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Evidence of partial deferment of digestion during diving in Steller sea lions (*Eumetopias jubatus*)

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A B S T R A C T

Past foraging success of diving air-breathing vertebrates can adversely affect future foraging capabilities and costs through changes in circulation or increased metabolic costs associated with digestion that are incompatible with efficient diving. This study tested the physiological interaction between digestion and diving by comparing the cost of diving in fasted and pre-fed trained Steller sea lions foraging under controlled conditions in the open ocean. Pre-dive and post-dive surface metabolism and diving metabolic rate were all higher in the pre-fed animals than the fasted animals, indicating an effect of digestion on metabolism. However, the sea lions displayed a significant reduction in the apparent additive effect of digestion during diving. The increase in rate of oxygen consumption associated with digestion was reduced by 54% during diving compared to the increase observed in pre-dive metabolism. This truncation of the additional cost of digestion rapidly disappeared following cessation of diving. The results suggest that Steller sea lions diving to depth demonstrate a partial deferment of digestion while actively foraging and that the classically held view that digestion and diving are incompatible processes may be much more variable and adaptable to specific diving conditions and behaviors than previously thought.

1. Introduction

The patterns and underlying physiological controls of foraging dives have been investigated in a number of air-breathing vertebrates, including seabirds (Elliott et al., 2013; Heath et al., 2007; Shoji et al., 2015), penguins (Hanuise et al., 2013; Shiomi et al., 2012), sea snakes (Cook and Brischoux, 2014), sea turtles (Bradshaw et al., 2007; Wallace and Jones, 2008), and a host of marine mammals. Current models of the cost of foraging in these diving animals and the resultant theories of optimal foraging strategies treat the acquisition and digestion of prey as physiological processes that are independent of one another (e.g., Burns et al., 2006; Mori, 1998; Sparling et al., 2007b; Thompson and Fedak, 2001). However, foraging bouts are often long-lasting, suggesting a potential temporal overlap between these two processes. Inherent conflicts between the physiological requirements for prey acquisition and prey assimilation could impact the foraging capacity of air-breathing vertebrates, including marine mammals, following successful bouts of foraging (Rosen et al., 2007).

During the normal course of digestion, blood flow is increased to the stomach and intestine to aid the physical and chemical breakdown of food and the absorption of nutrients. However, the changes in circulation that aid digestion of a meal are contradictory to the vasoconstriction required for efficient management of blood oxygen stores during diving. Studies of circulatory changes in diving pinnipeds (mostly phocid seals) during the classic dive response have shown extensive vasoconstriction of "non-essential" systems, turning them into what Scholander (1940) described as a "heart–lung–brain" machine. More detailed measurements of changes in redistribution of cardiac output and blood flow in a forcibly "dived" Weddell seal (*Leptonychotes weddellii*) confirmed the maintenance of blood flow to "essential" systems (the brain, spinal cord, adrenal glands, spleen, and placenta), while blood flow in other tissues was severely constrained (Zapol et al., 1979). This included an almost 90% reduction in blood flow at the ileum (small intestine), lending credence to the hypothesis that diving and digestion are non-compatible circulatory tasks. However, additional research on freely diving Weddell seals showed that their blood became lipemic during deep foraging dives, indicating that both digestion and intestinal absorption of fat continued over a 5- to 6-h foraging session (Davis et al., 1983).

A second potential conflict between the acquisition and digestion of prey relates to the increase in metabolism associated with meal digestion (the heat increment of feeding, HIF, also known as specific dynamic action, SDA), including the cost of warming prey to body temperature (Wilson and Culik, 1991). For some diving mammals this increase in metabolism may offset thermoregulatory costs (Costa and Kooyman, 1984; Rosen et al., 2007), although this does not appear to be the case with larger species (Rosen and Trites, 2003). Regardless, the increase in metabolism associated with the digestive process can potentially decrease the amount of time an individual can dive while relying upon

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aerobic metabolism. Aerobic diving is considered to be more "efficient" than reliance upon anaerobic metabolism (Carbone and Houstin, 1996). The maximum length of time that a marine mammal can remain submerged using only aerobic metabolism — their aerobic dive limit (ADL) — is a factor of their on-board oxygen reserves and their diving metabolic rate, the rate at which they consume the oxygen reserves (Kooyman et al., 1983). Therefore, any increases in metabolism while diving will decrease the ADL and result in reduced foraging efficiency.

