Journal of Experimental Marine Biology and Ecology 470 (2015) 70–77

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Low prey abundance leads to less efficient foraging behavior in Steller sea lions

Elizabeth T. Goundie *, David A.S. Rosen, Andrew W. Trites

Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada
Marine Mammal Research Unit, Fisheries Center, University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada

ARTICLE INFO

Article history:
Received 24 March 2015
Received in revised form 5 May 2015
Accepted 6 May 2015
Available online 22 May 2015

Keywords:
Dive behavior
Diving energetics
Foraging efficiency
Optimal foraging
Steller sea lion

ABSTRACT

Breath-hold divers should adjust their dive behaviors 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. We tested the effects of changes in prey availability on the foraging behavior and efficiency of Steller sea lions (*Eumetopias jubatus*) 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). We 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 we expected based on differences in food availability. Our results suggest that sea lions faced with reduced prey availability forage less efficiently and therefore would have greater difficulty obtaining their daily energy requirements.

1. Introduction

Animals should forage optimally such that they maximize net energy gain relative to the time and energy spent foraging (Charnov, 1976; Krebs, 1978; MacArthur and Pianka, 1966; McNamara, 1982). This means that foraging animals should alter their behavior 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 behaviors.

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 behavior 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.

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 and Trites, 2000, 2004; Rosen et al., 2000). However, only a few studies have investigated how such

---

Abbreviations: MR_S, surface metabolic rate; AMR, average metabolic rate over a dive cycle; ADL, aerobic dive limit; cADL, calculated aerobic dive limit.

* Corresponding author. Tel.: +1 778 714 1469.

E-mail addresses: e.goundie@fisheries.ubc.ca (E.T. Goundie), rosen@zoology.ubc.ca (D.A.S. Rosen), a.trites@fisheries.ubc.ca (A.W. Trites).

http://dx.doi.org/10.1016/j.jembe.2015.05.008

changes in prey may also impact foraging behavior and efficiency, and how they relate to the predictions of foraging models.

Tests of foraging models on marine mammals include studies where dive behavior 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 behavior, 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.

Our study tested how prey depth and abundance affect dive behavior and foraging efficiency by measuring diving metabolic rate, dive behavior, and food intake of 4 trained Steller sea lions diving in the open ocean on simulated prey patches of different densities at different depths. We thus empirically tested optimal foraging models for breath-hold divers by measuring energy gain and expenditure for animals diving in realistic conditions. Our 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. Materials and methods

2.1. Data collection

We measured changes in dive behavior, metabolic expenditure, and energy intake in 4 adult female Steller sea lions diving in simulated prey patches of varying qualities. 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 and 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.

2.2. Diving metabolic rate

We 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 s (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 min 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. 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 behavior. Each animal was outfitted with a tight-fitting harness holding a time depth recorder (ReefNet, Inc., Mississauga, ON, Canada) to record dive behavior. 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.

2.4. Foraging efficiency

We 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

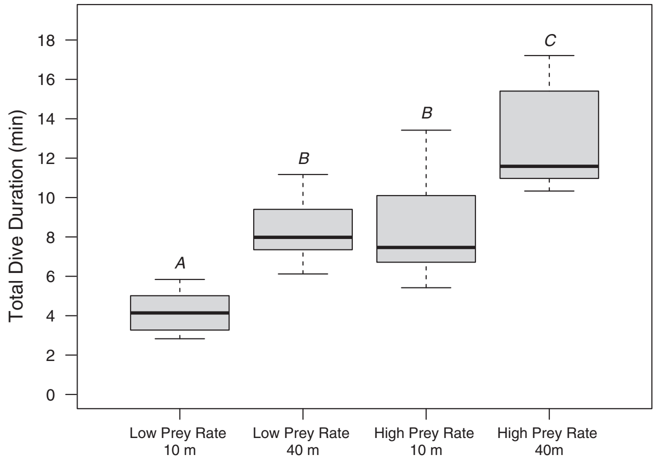

Fig. 1. Total dive durations for Steller sea lions diving to 10 and 40 m to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches. Dive durations are the sum of the five dives in a dive cycle. Each box represents 3 dive trials from each of the 4 animals for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

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).

