Examining the metabolic cost of otariid foraging under varying conditions

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1. Introduction

Marine mammal diving behavior is constrained by oxygen stores and gas exchange (Castellini et al., 1992; Fahlman et al., 2008a; Kooyman et al., 1980). Within physiological constraints dive behavior is plastic, which allows marine mammals to optimize their diving behavior as conditions change in order to maximize energy gain (Austin et al., 2006; Cornick and Horning, 2003; Cornick et al., 2006; Maresh et al., 2014; Van der Hoop et al., 2014; Yeates et al., 2007). Free ranging pinnipeds have been documented spending more time resting between dives to compensate for increased locomotion costs (Maresh et al., 2014). Several studies have also shown that behavior within dives is directly affected by prey availability during that particular dive (Austin et al., 2006; Heaslip et al., 2014; Sato et al., 2003).

Through varying prey encounter rates, Cornick and Horning (2003) demonstrated that dive duration, foraging time, and dive and foraging efficiency increased with increasing prey encounter rates in Steller sea lions (Eumetopias jubatus). An increase in the cost of locomotion elicited the same behavioral responses (e.g., dive duration, surface interval duration) as a reduction in prey encounter rate, but foraging efficiency was maintained over a series of dives by reducing surface interval durations by ~50% (Cornick et al., 2006). Increasing the cost of transport also causes an increase in oxygen consumption (VO2), carbon dioxide production (VCO2) and respiration rate (Cornick unpublished data; Fahlman et al., 2013; Maresh et al., 2014; Young et al., 2011). Changes in behavior, such as reducing surface interval durations (Cornick et al., 2006), decreasing dive and foraging durations (Cornick and Horning, 2003) and increasing the number of dives in a bout (Feldkamp et al., 1989; Boyd et al. 1995b), allow pinnipeds to maintain overall dive efficiency as foraging conditions change; however the extent to which an animal can change its behavior without accruing a physiological cost (e.g. increased O2 debt, increased CO2) has yet to be determined.

Many field studies of pinniped energetics are constrained by the techniques used to measure metabolic rate, such as heart rate (Boyd et al., 1995a), doubly labeled water (Sparring et al., 2008), and activity (e.g. body acceleration; Fahlman et al., 2008b). While respirometry is able to provide us with insight into free ranging metabolic rates of certain species (Kooyman, 1967; Castellini et al., 1992; Williams et al., 2004), the method has primarily been applied in captive settings in which animals are trained for voluntary respiratory measurements (Reed et al., 1994; Hastie et al., 2006; Fahlman et al., 2008a). These captive studies
are not without limitations. Hastie et al. (2006) were able to measure diving metabolism in trained Steller sea lions (Eumetopias jubatus), but were not able to provide a means of studying foraging metabolic rate, since the animals were not actively looking for prey. Fahlman et al. (2008a) addressed that limitation by simulating food patches of varying densities using a feeding tube, providing an estimate of foraging metabolism; however, the sea lions were mostly swimming vertically in the water column, providing no measurement of the cost of transit within and between prey patches. In order to understand the effects of changing behavior in response to changing conditions on the energetic cost of foraging, changes in behavior and metabolism were examined in response to varying prey densities and cost of transport using open flow respirometry. The goal of the study was to determine if metabolic rate and CO2 production changed at varying prey encounter rates and between standard and cost-increased dives, and to determine if changes in foraging behavior corresponded to changes in foraging metabolic rate and foraging CO2 production.

2. Methods

2.1. Study location and animals

Foraging trials were conducted using an adult male (M1; 15yo; 136 kg) and female (F1; 25yo; 80 kg) California sea lion (Zalophus californianus) at Moss Landing Marine Laboratories in Moss Landing, CA from March to December 2012.