Previous studies have demonstrated that the metabolism of Steller sea lions (*Eumetopias jubatus*) can more than double following ingestion of a meal (Rosen and Trites, 1997). Hence, the increased metabolism associated with the digestion of previous meals can theoretically limit future foraging success through decreased aerobic diving capacity. Both resting and diving metabolic rates in freely diving Weddell seals increased following feeding, both for dives during which fish were ingested as well as dives taking place as long as 5 h after successful foraging events (Williams et al., 2004). In contrast, gray seals (*Halichoerus grypus*) appear capable of deferring the costs of digestion until periods of active foraging are completed (Sparling et al., 2007a).

The potential conflicts between diving and digestion result in two competing hypotheses. First, that the heat increment of feeding will increase diving metabolic rate, effectively leading to decreases in foraging efficiency. Alternately, the circulatory changes that constitute part of the dive response will impede digestion during foraging bouts, delaying the benefits of successful foraging, but maintaining foraging efficiency. These hypothesized conflicts between digestion and diving were tested by measuring metabolic changes in trained Steller sea lions diving for prey in the open ocean under different digestive conditions. Our goal was to determine the effect of previous feeding events on the energetic cost of subsequent foraging episodes. The results contribute to understanding the nature and consequences of foraging decisions and metabolic costs on foraging efficiency under realistic physiological conditions.

2. Material and methods

2.1. Experimental protocol

Diving metabolic rate was measured in four adult, female Steller sea lions (ages 13–16 years, 143–222 kg) when they were either fasted overnight (at least 18 h), or 1 h after being fed a 3 kg meal of herring (Table 1). Animals each completed 4–5 trials for each experimental condition, and undertook only one trial each day. For both trial types, animals were fed a small amount of fish (<0.5 kg Pacific herring, *Clupea pallasii*) during transportation to the dive site. All sea lions were housed at the University of British Columbia's Open Water Research Laboratory (Port Moody, BC), where they have been actively diving in the open ocean for research purposes for between 6 and 10 years. The animals performed all behaviors voluntarily under trainer control. All experiments were conducted under animal care Permit A11-0397.

Each dive trial consisted of a bout of four, 3-minute dives with 1-minute inter-dive surface intervals. Each bout was preceded by a pre-dive resting metabolic rate (RMRpre) measurement. This was quantified as the last 3 min of a 5–8 minute measurement period, when $\dot{V}_{O_2}$ was constant. The diving bout was then followed by a recovery period (4–5 min) and post-dive resting metabolic rate measurement (RMRpost); taken as the lowest 3 minute average of a 4–5 minute period after $\dot{V}_{O_2}$ returned to pre-dive levels and remained constant.

The animals were trained to dive between a small (100 L) respirometry dome floating at the surface and two feeding tubes (~9 m apart) set at a depth of 40 m. Herring pieces (~20 g) were alternately pumped to the bottom of these tubes to create a prey patch at depth and simulate a foraging dive by having the sea lion travel continuously between the two tubes. The rates of O_2 consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were measured using flow through respirometry, as detailed in Gerlinsky et al. (2013). Briefly, air was drawn through the dome at a rate of 475 L min^{-1} by a 500H mass flow generator and controller (Sable Systems Inc., Las Vegas, NV, USA), and a dried subsample of excurrrent air was analyzed for oxygen and carbon dioxide concentrations using Sable System FC-1B and CA-1B analyzers, respectively. Changes in oxygen and carbon dioxide concentrations were recorded every 0.5 s in relation to ambient air. Metabolic data was analyzed using Lab Analyst X (Warthog Systems, University of California) and rates of oxygen consumption were calculated using Eqs. (11.7) and (11.8) in Lighton (2008).

Diving metabolic rate was calculated two ways. DMRdive was calculated by dividing all excess oxygen consumed above resting $\dot{V}_{O_2}$ during the post-dive recovery period and inter-dive surface intervals, by total dive duration. DMRcycle represents the average rate of oxygen consumption over the entire dive bout (on the assumption that it is a complete physiological event) and was calculated as the average $\dot{V}_{O_2}$ over the four dives, three surface intervals and recovery period.

Activity levels while diving and at the surface was quantified by calculating overall dynamic body acceleration (ODBA, following methods in Wilson et al., 2006) using data from a 3-d accelerometer (USB Accelerometer, X6-2mini, Gulf Coast Data Concepts, Waveland, MS, USA) attached to a custom-built harness worn by the sea lions. The purpose of the ODBA measurements was to test for differences in activity levels between trial types.