2.5. 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 ANOVAs 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 values and scaled to body mass (i.e., per kg). Results did not differ between methods, so scaled data were reported to facilitate comparison to other studies. All values are reported as means ± SD.

3. Results

3.1. Dive energetics

Average diving metabolic rate (AMR) for all trials ranged from 8.9 to 13.4 mL O_2 min^{-1} kg^{-1}. 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.

3.2. Dive behavior

A variety of dive characteristics were measured to test for differences in diving behavior among the four foraging conditions. 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 min) and the shortest cycles were in low-density patches at 10 m (10.0 ± 1.1 min). 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 min).

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 min) and the shortest were in low-density prey patches at 10 m (4.2 ± 1.0 min). In fact, the increase in dive cycle duration was primarily due to these increases in total dive duration (Fig. 1).

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 min for 10 m dive bouts and 4.2 ± 0.4 min 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 min, low-density patches: 3.6 ± 1.3 min; 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

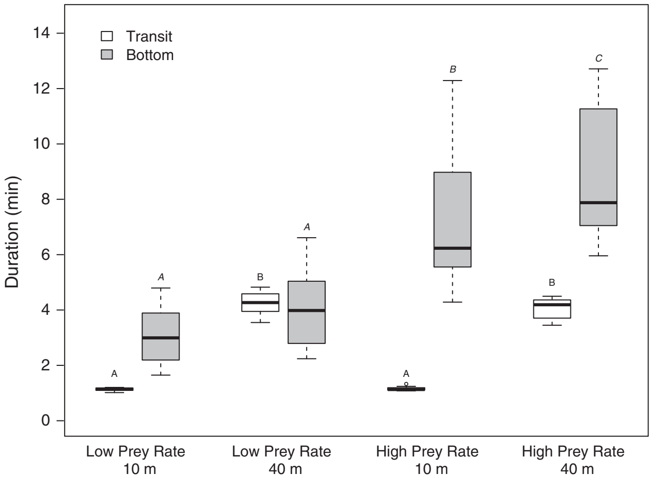

Fig. 2. Differences in transit and bottom durations for Steller sea lions diving to 10 and 40 m to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches. Transit durations (in white) include the sum of descent and ascent times for all five dives in a dive cycle. Bottom durations (in gray) 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 indicate significant differences between foraging conditions.

(40 m: 8.9 ± 2.4 min, 10 m: 7.2 ± 2.4 min; 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).

Total surface duration (sum of 4 inter-dive surface intervals and post-dive recovery period) increased directly with total dive duration (ANOVA, $F = 12.04$, $P = 0.0012$). 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, $F = 77.04$, $P < 0.0001$). In contrast, dive duration had no effect on post-dive recovery time (ANOVA, $F = 0.19$, $P = 0.67$). 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, $P < 0.0001$), 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, $P = 0.02$). The shortest total surface durations (5.8 ± 1.0 min), 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 min), seen with dives to high-density prey patches at 40 m, are due to both long surface interval durations and recovery times.

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. 3). 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.

