

Effects of increased swimming costs on foraging behavior and efficiency of captive Steller sea lions: Evidence for behavioral plasticity in the recovery phase of dives

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Abstract

A significant component of foraging energetics is the cost of locomotion, which for marine animals, is the cost of swimming. Increases in the cost of swimming may have significant impacts on foraging efficiency. Minimizing the cost of swimming can contribute to the optimization of foraging strategies by reducing the energetic cost of foraging. Results of several field studies suggest that an increase in the cost of locomotion may have comparable effects on foraging behavior and efficiency to a decrease in prey availability. We tested the hypothesis that an increased cost of swimming, brought on by increased hydrodynamic drag, has the same effect on dive behavior and efficiency as reduced prey availability under standard locomotion. Experiments were performed using two adult female Steller sea lions at the Alaska SeaLife Center in Seward, AK, using the same animals and general experimental design previously used to test the effects of reduced prey encounter rate on dive behavior and efficiency. Animals were fitted with a drag-inducing harness for half of the 500 simulated foraging dives in order to increase the cost of swimming. Individual dive duration and foraging time were significantly reduced in all cost-increased dives, comparable to the effects of reduced prey encounter rate. However, on a bout-by-bout basis, dive and foraging efficiency were only slightly reduced, which is likely due to an average 50% reduction in post-dive surface recovery duration during cost-increased dives. Increased heat flux across the body surface measured in a parallel study confirmed a significant increase in work during drag-increased dives. These results suggest that sea lions are able to compensate for changes in the cost of foraging and maintain their foraging efficiency by altering their dive strategy over an entire bout of dives when operating well within their aerobic scope.

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1. Introduction

A significant component of foraging energetics is the cost of locomotion, which for marine animals, is the cost of swimming. Marine mammals have evolved a number

of adaptations that minimize the cost of swimming, including a fusiform body shape, minimization of body contouring aided by sub-cutaneous blubber, and in some species, reduction or loss of hair (Pabst et al., 1999). Behavioral adaptations allow a further reduction in the cost of swimming. Such adjustments include avoiding higher swimming speeds with exponentially increasing drag by swimming near minimum cost of transport

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(MCT) speeds ($\sim 1.0\text{--}3.6\text{ m s}^{-1}$). Typical swim speeds are often near the lower end of this range (Ponganis et al., 1990; Thompson et al., 1993; Williams et al., 1993; Boyd et al., 1995; Hindell and Lea, 1998; Hindell et al., 2000; Crocker et al., 2001; Rosen and Trites, 2002). The use of different swimming modes during periods of exercise (i.e., foraging, traveling), such as wave-riding (Williams et al., 1992), porpoising (Au and Weihs, 1980), and burst-and-glide locomotion and prolonged gliding on deep dive descents (Costa and Gales, 2000; Williams et al., 2000; Williams, 2001) also facilitate reduced costs of foraging (Skrovan et al., 1999; Sato et al., 2003; Williams et al., 2004). As a result, short dives often require as little as 1.5 times the energy as sleeping (Castellini et al., 1992; Castellini and Castellini, 2004; Williams et al., 2004). Minimizing the cost of swimming by exploiting behavioral plasticity can contribute to the optimization of foraging strategies. These behavioral adjustments are especially critical for breath-hold diving animals, as increased exercise costs result in more rapid depletion of oxygen reserves (Skrovan et al., 1999; Sato et al., 2003), and thus reduced aerobic dive durations.

Increases in the cost of swimming, such as those resulting from loss of fusiform shape due to extreme loss of fat reserves (i.e., animals under nutritional stress), injury or the attachment of large instrumentation, can have significant impacts on the overall cost of foraging, and thus foraging efficiency. Increasing or decreasing swimming speed outside of the MCT range and increases in hydrodynamic drag have all been shown to increase the cost of transport (Feldkamp, 1987; Boyd et al., 1997; Hind and Gurney, 1997; McCafferty et al., 1998). Gentry et al. (1986) showed that increased drag created by telemetry devices resulted in significant changes in foraging trip durations of several species of fur seals. Boyd et al. (1997) developed this effect into an experimental design and demonstrated that increasing the cost of swimming through the addition of a drag-producing device produced significant changes in foraging behavior in female Antarctic fur seals (*Arctocephalus gazella*, Peters). Females with higher profile instruments made shorter, shallower dives, had a higher dive frequency, and made a greater number of total dives than those with smaller instruments. McCafferty et al. (1998) observed that in years of reduced krill abundance, females of the same species exhibited a similar response to that of the increased drag (Boyd et al., 1997), increasing their foraging effort in order to maintain foraging efficiency and match pup demand, suggesting that the effects of drag increases may be comparable to those of reduced prey abundance. Horning and Trillmich (1999) revealed that juvenile Galapagos fur seals (*A. galapagoensis*, Heller)

