et al., 2008c; Young et al., 2011). However, this method provides a simple way to estimate the energetic costs of diving by wild animals, without the need for more complicated and expensive tags and procedures. It also permits reanalysis and energetic quantification of historical dive behaviour records from wild Steller sea lions.

4.2 Strengths and Weaknesses

As with all studies, my thesis has its strengths and weaknesses. A notable strength was the ability to undertake controlled experiments with sea lions diving in a realistic setting. Working with trained animals in the open ocean helped to bridge the gap between precisely controlled laboratory experiments conducted in restricted physical conditions and wild studies where there is very little if any control over experimental conditions or manipulations.

With the experimental set-up I used, I was able to directly measure oxygen consumption for animals performing dives at depths and durations similar to those observed in wild Steller sea lions (Loughlin et al., 1998; Merrick et al., 1994; Merrick and Loughlin, 1997). This allowed me to directly measure the energetic costs of changes in dive behaviour in response to changes in foraging conditions. This is a vast improvement over previous studies, which could only measure behavioural changes (under a limited set of highly artificial conditions), but could not quantify the impact of those observed changes (Cornick and Horning, 2003; Sparling et al., 2007).

Measuring oxygen consumption also allowed me to produce a predictive model that estimated oxygen consumption rates based on simple behaviour categorization of diving. Rates of oxygen consumption are generally recognized to be the most accurate method for determining energy expenditure. However, it is rare to get the opportunity to use this method with diving marine mammals. Measuring field metabolic rate though the use of doubly labeled water is often used, but provides only a single value of energy expenditure and does not allow for differentiation between activities (Boyd et al., 1995b; Dalton et al., 2014; Sparling et al., 2008). Similarly, activity budgets with multipliers of resting basal metabolic rate can be used to estimate total diving costs, but applies only a single cost to diving and does not consider the variation in activity during different dive types (e.g., Costa et al., 1989; Winship et al., 2002).

Working with trained captive animals allowed me to study particular aspects of foraging energetics that would otherwise have not been possible. The purpose of my study was to measure foraging efficiency under various conditions and to separate the costs of specific dive portions and types. Without the ability to manipulate foraging conditions or dive types, this data would have been unattainable. Studying marine mammals in the wild can be challenging when looking to answer very specific questions, and it can be difficult to tease out specific causes and effects from many confounding variables.

Although working with trained sea lions in the open ocean helps to combine the control of laboratory experiments with the realistic conditions of field studies, there are some limitations as well. As these are trained animals, there was the potential for some effects of training to influence their behaviour. However this should not have had any effect on physical or physiological responses. The sea lions had been trained to dive and use the experimental equipment for 4-8 years, so they were familiar and comfortable around the equipment and trainers. Also, these animals dive on a regular basis, making their activity levels more similar to wild animals than sea lions in other captive settings.

One of the aims of my study was to determine changes in behaviour and energy expenditure of the sea lions in response to changes in prey. However, food was used as reinforcement for animals surfacing in the metabolic dome, which could affect diving decisions given that the sea lions knew food was always available at the surface. However, this feeding was kept at a small fraction of what the animals received at depth. Although this may have slightly influenced behaviour, I do not believe it had any major effects on the foraging decisions of the animals. The fact that I did see changes in behaviour with trained animals and that these behaviours matched those observed in wild animals (Boyd and Arnbom, 1991; Dolphin, 1987; Thompson et al., 1991), indicated that my sea lions made similar foraging decisions to their wild counterparts, despite being trained animals.

A limitation with my experimental set-up was the inability to create a situation where the sea lions had to search for and chase prey. This resulted in what were likely overestimates of foraging efficiency. Logistically, I could not feed live prey to the sea lions or create a scenario where they did not know where food was going to come from. While I was able to make direct comparisons between experimental foraging conditions, it is important to note that these values of foraging efficiency are not representative of foraging efficiencies of free-ranging animals with less predictable prey sources.

A weakness of my study was the small sample size of only 4 animals, which is not uncommon when working with marine mammals, both in laboratory and field settings. This highlights the challenges associated with studying large mammals, especially those that spend a large portion of their time at sea. Furthermore, it is difficult to have large sample sizes with captive marine mammals, due to the logistics of keeping the animals and providing the training for voluntary work in the open ocean. Often studies with small sample sizes pool data from a few animals. However, the use of mixed effects models for the statistical analysis of my data helped to account for repeated measures and inter-animal variation. This increased the statistical power allowing me to more confidently make inferences about the population from a small sample size.