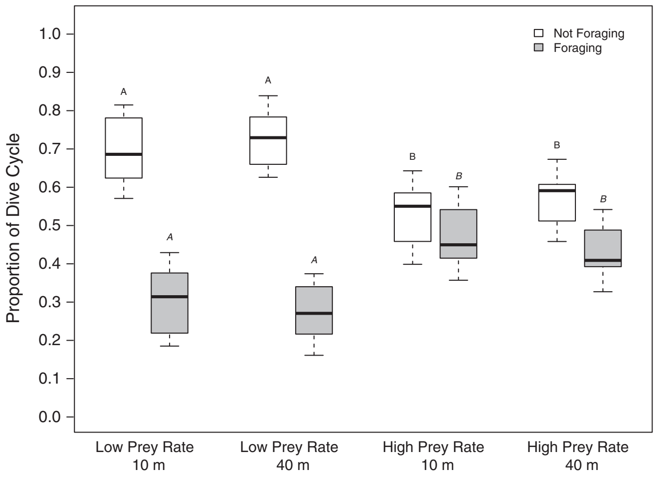

Fig. 3. Differences in the proportion of a dive cycle spent foraging (gray) and not foraging (white) for Steller sea lions diving to 10 and 40 m in low-density (4 fish pieces min^{-1}) and high-density (12 fish pieces min^{-1}) prey patches. “Foraging” includes only the total time spent at depth consuming 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 indicate significant differences between foraging conditions.

3.3. Foraging efficiency

Foraging efficiency is the outcome of the rate of energy intake and energy expenditure (Table 1). As previously noted, the rate of energy expenditure was independent of dive cycle duration (ANOVA, $F = 2.33$, $P = 0.13$) and was constant across all experimental conditions (Fig. 4A). Therefore, any differences in foraging efficiency between experimental conditions were the result of changes in the rate of energy intake.

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 behavior 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. 4B).

The proportion of the dive cycle spent foraging was independent of dive cycle duration within each prey patch density (high-density patches, ANOVA, $F = 0.58$, $P = 0.46$; low-density patches, ANOVA, $F = 0.18$, $P = 0.68$). Hence, rate of energy intake was also independent of dive cycle duration within each prey patch density (high-density patches, ANOVA, $F = 0.91$, $P = 0.35$; low-density patches, ANOVA, $F = 0.64$, $P = 0.43$). 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, $P = 0.27$).

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. 5). 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.

4. Discussion

Mathematical models have largely been the basis for current understanding of the effects that prey depth, prey density, and aerobic

Table 1
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)	AMR (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

dive limits have on the foraging behaviors 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 behavioral and energetic effects that changes in prey can have on the foraging efficiencies of air-breathing diving predators.

Consistent with the predictions of behavioral foraging models, we 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.

4.1. Effects of depth on dive behavior

Houston and Carbone's (1992; 1996) model predicted changes in foraging behavior 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, our 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 min at 10 m depths and 2.1 min at 40 m. In comparison, the calculated ADL (cADL) of these same Steller sea lions is 3 min (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 we measured to 40 m correspond

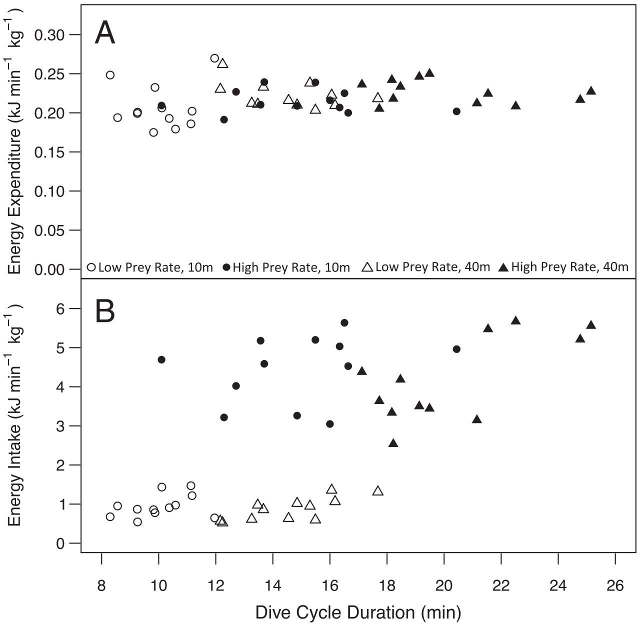

Fig. 4. Rate of (A) energy expenditure and (B) energy intake for 48 dive cycles as a function of cycle duration for 4 Steller sea lions. Each point represents a single dive cycle. Filled symbols are dives in high-density prey patches (12 fish pieces min^{-1}) and open symbols are dives in low-density 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.