likely had reduced foraging efficiency during full moon periods when vertically migrating prey remained at greater depths, thus requiring a greater up-front cost of foraging.

The results of these studies suggest that an increase in the cost of locomotion may have comparable effects on foraging efficiency to reduced prey availability. Results from a preliminary series of cost-increased dives during optimal foraging experiments with captive Steller sea lions (*Eumetopias jubatus*, Schreber) suggested reduced dive durations and foraging times during 45 cost-increased dives, providing preliminary support for this hypothesis (Cornick and Horning, 2003). In this study, we specifically test the hypothesis that an increased cost of locomotion has the same effect on dive behavior and foraging efficiency as a reduced prey encounter rate under standard locomotion. These experiments seek to further validate the use of locomotor cost manipulation as an experimental approach, and examine the validity of testing responses of free-ranging animals to reductions in prey availability by monitoring their responses to cost manipulations.

2. Materials and methods

Simulated foraging sessions were conducted using two adult (9 years, 198 ± 0.69 and 188 ± 0.43 kg) female Steller sea lions at the Alaska SeaLife Center in Seward, AK from June to August 2002. The same animals and general experimental design described in detail in Cornick and Horning (2003) were used in the present study. Each animal was fitted with a swim speed indicator (Ultramarine Instruments, Galveston TX). Three ABS plastic fish feeder tubes with remotely controlled light targets and trap door releases were mounted on the observation glass at the top of the sea lion enclosure. Four real-time video cameras were mounted around the enclosure, one recording each feeder opening and one recording at the water's surface. Lit targets cued the sea lions to swim between feeders for simulated dive descent phases during which no prey items were released, and subsequent foraging phases with prey item releases timed to simulate a range of prey encounter rates. Sixty experimental sessions (37 standard locomotion, 23 cost-increased) were conducted, resulting in 270 standard locomotion dives and 230 cost-increased dives. Prey encounter rates ranged from 0–7 fish/dive cycle (dive duration + post-dive surface interval). Each session of multiple dives was assumed to be comparable to the typical series of foraging dives, or dive bout, observed in free-ranging sea lions. Dives were terminated voluntarily by the animal.

For cost-increased dives, sea lions were fitted with a drag-inducing harness constructed of nylon strapping secured by buckles on two girth straps and two length straps (Fig. 1). The external surfaces of the strapping material were covered with plastic sheeting similar to Astroturf™, which disrupted the boundary layer of water across the body surface, thereby increasing hydrodynamic drag, and subsequently the cost of locomotion. In order to determine the magnitude of the cost increase produced by the harness, passive drag coefficients were calculated during a series of 30 glides performed by both animals with and without the harness. The animals were trained to stroke once and glide in a straight line at constant depth across a pool. Underwater and overhead video cameras were positioned to record the complete glide phase. Video analysis on the glides was conducted using ImageExpress® software (Sensors Applications Inc., v. 5.5R).

Dive duration, foraging time, dive efficiency (foraging time per dive cycle), foraging efficiency (mass of fish (g) ingested per dive cycle), and post-dive surface interval duration were calculated from the videotape time stamp data for each standard and cost-increased dive. Dive efficiency (foraging time per dive cycle) and foraging efficiency (catch-per-unit-effort in g fish per dive cycle) were also calculated for each session/bout. Stroke frequency (strokes/min) was calculated from video data for each dive by counting the number of strokes per dive and dividing by the dive duration. Mean swim speed (m s^{-1}) was measured during each bout using a flow-

through swim speed data logger (Ultramarine Instruments, Galveston, TX) with a resolution of 0.05 m s^{-1} .