2.2. Statistical analysis

All data was analyzed using R software (R Development Core Team, 2011). Data from each animal were treated as repeated measures by including animal ID as a random effect, using linear mixed-effects models (lme) from the nlme package. Trial type and digestion time were also tested as potential fixed effects, with body mass as a covariate. Nested models (with or without a fixed effect) were compared using a log likelihood ratio test to determine the best overall model (including the null model with no fixed effects) to fit the data (Pinheiro and Bates, 2009). Final models were then run using restricted maximum likelihood. Values are reported as means (± s.d.) and significance was set at $\alpha = 0.05$. Metabolic rates were tested as absolute values and when scaled to body mass ($M_b^{-1.0}$).

Table 1
Average increase in rates of oxygen consumption following a 3 kg meal as compared to fasted trials. Data are presented for resting metabolic rate prior to (RMRpre) and following (RMRpost) a dive bout, as well as diving metabolic rate calculated over the entire dive cycle (DMRcycle), as well as just over the submerged portion of the bout (DMRdive). Mean body mass, number of trials and mean digestion time (between 3 kg meal and beginning of the dives) are also presented.

Animal	Mass (kg)	No. trials		Average increase in MR when pre-fed (ml O_2 min^{-1})				Mean digestion time (min ± s.d.)
		Fasted	Fed	RMRpre	RMRpost	DMRcycle	DMRdive	
F97BO	143.7	4	5	233	228	114	62	83 (2.7)
F93HA	170.2	5	4	288	231	144	87	84 (9.9)
F97YA	207.3	5	4	342	235	210	243	83 (2.5)
F93SI	222.4	5	4	295	305	206	144	76 (6.2)

3. Results

All dive bouts consisted of 4 dives (3.01 ± 0.25 min) and 3 surface intervals (1.01 ± 0.05 min) followed by a post-dive recovery period. As per experimental design, average dive and inter-dive surface durations were the same for both fasted and pre-fed trials. Average digestion time for feeding trials (from end of meal to start of trials) was 81.4 ± 6.1 min (range 68–95 min), and neither RMR (resting at the surface) nor either measure of DMR varied with digestion time (Table 1). Both pre-dive RMR ($p < 0.001$) and post-dive RMR ($p < 0.001$) were higher in pre-fed versus fasted trials (Fig. 1). Diving metabolic rate was also higher during the pre-fed trials, whether calculated as DMRdive ($p = 0.013$) or DMRcycle ($p < 0.001$; Fig. 2). The same results were seen when RMR, DMRdive and DMRcycle were scaled to body mass. There were no changes in ODBA between trial types, whether averaged over the bout, cycle (with recovery) or just the dive portion, suggesting that foraging activity did not change between trial types.

Although both the pre- and post-dive surface metabolism and diving metabolism were greater during the pre-fed trials, the extent of the effect differed; there was a greater increase in RMR due to feeding compared to the increase observed in DMR. Pre-dive RMR increased on average by 289 ml O_2 min^{-1} (16.7 ± 2.5%) and post-dive RMR by 250 ml O_2 min^{-1} (13.6 ± 1.1%). DMRcycle (which included post-dive recovery) increased on average by 168 ml O_2 min^{-1} (6.4 ± 0.8%) and DMRdive increased the least, by 133 ml O_2 min^{-1} (4.1 ± 1.9%) (Table 1).