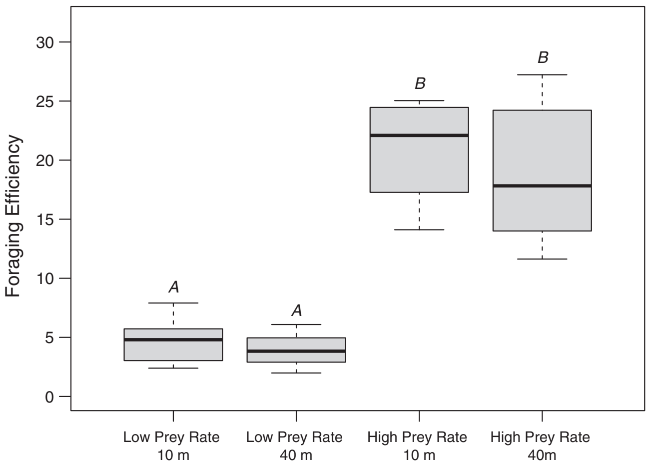

Fig. 5. Foraging efficiency for Steller sea lions diving to either low-density (4 fish pieces min^{-1}) or high-density (12 fish pieces min^{-1}) prey patches at 10 and 40 m. Foraging efficiency was calculated as energy intake divided by energy expenditure and represents the amount of energy gained for 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 indicate significant differences between foraging conditions.

to measurements on wild Steller sea lions, where dive durations to depths of 20–50 m averaged 1.9–2.4 min, also well below the cADL (Loughlin et al., 1998; Merrick et al., 1994). This indicates that the sea lions in our study were making similar foraging decisions to those of their wild counterparts. It is possible that our 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 behavior 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., 2008; Kooyman et al., 1973). During subsequent inter-dive surface intervals, these oxygen reserves are thought to be only partly 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.

4.2. Effects of patch quality on dive behavior

A model by Thompson and Fedak (2001) predicted that diving behavior 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 our study diving in high-density prey patches dove longer than in low-density prey patches. Due to the logistics of having animals reliably dive, our study did not use 0 prey rates (as described in Thompson and Fedak, 2001). However, given that our sea lions abandoned their dives earlier in low-density patches, the results of our 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 behavior 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 behavior, 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 behavior. 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 min (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.

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 aerobic 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 our 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 our 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, our 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 our 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.

4.3. Foraging efficiency

Foraging efficiency may be the most inclusive measure of the impacts of changes in prey availability, as it incorporates changes in behavior 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 behavior 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 our study, we quantified foraging efficiency in relation to the behaviors 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 our foraging conditions, differences in foraging efficiency were solely the result of changes in overall rate of energy intake. In our 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, our 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, our 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., 2006). For our study, depth was limited to 40 m; however, in the wild Steller sea lions rarely dive beyond 50 m, making the depths used in our study relevant (Merrick and Loughlin, 1997).

Although the observed changes in diving behavior agreed with model predictions and the majority of previous studies, these behaviors 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 our 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 we observed between prey patch conditions. It is possible that our 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. Our 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 we underestimated the costs of 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 we 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.

4.4. Conclusions

The changes in foraging behavior observed in our sea lions were similar to those reported in several studies of marine birds, reptiles, and mammals in the wild, where dive behavior 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 behaviors and captive studies such as ours help create a more complete picture of foraging conditions and energetics in relation to the behaviors 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. Our 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.