In order to determine the overall effect of increased cost of swimming on foraging behavior and efficiency, mean values between standard and cost-increased dives and bouts were compared for each variable across all prey encounter rates using one-way Analysis of Variance (ANOVA). Significance was set at $p < 0.05$. In order to examine the combined effects of the cost of locomotion and prey encounter rate, means for each variable were then calculated at each prey encounter rate on a dive-by-dive and bout-by-bout basis for both standard and cost-increased dives. These values were then regressed on prey encounter rate using forward stepwise polynomial regression (Cornick and Horning, 2003) in order to determine the best-fit (highest adjusted R^2) functional response curve (Manly and Jamieson, 1999). Slopes were compared between standard and cost-increased dives using Student's t -test (Zar, 1999).

Heat flux (W m^{-2}) between the animal's skin surface and water was measured for a concurrent study using heat flux sensors (Thermonetics Corporation, San Diego, CA) during 11 experimental sessions, 5 of which included the drag harness (Willis et al., 2005). Methods for collection and analysis of heat flux measurements are described in detail in Willis et al. (2005). Sensors were placed against a small (3 cm diameter) area of shaved skin just prior to experimental foraging sessions at 4 locations (shoulders, axillary girth, mid-girth, hips) along the body of 1 female sea lion using custom-

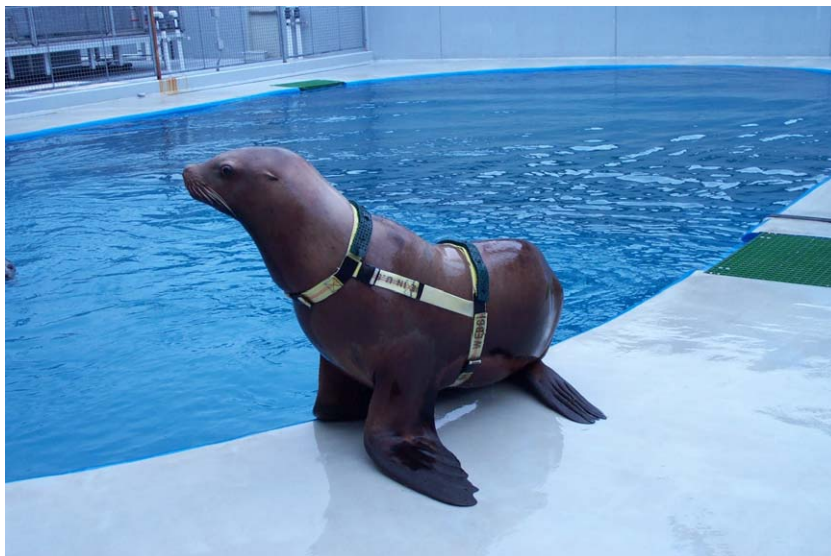


Fig. 1. Sea lion with drag harness showing location of girth straps with drag-increasing material. Swim speed indicator unit was glued directly to the dorsal fur of the animal using epoxy, and was located behind the anterior girth strap. Heat flux sensors were placed at the shoulders, axillary girth, mid-girth and hips (Willis and Horning, 2005). Photo courtesy of Alaska SeaLife Center.

designed sensor holders (Willis and Horning, 2005), which facilitated firm contact between the sensors and the skin throughout each session. Sensor holders were glued to the fur surrounding the shaved area. In the present study, heat flux was used as a proxy for metabolic heat production, in order to confirm an increased work load for cost-increased versus standard dives.

3. Results

Results of the ANOVA are summarized in Table 1. All values are reported as mean±SE. On a dive-by-dive basis, mean dive duration, foraging time, surface interval duration, dive efficiency, and foraging efficiency were all significantly reduced during cost-increased dives. Over bouts of dives, mean dive efficiency was significantly reduced with increased cost of swimming. In contrast, mean foraging efficiency during cost-increased bouts was slightly lower than that of standard locomotion bouts, but the effect was not significant (Table 1). Stroke frequency was significantly higher and swim speed was significantly reduced during cost-increased versus standard dives. Metabolic heat production was significantly greater during cost-increased dives, as indicated by a significant increase in heat flux across all locations (Willis et al., 2005).