2.2. Experimental design

Metabolic measurements were done with a Sable Systems TurboFox 500 P series open flow respirometer. The breathing dome was constructed of Plexiglas (7.01 m x 7.01 m x 7.32 m; 5.69 ft³ volume) and rested on starboard plastic, with a rubber bumper secured to the underside of the starboard to create an airtight seal at the water surface and rested on starboard plastic, with a rubber bumper secured to the buoys. The inflow hole was located on the top of the chamber and also served as the provisioning hole during baseline periods. The outflow hole was located on the opposite side panel of the chamber. Air was drawn through the dome at a constant rate of 500 L min⁻¹. Carbon dioxide (CO₂) and oxygen (O₂) concentration (% barometric pressure compensated), water vapor pressure (WVP in kPa), flow rate (L min⁻¹) and barometric pressure (BP; kPa) were sub-sampled every second. Data were recorded directly from the TurboFox using Sable Systems Expedata software (v. 2.0; Sable Systems 2010). The TurboFox was calibrated daily according to manufacturer instructions using dry nitrogen, 2% CO₂/N₂ mixed gas and a magnesium perchlorate-ascarite scrubber.

Feeding trials were conducted following Cornick and Horning (2003) and Cornick et al. (2006). Three ABS plastic fish feeder tubes with trap door releases were mounted around a 43,000 L circular pool. Kennel grating covered in a shade cloth was placed over the surface of the pool to prevent the sea lions from surfacing outside of the breathing dome. Four real-time video cameras were set in waterproof housing. Three cameras were mounted downward in the kennel grating facing the bottom of each fish feeder. The fourth camera was mounted on the side of the enclosure facing the dome. Behavioral data were recorded using a Lorex video system (120WDB800 series). Water temperature during trials averaged 11.6 ± 0.2 °C.

2.3. Experimental procedure and measurements

Sea lions were exposed to either high (36 fish released per session) or low (6 fish released per session) prey encounter rates. To simulate an increased cost of foraging, each sea lion was fitted with a drag harness for half of the trials (Cornick and Horning, 2003; Cornick et al., 2006).

Each trial was conducted using a single fasted sea lion. Trials started with the animal stationed in the dome for 4 min prior to foraging to measure resting metabolic rate (RMR). The sea lion was then released from the chamber to forage freely. Tubes were opened one at a time by an intern, 12 s apart. For high-density prey encounter rates each tube released 1 fish per opening. For low-density prey encounter rates each tube released 3 fish per opening. During the pre-trial and post-trial periods the sea lions were fed minimally to prevent them from leaving the dome. The sea lions were not provisioned at the surface during the foraging trials.

2.4. Data analysis

Because the animals were stationed in the chamber following the end of each session, the surface interval duration for the last dive of each bout was calculated using the mean surface interval for the other dives in that session (Cornick et al., 2006). Surface intervals lasting <1 s were recorded as 0.5 s. A single dive cycle (DC) consisted of the

Fig. 1. Left: Breathing dome. A nylon hose connected the dome to the TurboFox respirometer for data collection. Air was pulled through the chamber at 500 L min⁻¹. The white arrow on the top of the respirometry chamber indicates the flow of ambient air into the chamber. The white arrow perpendicular to the top arrow indicates the direction of airflow though the outflow hole leading to the respirometer. Middle: M1 in the drag harness used during cost increased trials. Right: F1 in the drag harnesses used during cost increased trials.
total dive duration (DD) plus the subsequent post-dive surface interval (SI) duration. Dive duration, foraging time (FT), SI, and dive efficiency (FT/DD) were calculated from the time-stamped video data (Cornick et al., 2006). Mass-specific foraging metabolic rate (FVO$_2$), mass specific foraging CO$_2$ elimination (FVCO$_2$) and foraging efficiency (FVO$_2$/DC) were calculated using Sable Systems Expedata software.

Each experimental session was defined as a dive bout, and data were analyzed for bout-by-bout differences (Cornick et al., 2006). Each bout was considered an independent event, because each session was a new, fasted foraging event, and because treatments were randomized, the animals had no prior knowledge or expectation of the prey encounter rates they would experience in a bout. In order to remove autocorrelation of dives within a bout, the mean and median were calculated for each bout for dive duration, foraging duration, post-dive surface interval, dive efficiency, FVO$_2$, and FVCO$_2$. Subsequent analyses were conducted on bout means or medians, depending on which measure was the best representation of central tendency for that variable. Statistical analyses were conducted using SPSS v.20 for Mac (IBM Corp. 2011). Alpha levels were set to $p < 0.05$. An initial one way Analysis of Variance (ANOVA) was performed across all variables and sessions to assess individual variability between sea lions.