Acknowledgments

We thank the research technicians and husbandry staff at the UBC Open Water Research Laboratory for their assistance with data collection and animal training. We would also like to thank the reviewers for comments on this manuscript and Beth Volpov and Carling Gerlinsky for their assistance with statistical analysis. Financial support was provided by the US National Oceanic and Atmospheric Administration (Grant #NA11NMF4390124) to the North Pacific Universities Marine Mammal Research Consortium. All experimental protocols were approved by Animal Care Committees of the University of British Columbia and the Vancouver Aquarium and were conducted under UBC Animal Care Permit #A11-0397.**[SS]**

References

Atkinson, S., Calkins, D., Burkanov, V., Castellini, M., Hennen, D., Inglis, S., 2008. Impact of changing diet regimes on Steller sea lion body condition. Mar. Mamm. Sci. 24, 276–289.

Boyd, I., Arnbom, T., 1991. Diving behavior in relation to water temperature in the Southern elephant seal — foraging implications. Polar Biol. 11, 259–266.

Butler, P.J., 1988. The exercise response and the "classical" diving response during natural submersion in birds and mammals. Can. J. Zool. 66, 29–39.

Butler, P.J., Jones, D.R., 1997. Physiology of diving of birds and mammals. Physiol. Rev. 77, 837–899.

Carbone, C., Houston, A.I., 1994. Patterns in the diving behaviour of the pochard *Aythya ferina*: a test of an optimality model. Anim. Behav. 48, 457–465.

Carbone, C., Houston, A.I., 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. Anim. Behav. 51, 1247–1255.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Cornick, L.A., Horning, M., 2003. A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. Can. J. Zool. 81, 1799–1807.

Costa, D.P., Croxall, J.P., Duck, C.D., 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. Ecology 70, 596–606.

Dolphin, W.F., 1987. Dive behavior and estimated energy expenditure of foraging humpback whales in southeast Alaska. Can. J. Zool. 65, 354–362.

Doniol-Valcroze, T., Lesage, V., Giard, J., Michaud, R., 2011. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. Behav. Ecol. 22, 880–888.

Elliott, K.H., Davoren, G.K., Gaston, A.J., 2008. Time allocation by a deep-diving bird reflects prey type and energy gain. Anim. Behav. 75, 1301–1310.

Fahlman, A., Svard, C., Rosen, D.A.S., Jones, D.R., Trites, A.W., 2008. Metabolic costs of foraging and the management of O_2 and CO_2 stores in Steller sea lions. J. Exp. Biol. 211, 3573–3580.

Gerlinsky, C.D., Rosen, D.A.S., Trites, A.W., 2013. High diving metabolism results in a short aerobic dive limit for Steller sea lions (*Eumetopias jubatus*). J. Comp. Physiol. B. 183, 699–708.

Gerlinsky, C.D., Trites, A.W., Rosen, D.A.S., 2014. Steller sea lions (*Eumetopias jubatus*) have greater blood volumes, higher diving metabolic rates and a longer aerobic dive limit when nutritionally stressed. J. Exp. Biol. 217, 769–778.

Hastie, G.D., Rosen, D.A.S., Trites, A.W., 2006. The influence of depth on a breath-hold diver: predicting the diving metabolism of Steller sea lions (*Eumetopias jubatus*). J. Exp. Mar. Biol. Ecol. 336, 163–170.

Hays, G.C., Houghton, J.D.R., Issacs, C., King, R.S., Lloyd, C., Lovell, P., 2004. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. Anim. Behav. 67, 733–743.

Heath, J.P., Gilchrist, H.G., Ydenberg, R.C., 2007. Can dive cycle models predict patterns of foraging behaviour? Diving by common eiders in an Arctic polynya. Anim. Behav. 73, 877–884.

Houston, A.I., Carbone, C., 1992. The optimal allocation of time during the diving cycle. Behav. Ecol. 3, 255–265.

Jeanniard du Dot, T., Rosen, D.A.S., Richmond, J.P., Kitaysky, A.S., Zinn, S.A., Trites, A.W., 2009. Changes in glucocorticoids, IGF-I and thyroid hormones as indicators of nutritional stress and subsequent refeeding in Steller sea lions (*Eumetopias jubatus*). Comp. Biochem. Physiol. A Mol. Integr. Physiol. 152, 524–534.