All of the dive behavior and efficiency variables as a function of prey encounter rate produced Type II

functional response curves (Holling, 1959; Stephens and Krebs, 1986) in both standard and cost-increased dives (Fig. 2a–f). Dive duration ($t_8=3.31, p<.05$) and foraging time ($t_8=3.55, p<.05$) decelerated at a greater rate in cost-increased dives (Fig. 2a–b). There were no significant differences in the slope of functional response curves for dive efficiency and foraging efficiency on either a dive-by-dive or bout-by-bout basis (Fig. 2c–f). There was also no relationship between surface interval duration and prey encounter rate. Surface interval durations were constant across all prey encounter rates within each locomotor cost (standard versus cost-increased).

Underwater video analysis revealed that the harness induced early boundary layer separation, significantly increasing the hydrodynamic drag imposed on the animal (ANOVA, $F_{2,5}=3.53, p<0.001$). The harness produced a hydrodynamic drag augmentation of $23\pm 1.06\%$.

4. Discussion

Mean passive drag coefficients for Steller sea lions (0.0056, Stelle et al., 2000) are not substantially higher than the theoretical values for a streamlined body. Therefore, any increase in drag is likely to create a substantial increase in the work performed during swimming at comparable speeds in order to overcome this force. The cost of transport is further increased if swimming speed is reduced in response to the added drag (Feldkamp, 1987; Culik and Wilson, 1994). During cost-increased dives, both sea lions had significantly reduced swim speed (Table 1), despite an attendant increase in stroke frequency (Table 1). This suggests a substantial increase in the cost of transport between standard and cost-increased dives. It should be noted that the range of swim speeds in this study ($\sim 1\text{--}1.3\text{ ms}^{-1}$) are slightly below values reported as minimum cost of transport for Steller sea lions ($1.7\text{--}3.6\text{ ms}^{-1}$; Stelle et al., 2000; Rosen and Trites, 2002). This is likely due to the shorter swimming distances between the feeders in the captive environment relative to a natural environment, as well as the lack of live prey which would require active pursuit.

The relationship between stroke frequency and locomotor cost has also been demonstrated in free-ranging Weddell seals, which exhibited a linear increase in total oxygen consumption ($\text{ml O}_2\text{ kg}^{-1}$) and locomotor costs with an increase in the total number of strokes per dive (Williams et al., 2004). When this relationship is extrapolated to a point of 0 strokes, oxygen consumption is that predicted by the Kleiber (1975) relationship for BMR as a function of body mass (Williams et al., 2004), indicating the substantial energy savings associated with minimizing the number of strokes in a dive. In this study,

Table 1
Results of one-way ANOVA

	Standard mean±SE (n)	Cost-increased mean±SE (n)	p
Dive duration (s)	42.88±1.10 (270)	33.83±0.88 (230)	<0.001
Foraging time (s)	29.91±1.13 (266)	19.73±0.99 (228)	<0.001
Surface interval (s)	4.44±0.24 (233)	2.65±0.16 (207)	<0.001
Dive efficiency (FT/DC)	0.567±0.015 (229)	0.479±0.018 (205)	<0.001
Foraging efficiency (CPUE/DC)	12.85±0.42 (233)	10.86±0.40 (207)	0.001
Dive efficiency– bout	0.628±0.020 (37)	0.550±0.03 (23)	0.026
Foraging efficiency– bout	13.59±0.74 (37)	11.71±0.92 (23)	0.120 (NS)
Stroke frequency (strokes/min)	0.29±0.01 (136)	0.38±0.01 (229)	<0.001
Swim speed (m/s)–bout	1.3±0.02 (34)	1.0±0.01 (19)	0.004

Mean values for each variable compared between standard and cost-increased dives across all prey encounter rates.

Values reported are mean±SE, n=number of samples per analysis. p=significance at $\alpha<0.05$, NS=not significant. Dive efficiency is defined as foraging time (FT) per dive cycle (DC). Foraging efficiency is defined as catch-per-unit-effort (CPUE) in mass of fish (g) per DC.