To determine the effect of increased cost of swimming on foraging behavior and efficiency, standard and cost-increased dives and bouts were compared for each variable across all prey encounter rates using ANOVA (Cornick et al., 2006). Simple linear regression was used to examine the relationship between foraging behavior (dive duration, foraging duration, surface interval duration) and foraging energetics (FVO$_2$ and FVCO$_2$). All values are reported as median or mean ± 1 SE.

**3. Results**

Fifty-two experimental sessions (26 standard locomotion, 26 cost increased) were conducted, resulting in 182 standard locomotion dives and 172 cost increased dives. Metabolic data were collected in 32 (16 standard locomotion, 16 cost increased) of the 52 sessions, resulting in 105 standard and 105 cost increased dives.

There were significant differences between the two sea lions for all variables except dive efficiency, so subsequent analyses were performed on each subject individually (see supplementary Table 1).

3.1. FVO$_2$ analysis

For F1, the explanatory power of dive duration ($R^2 = 0.13, F_{1,14} = 2.17, p = 0.16$; Fig. 2A) and foraging duration ($R^2 = 0.18, F_{1,14} = 3.05, p = 0.11$; Fig. 3A) on FVO$_2$ variability was less than would be expected by chance. For M1, dive duration explained 64% of the variability in FVO$_2$ ($F_{1,14} = 25.35, p < 0.001$; Fig. 2A) and foraging duration explained 61% of the variability in FVO$_2$ ($F_{1,14} = 21.79, p < 0.001$; Fig. 3A). Surface interval duration was not a significant predictor of FVO$_2$ for either animal (F1: $R^2 = 0.01, F_{1,14} = 0.13, p = 0.73$; M1: $R^2 = 0.004, F_{1,14} = 0.06, p = 0.81$).

3.2. FVCO$_2$ analysis

Dive duration explained 34% of the variability in FVCO$_2$ for F1 ($F_{1,14} = 7.33, p = 0.02$; Fig. 2B) and 71% for M1 ($F_{1,14} = 34.36, p < 0.01$; Fig. 2B). Foraging duration explained 36% of the variability in FVCO$_2$ for F1 ($F_{1,14} = 7.83, p = 0.01$; Fig. 3B), and 66% for M1 ($F_{1,14} = 27.36, p < 0.01$; Fig. 3B). Surface interval duration was not a significant predictor of FVCO$_2$ for either animal (F1: $R^2 = 0.001, F_{1,14} = 0.009, p = 0.93$; M1: $R^2 = 0.006, F_{1,14} = 0.09, p = 0.77$).

3.3. Behavioral analysis

Results of the ANOVA comparing all variables between prey encounter rates are summarized in Table 1. For F1, dive efficiency and dive duration were significantly higher during high prey encounter rates. There was no significant difference in FVO$_2$ between low and high prey encounter rates (Fig. 4A); however FVCO$_2$ was significantly higher during low prey encounter rates (Fig. 4B). M1 showed a significant increase in dive duration, foraging duration, dive efficiency, foraging efficiency, recovery VO$_2$ and recovery VCO$_2$ under high prey encounter rates; however FVO$_2$ and FVCO$_2$ were significantly lower in high prey encounter rates (Fig. 4).

There were no statistically significant differences in any variable analyzed between standard and cost increased dives for either animal (supplementary Table 2); however, both FVO$_2$ and FVCO$_2$ were maintained or showed an increasing trend in cost-increased bouts (Fig. 5) for both animals. Surface interval duration also decreased during cost-increased dives for both animals (Fig. 6).

4. Discussion

Foraging metabolic rates (4.07–25.68 mL min$^{-1}$ kg$^{-1}$) and overall dive durations (12–82 s) were consistent with those reported in other studies on California sea lions (Butler et al., 1992; Feldkamp, 1985). Both animals increased dive duration in response to increased prey encounter rates. This is consistent with the results of previous captive foraging experiments (Cornick and Horning, 2003; Cornick et al., 2006).