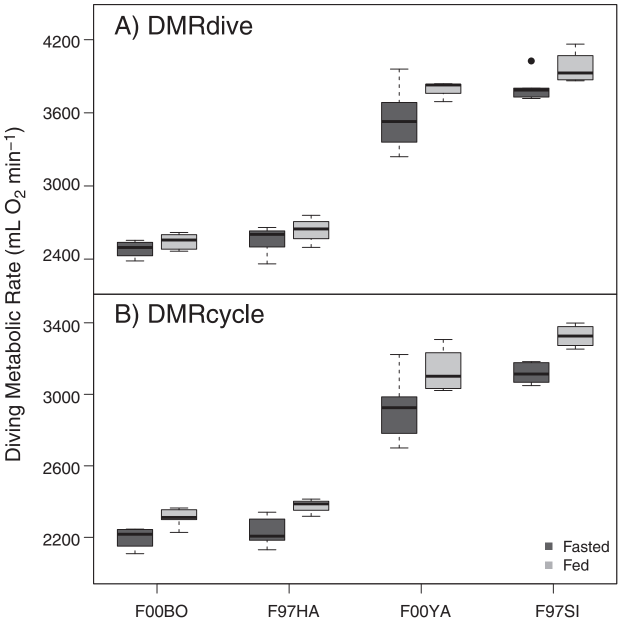

Fig. 2. Effect of meal ingestion on diving metabolic rate of sea lions. Diving metabolic rate (mL O_2 min^{-1}) of four Steller sea lions, A: measured over the dive only and, B: averaged over the dive and recovery cycle when fasted and following a 3 kg meal. DMR was significantly higher in pre-fed (lt. gray) than in fasted (dk. gray) trials.

4. Discussion

Air-breathing vertebrates such as marine mammals face unique physiological challenges when diving for prey. The most fundamental is the limitation placed on their ability to dive aerobically during a single foraging episode by their on-board oxygen reserves. Considerable research has been undertaken on understanding the physiological, anatomical, and behavioral adaptations that diving mammals use to maximize their potential bottom time. Some have suggested that their resulting strategies can be viewed as a modified optimal foraging model (Carbone and Houstin, 1996; Halsey et al., 2003; Hindell, 2008; Mori, 1999; Thompson and Fedak, 2001). Despite this interest, relatively little experimental work has been undertaken to clarify the potential conflict between the physiological requirements for foraging and digestion (Rosen et al., 2007; Sparling et al., 2007a).

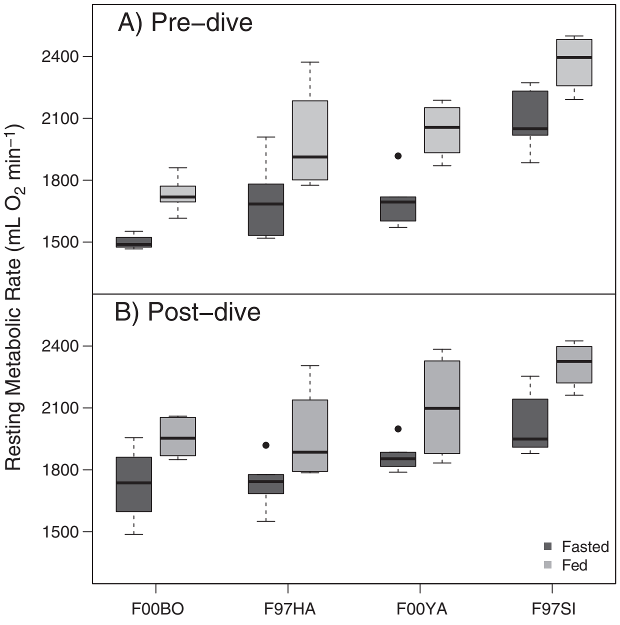

Fig. 1. Effect of meal ingestion on metabolism of sea lions resting at the surface. A: Pre- and B: post-dive resting metabolic rate (mL O_2 min^{-1}) of four Steller sea lions when fasted and following a 3 kg meal. RMR was significantly higher in pre-fed (lt. gray) than in fasted (dk. gray) trials.

One possible solution to the potential problems of incompatible circulatory demands and increased foraging costs is to rely upon a temporal and physiological disjunction between foraging and digestive activities. For example, animals can concentrate solely on prey capture until their immediate gut capacity has been reached, after which they are forced to rest while digesting, rather than continue foraging (Crocker et al., 1997). Drift dives in seals, characterized by episodes of languid, non-powered ascents or descents (Biuw et al., 2003; Crocker et al., 1997) have been hypothesized to function as a period of inter-foraging digestion (as well as an opportunity to purge metabolic waste; Crocker et al., 1997). However, most marine mammals do not undergo such intense, isolated foraging bouts, and there is evidence from other mammals that fragmented foraging periods may increase maximum intake levels (Zynel and Wunder, 2002).