Kooyman, G.L., 1989. Diverse Divers: Physiology and Behavior. Springer-Verlag.

Kooyman, G.L., Kerem, D.H., Campbell, W.B., Wright, J.J., 1973. Pulmonary gas exchange in freely diving Weddell seals *Leptonychotes weddelli*. Respir. Physiol. 17, 283–290.

Kramer, D.L., 1988. The behavioral ecology of air breathing by aquatic animals. Can. J. Zool. 66, 89–94.

Krebs, J.R., 1978. Behavioural Ecology: An Evolutionary Approach. Wiley.

Loughlin, T.R., Perlov, A.S., Baker, J.D., Blokhin, S.A., Makhnyr, A.G., 1998. Diving behavior of adult female Steller sea lions in the Kuril Islands, Russia. Biosphere Conserv. Nat. Wildl. Hum. 1, 21–31.

MacArthur, R., Pianka, E., 1966. On optimal use of a patchy environment. Am. Nat. 100, 603–609.

McNamara, J., 1982. Optimal patch use in a stochastic environment. Theor. Popul. Biol. 21, 269–288.

Merrick, R.L., Loughlin, T.R., 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Can. J. Zool. 75, 776–786.

Merrick, R.L., Loughlin, T.R., Antonelis, G.A., Hill, R., 1994. Use of satellite-linked telemetry to study Steller sea lion and northern fur seal foraging. Polar Res. 13, 105–114.

Mori, Y., Boyd, I.L., 2004. The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. Ecology 85, 398–410.

Nolet, B.A., Wansink, D.E.H., Kruuk, H., 1993. Diving of otters (*Lutra lutra*) in a marine habitat: use of depths by a single-prey loader. J. Anim. Ecol. 62, 22–32.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects Models in S and S-PLUS. Springer.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2015. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-120.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosen, D.A.S., Trites, A.W., 1997. Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. Comp. Biochem. Physiol. Physiol. 118, 877–881.

Rosen, D.A.S., Trites, A.W., 2000. Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. Can. J. Zool. Rev. Can. Zool. 78, 1243–1250.

Rosen, D.A.S., Trites, A.W., 2004. Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*). Can. J. Zool. Rev. Can. Zool. 82, 1061–1069.

Rosen, D.A.S., Williams, L., Trites, A.W., 2000. Effect of ration size and meal frequency on assimilation and digestive efficiency in yearling Steller sea lions, *Eumetopias jubatus*. Aquat. Mamm. 26, 76–82.

Scholander, P.F., 1940. Experimental Investigations on the Respiratory Function in Diving Mammals and Birds. Det Norske Videnskaps-Akademi I Oslo, Oslo.

Sparling, C.E., Georges, J.Y., Gallon, S.L., Fedak, M., Thompson, D., 2007. How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. Anim. Behav. 74, 207–218.

Thompson, D., Fedak, M.A., 2001. How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. Anim. Behav. 61, 287–296.

Thompson, D., Hammond, P.S., Nicholas, K.S., Fedak, M.A., 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). J. Zool. 224, 223–232.

Thums, M., Bradshaw, C.J.A., Sumner, M.D., Horsburgh, J.M., Hindell, M.A., 2013. Depletion of deep marine food patches forces divers to give up early. J. Anim. Ecol. 82, 72–83.

Trites, A.W., Donnelly, C.P., 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mamm. Rev. 33, 3–28.

Wallace, B.P., Zolkewitz, M., James, M.C., 2015. Fine-scale foraging ecology of leatherback turtles. Behav. Evol. Ecol. 3, 15.

Weathers, W.W., Sullivan, K.A., 1991. Foraging efficiency of parent juncos and their young. Condor 93, 346–353.

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