Foraging VCO$_2$ explained over 30% of the variability in dive and foraging durations and showed a significant decrease under high prey encounter rates for both animals. These results are consistent with Boutilier et al.’s (2001) observations on grey seals (Halichoerus grypus) that as dive duration increases, the respiratory quotient (ratio of CO$_2$ output to O$_2$ uptake) decreases. Because FVO$_2$ decreased in high prey encounter rates, a decrease in FVCO$_2$ would be expected due to the nature of
Foraging duration and metabolic cost of foraging

Most studies that examine foraging costs in pinnipeds use O2 consumption and MR as physiological markers (Hind and Gurney 1997; Hastie et al., 2006, 2007; Fahlin et al., 2008a); however, CO2 could be a more sensitive indicator of foraging costs than FVO2 because the dive response, and thus the magnitude of hypometabolism, is voluntary (Davis and Williams 2012; Kooyman, 1973; Kooyman et al., 1980, 1983; Hill, 1986; Hurley and Costa, 2001; Thorson, 1993). Hindle et al. (2010) demonstrated that Steller sea lions trained to voluntarily dive to depths up to 40 m decreased their heart rate by 40%, and noted that mean badycardia was 9% greater during shallow (10 m) dives when compared to deep dives. The sea lions also exhibited tachycardia prior to surfacing (Hindle et al., 2010) to increase the saturation rate of O2 in the blood and tissues and the rate of CO2 removal (Hastie et al., 2007).

Conversely, CO2 exchange is not within the voluntary control of the animal. Carbon dioxide stores take more time to balance than O2 stores at the surface. Boutiller et al. (2001) concluded that by rapidly reloading O2, seals can cut their surface interval short, maintain aerobic diving, tolerate the added CO2 burden during diving, and repay the O2 debt at the end of a dive bout. Fahlin et al. (2008a) demonstrated this during a foraging experiment with Steller sea lions. In their experiments, the sea lions spent enough time at the surface to optimize O2 uptake and remove enough CO2 that there would not be a significant accumulation to hinder diving. They hypothesized that maintaining extremely short dive durations over an entire bout would lead to elevated tissue and blood CO2 levels that would eventually force the end of the bout.

### Table 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>Low PER</th>
<th>High PER</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dive duration (s) median ± SE (n)</td>
<td>15 ± 1 (12)</td>
<td>20.5 ± 2 (14)</td>
<td>0.02</td>
</tr>
<tr>
<td>Foraging duration (s) median ± SE (n)</td>
<td>14.5 ± 2 (12)</td>
<td>17.5 ± 2 (14)</td>
<td>0.27 (NS)</td>
</tr>
<tr>
<td>Surface interval (s) median ± SE (n)</td>
<td>1 ± 2.00E − 05 (12)</td>
<td>1 ± 2.00E − 05 (14)</td>
<td>0.61 (NS)</td>
</tr>
<tr>
<td>Dive efficiency (FT/DC) median ± SE (n)</td>
<td>0.64 ± 0.03 (12)</td>
<td>0.73 ± 0.02 (14)</td>
<td>0.03</td>
</tr>
<tr>
<td>Foraging efficiency (FVO2/DC) median ± SE (n)</td>
<td>7.02 ± 0.68 (8)</td>
<td>5.04 ± 0.75 (14)</td>
<td>0.07 (NS)</td>
</tr>
<tr>
<td>Baseline metabolic rate (mL min⁻¹ kg⁻¹) mean ± SE (n)</td>
<td>15.47 ± 0.83 (8)</td>
<td>16.01 ± 0.78 (8)</td>
<td>0.64 (NS)</td>
</tr>
<tr>
<td>Foraging metabolic rate (mL min⁻¹ kg⁻¹) mean ± SE (n)</td>
<td>23.26 ± 0.54 (8)</td>
<td>21.83 ± 0.70 (8)</td>
<td>0.13</td>
</tr>
<tr>
<td>Foraging VCO2 (mL min⁻¹ kg⁻¹) mean ± SE (n)</td>
<td>17.96 ± 0.57 (8)</td>
<td>15.83 ± 0.66 (8)</td>
<td>0.03</td>
</tr>
<tr>
<td>Post-bout metabolic rate (mL min⁻¹ kg⁻¹) mean ± SE (n)</td>
<td>17.52 ± 0.79 (8)</td>
<td>18.89 ± 0.79 (8)</td>
<td>0.24 (NS)</td>
</tr>
<tr>
<td>Post-bout VCO2 (mL min⁻¹ kg⁻¹) mean ± SE (n)</td>
<td>16.83 ± 0.76 (8)</td>
<td>18.52 ± 0.53 (8)</td>
<td>0.09 (NS)</td>
</tr>
</tbody>
</table>