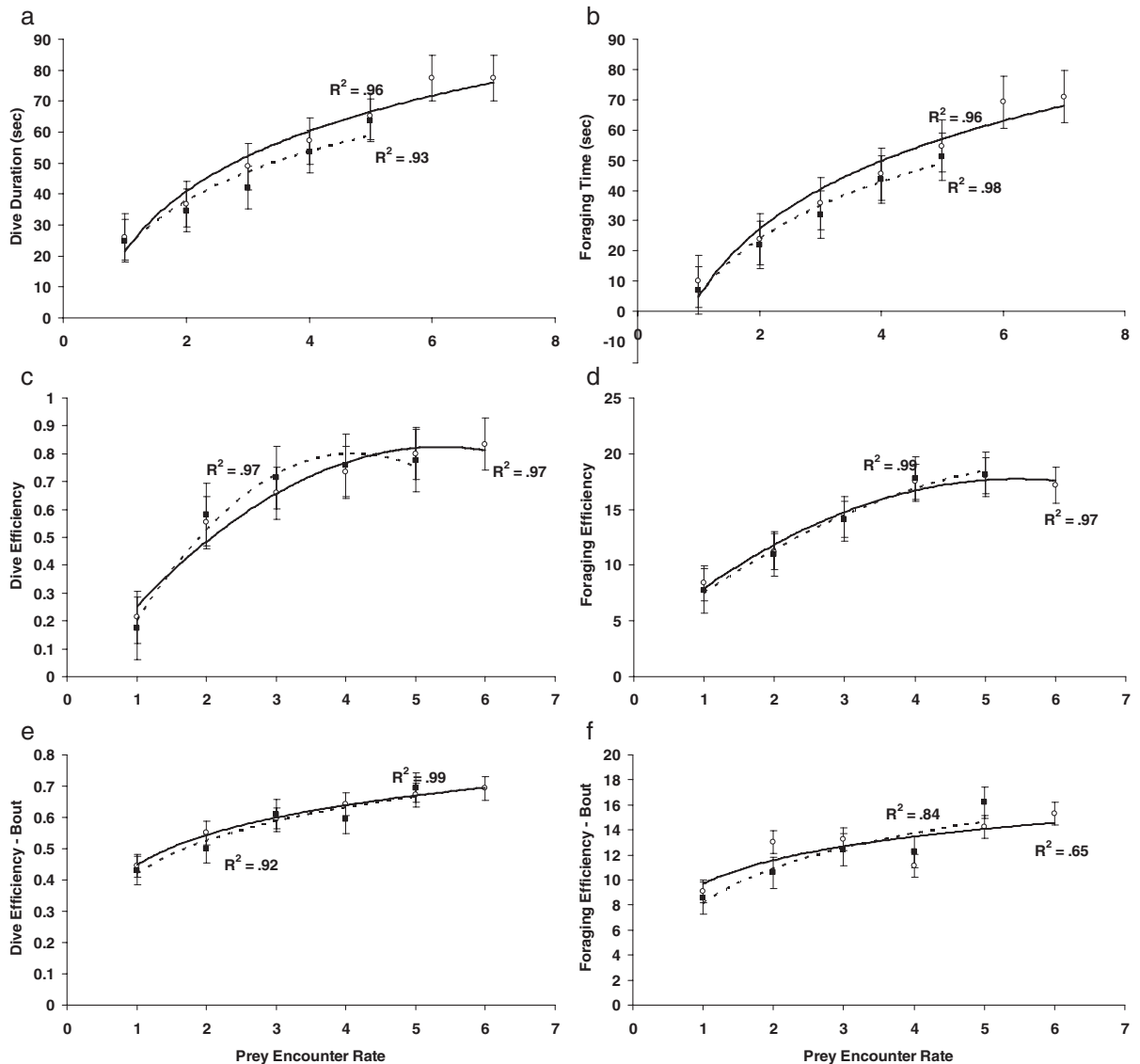


Fig. 2. Functional response curves for dive-by-dive and bout-by-bout dive behavior and efficiency as a function of prey encounter rate (fish/dive cycle). Solid lines represent standard locomotion and dotted lines represent cost-increased locomotion. Error bars represent 1 SE of the mean. (a) Mean dive duration, dive-by-dive. Standard: $R^2=0.96$; cost-increased: $R^2=0.93$. (b) Mean foraging time, dive-by-dive. Standard: $R^2=0.96$; cost-increased: $R^2=0.98$. (c) Mean dive efficiency, dive-by-dive. Standard: $R^2=0.97$; cost-increased: $R^2=0.97$. (d) Mean foraging efficiency, dive-by-dive. Standard: $R^2=0.97$; cost-increased: $R^2=0.99$. (e) Mean dive efficiency, bout-by-bout. Standard: $R^2=0.99$; cost-increased: $R^2=0.92$. (f) Mean foraging efficiency, bout-by-bout. Standard: $R^2=0.65$; cost-increased: $R^2=0.84$.

sea lions employed burst-and-glide locomotion during standard dives, but exhibited nearly constant stroking in cost-increased dives, suggesting that the power required to overcome the effects of the increased drag inhibited their ability to minimize the costs associated with propulsion by minimizing the number of strokes.