The predictive equation I generated for determining metabolic costs based on dive behaviour provides a new approach for estimating foraging costs of free-ranging animals. However, it is important to note that it is species-specific for adult female Steller sea lions. Adult females are likely to have a larger impact on population trends than males, so although this study does not provide data for all age and sex classes, it does target a key group in the population.

My predictive equations, combined with time-depth recorder (TDR) data, can be used to determine how much energy animals spend while foraging. Changes can be monitored and comparisons can be made with regards to this aspect of foraging. However, energy expenditure is only half of the information—and needs to be balanced with the amount of energy animals gain while foraging. Unfortunately, it remains a challenge to determine when animals are actively foraging, what they are feeding on, and when they make successful prey capture attempts. Some methods have been developed to determine prey captures, such as accelerometry and animal-borne cameras (Bowen et al., 2002; Parrish et al., 2005; Viviant et al., 2009; Volpov et al., in press). Obtaining the full picture of foraging efficiency using my predictive model and TDR data to quantify energy expenditure, will require an additional technique to determine the amount of prey an animal is consuming (i.e., energy intake).

4.3 Applications and Importance of Research

My results indicate that Steller sea lions faced with reduced prey availability become less efficient foragers. Understanding how the energy balance of individuals is affected by changes in the environment is important for determining the health of the entire population. Animals that not only have less food available to them, but also use less efficient foraging behaviours will either end up at a lower nutritional status or will have to dedicate more time to foraging. This would take time and energy away from other essential activities, such as predator avoidance or maternal care, and could have serious implications for the recovery of declining populations.

Steller sea lions are not the only species of concern in Alaska and the Bering Sea. Several other species of top marine predators have also experienced similar population declines corresponding with changes in prey availability (Trites and Donnelly, 2003), indicating a possible ecosystem-wide issue. The findings of this study could be extended beyond Steller sea lions and may also shed light on the challenges facing other declining species.

The results of my study also provide a tool for assessing foraging costs of wild Steller sea lions. Understanding whether or not animals in the wild are foraging efficiently requires a means to interpret observed behaviours and monitor how these behaviours and associated costs may be changing with changes to the environment over time. The predictive equation I derived for estimating dive costs provides the unique opportunity to examine energy expenditure from both historical and current behavioural dive data. With this, current data from populations that have declined can be compared to and put into the context of data from the same populations at different stages of their population decline. This can provide quantitative data on the relationship between changes in population numbers and ecosystem conditions.

4.4 Future Research

Future work could be geared towards creating increasingly realistic dive settings to measure foraging costs to further bridge the gap between captive and wild studies. As previously mentioned, my measures of foraging efficiency are likely overestimates. Increasing the number and distance between feeding stations and randomizing where fish were delivered would help to create more realistic searching behaviours. A similar method was used with animals swimming horizontally in a pool (Cornick and Horning, 2003), and incorporating this idea with the dive set-up used in my study could provide further information on foraging decisions based on prey availability.

Similarly, another aspect that I was unable to include in my study was the actual pursuit of prey. This could be overcome by using live prey items. While using live prey would be extremely difficult in an open ocean setting, this aspect of foraging could perhaps be tested in a pool. Increasing the activity level of the simulated foraging dives through increasing search and/or chase efforts may provide a better picture of forging decisions in the context of the animals' physiological capacity (e.g., ADL) and create a better understanding of the physiological constraints of diving.

Further studies could also be conducted using the results of my predictive equation for estimating foraging costs for wild animals. Studies using this equation to compare foraging strategies and costs between different populations of Steller sea lions could help to further elucidate the reasons behind the observed population decline in Alaska and Russia. Combining TDR data for free-ranging animals from both the Eastern stock and the declining Western stock with my values for diving costs could help to highlight the differences in foraging strategies and costs between the two populations. This information could shed some light on the population decline in the Western stock and help to inform management decisions. In addition, this type of data could be used to inform and update bioenergetic models for Steller sea lions (Winship et al., 2002).

Finally, further development of techniques for determining energy intake of foraging marine mammals needs to be undertaken. Current methods available include jaw or head mounted accelerometers to detect movements associated with prey capture attempts (Viviant et al., 2009; Volpov et al., in press), internal stomach sensors to determine changes in temperature with feeding (Andrews, 1998; Kuhn and Costa, 2006), and animal-mounted video cameras to visually detect feeding events (Bowen et al., 2002; Parrish et al., 2005). All methods have advantages and disadvantages to them. However, there is room for improving accuracy and the amount of information provided (i.e., type and size of prey) in all methods. Accurate detection of successful prey captures combined with estimates of energy expenditure from my predictive equations could allow for foraging efficiency to be determined in free-raging animals and provide a more complete picture of what these animals are doing beneath the surface of the water and how they are affected by changes in their environment.

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