Values for each variable compared between low and high prey encounter rates (PER) across all dives for F1 and M1. Values reported are mean ± SE. n = number of bouts. p = significance at p = 0.05. VCO2 = amount of carbon dioxide eliminated, high PER = 36 pieces of fish per trial released, low PER = 6 pieces of fish per trial released, NS = not significant. Dive efficiency is defined as foraging time (FT) per dive cycle (DC). Foraging efficiency is defined as mass specific foraging metabolic rate (FVO2) (mL min⁻¹ kg⁻¹) per dive cycle (DC).
Although differences in surface interval duration between standard and cost increased dives were not statistically significant, the trend for surface interval to decrease in order to maintain efficiency when the cost of transport increases supports the findings of Boutlier et al. (2001) and Cornick et al. (2006), and the hypothesis that there is plasticity in how these animals manage the cost of foraging when prey conditions warrant continuing to forage. Decreasing surface interval durations to maintain efficiency within aerobic diving when the cost of foraging increases suggests it may be easier to tolerate marginal increases in CO2 over the course of a bout and maintain contact with prey, rather than accumulating a more significant O2 debt by exceeding the aerobic dive limit (ADL) on a single dive.

Due to the size and shape of the enclosure, which required very little active swimming to move between feeders, the additional effect of swimming within a prey patch on CO2 could not be measured. Therefore, the results are likely an underestimate of the true metabolic cost of changing foraging conditions that either reduce the prey encounter rate (e.g., overfishing) or increase the cost of accessing prey (e.g., prey depth suppression due to El Nino). The results make clear that CO2 should be more closely examined in the context of foraging studies, and may provide a more sensitive marker when determining the metabolic cost of foraging behavior under varying conditions in pinnipeds. Total O2 stores, and the rate at which they are used, dictate the maximal diving capability of foraging marine mammals; the distribution, abundance, depth and energy content of prey dictate dive behavior (Costa and Gales, 2000; Cornick and Horning, 2003; Cornick et al., 2006). Boutlier et al. (1993, 2001) and Fahlman et al. (2008a) suggest that surface interval duration is driven by the need to optimize O2 stores while simultaneously removing enough CO2 to continue diving. As prey availability changes under the myriad stressors of changing ocean conditions, pinnipeds may reach the limits of both behavioral plasticity and maximal physiological costs, which could result in population-level effects over time.

5. Conclusions

Understanding how pinnipeds respond physiologically to changes in the prey field provides greater insight into their behavioral limits. As natural and anthropogenic changes in ocean conditions cause prey populations to migrate into deeper waters and further offshore in response to changes in their preferred temperature profiles, pinnipeds will be forced to dive deeper and travel further for food, increasing the amount of time and energy spent foraging. California sea lion strandings in 2015 were 10 times the average stranding levels recorded during the same months in 2004–2012 (NOAA Fisheries, 2015). NOAA Fisheries (2015) listed change in prey availability as one of the likely contributors to the increase in strandings. The increase in strandings illustrates that the subsequent increase in the metabolic cost of foraging may exceed the ability to adapt. Closer examination of CO2 as a marker for the metabolic cost of foraging will provide greater understanding of both the behavioral and physiological limits of these iconic marine predators.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2016.11.001.
Fig. 6. Mean surface interval duration for standard (dark grey) and cost-increased (light grey) bouts for F1 (n = 8) and M1 (n = 8). Error bars represent 1 standard error of the mean.

References


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Glossary

DC: dive cycle
DD: dive duration
FT: time spent foraging
FMD: mass-specific foraging metabolic rate
FVC02: mass-specific foraging carbon dioxide elimination
SI: surface interval duration