The sea lions in our study displayed a significant reduction in the apparent additive effect of digestion during diving. The HIF, as measured by the differences in pre-dive metabolic rates between fasted and pre-fed states, was 289 ml O_2 min^{-1}. In comparison, the average difference in oxygen consumption rates between fasted and pre-fed animals when diving was only 133 ml O_2 min^{-1}. The lack of differences in ODBA during dives between pre-fed and fasted individuals confirms that this difference in metabolism was not due to changes in behavior; e.g.; fed individuals were not more lethargic when diving. These differences in measured metabolism suggest a 54% decrease in the apparent effect of digestion during diving. Immediately following a dive, there was a rapid, almost complete return to pre-dive levels of metabolism, with the measured cost of digestion reaching 250 ml O_2 min^{-1}. These results suggest a significant, but incomplete suspension of digestive processes during voluntary dives of a duration and depth that are typical of the majority of foraging dives observed in the wild (Loughlin et al., 2003).

It is important to remember that balancing competing circulatory demands are a normal part of a pinniped's diving physiology. There are three responses associated with the classic "dive response": apnea, bradycardia, and peripheral vasoconstriction (Scholander, 1940). Many studies have examined the potential clash between the increased blood flow and oxygen use associated with exercise in terrestrial mammals and the peripheral vasoconstriction associated with maximizing bottom time in diving mammals (e.g., Castellini et al., 1985; Davis and Williams, 2012; Williams et al., 1999). Although bradycardia can be thought of as a secondary response — it functions to maintain reasonable blood pressure in the face of vasoconstriction — it can serve as a readily measurable indicator of systemic changes in blood flow. In other words, the hypothesized changes in circulation that are postulated to account for the observed decreases in the HIF effect during diving should be matched by parallel decreases in heart rate.

While heart rate was not measured in the current study, past research with some of the same captive animals has shown that the mean heart rate of Steller sea lions trained to voluntarily dive to depths up to 40 m dropped by 40% while diving, and minimum instantaneous heart rate decreased consistently with dive duration (Hindle et al., 2010). These results suggest that Steller sea lions diving voluntarily to depth exhibit the type of bradycardia and vasoconstriction that has been directly demonstrated in freely diving phocid seals (e.g., Cherepanova et al., 1993; Hindell and Lea, 1998; Murphy et al., 1980; Ponganis et al., 1997). These circulatory changes should be associated with decreased digestion.

Less intense drops in mean heart rate have been seen in Steller sea lions performing shallower dives (Hindle et al., 2010), suggesting that deferment of digestion may not be dramatic in these types of foraging dives. This agrees with results from gray seals that found decreasing dive times and increased effect of digestive costs during short, "shallow" foraging dives, and an almost complete deferment of the metabolic effects of digestion on diving metabolism or behavior during simulated "deep-water" foraging (Sparling et al., 2007a). Previous work with the same sea lions used in the present study has also demonstrated that the cost of diving decreases with dive duration (Fahlman et al., 2008), facilitated by increased bradycardia (Hindle et al., 2010).

The experimental protocol of the current study kept dive times and interdive surface intervals constant between treatment conditions in order to eliminate any potential confounding effects of digestive state on dive cost through changes in dive behavior. However, there are several reasons to believe that digestive state can affect diving patterns. First, there is likely a link between increasing satiation and decreased dive times due to diminishing motivation for food acquisition. Second, if past foraging success results in an increase in diving metabolic rate, it will effectively decrease aerobic dive limit. The aerobic dive limit of these same Steller sea lions has been calculated to be 2.5–3.0 min, depending on dive type (Gerlinsky et al., 2013). A 4–6% increase in DMR would, in theory, decrease ADL by a similar amount resulting in a slight shortening (~8–10 s) of each dive (with concurrent minor decreases in effective foraging efficiency). Alternately, if dive times stay constant, the increased metabolism due to digestive costs could make each dive more anaerobic, requiring proportionally increasing post-dive surface recovery times. This post-dive recovery could be extended even further due to the higher apparent post-dive resting metabolic rates that might serve to decrease aerobic recovery. Such a response would likely have a greater impact on overall foraging efficiency than compensatory changes in dive behavior resulting from decreases in ADL.

5. Conclusions

Overall, the results of the present study demonstrate a partial deferment of digestion while actively foraging. This study suggests that the classically held view that digestion and diving are incompatible processes may be much more variable than previously thought. It further suggests that otariids could have a range of possible digestive states while diving depending on behavior; short, shallow dives may allow them to continue digesting while maintaining a higher foraging rate or they may be capable of delaying digestion if deeper, longer dives increase foraging success. The lack of a complete "switch" to a classic diving state with its inherent restrictions in circulation appears to be one more example of plasticity in the physiological response of otariids to competing demands while diving.

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