Increased heat flux across all measured locations on the body during cost-increased dives (Willis et al., 2005) further supports the conclusion that the changes in dive behavior during cost-increased versus standard dives

were a result of adjustments to increased work, and a concomitant increase in metabolic heat production, rather than an adverse behavioral effect from the presence of the harness itself. These results also support the contention that the costs of propulsion and thermoregulation in a swimming homeotherm are functionally linked (Hind and Gurney, 1997).

Mean dive duration, foraging time, dive efficiency, and foraging efficiency were all significantly reduced on a dive-by-dive basis during cost-increased dives (Table 1).

These values were all similarly reduced for lower prey encounter rates in previous experiments examining the effects of reduced prey availability on dive behavior and efficiency (Cornick and Horning, 2003). In that study, dive-by-dive foraging time and dive efficiency were also reduced with increased search time, which could be interpreted as an increased cost. These combined results support the primary hypothesis that an increased cost of locomotion while foraging has the same fundamental effect on dive behavior and efficiency as reduced prey availability. For example, increased swimming effort may be required to capture prey in lower density patches, resulting in a higher cost per unit energy gained during the dive.

Over an entire bout of dives, however, animals were largely able to maintain foraging efficiency even as the cost of locomotion increased. Because cost-increased dives were terminated earlier than standard locomotion dives at the same prey encounter rate, maintaining foraging efficiency across a bout of dives necessitates some means of compensation for changes in dive duration and foraging time in order to consume a comparable amount of prey in the face of increased work. Diving mammals may have a number of physiological and behavioral choices available to them in order to compensate for increased foraging costs related to environmental or energetic factors. Recent data from New Zealand sea lions suggest a region of metabolic compensation (e.g., increased metabolic suppression) in the face of increasing environmental perturbation that may not result in observable changes in typically measured behavioral variables, such as foraging trip duration (Costa, 2004). In this study, we suggest this compensation may come from an approximate 50% reduction in the post-dive surface recovery period (Fig. 3). This implies that, even in the recovery phase of the dive, there is a substantial amount of plasticity in behavior when the animal is operating well within its aerobic capacity.

Assuming that the duration of the surface interval is largely driven by physiological constraints, how is this much flexibility manageable over a bout of dives? Physiological measurements taken during the surface interval (e.g., end-tidal PO_2 and PCO_2) have primarily been used to examine the physiology of the dive phase (i.e., as a measure of oxygen consumption rates (Kooyman et al., 1973; Kooyman et al., 1980; Castellini, 1991; Williams et al., 1993; Burns and Castellini, 1996; Butler and Jones, 1997). Questions remain about the physiological cues that drive the recovery period itself. Data from grey seals (*Halichoerus grypus*, Fabricius) and harbor porpoise (*Phocoena phocoena*, Linnaeus) suggest that the assumption that surface recovery is driven by oxygen depletion

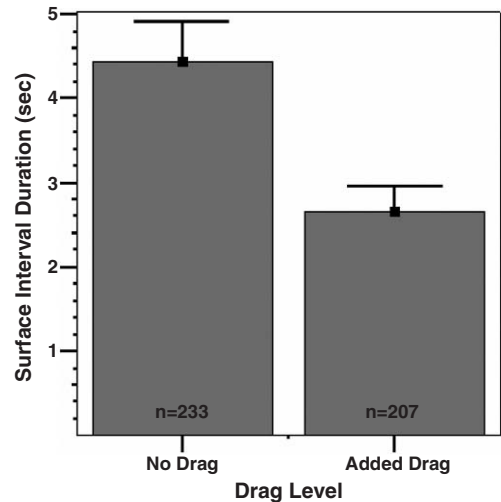


Fig. 3. Surface interval duration (mean \pm SE) during standard (4.44 ± 0.24) and cost-increased (2.65 ± 0.16) dives across all prey encounter rates.

may be imperfect (Reed et al., 1994; Reed et al., 2000; Boutilier et al., 2001). Their data show that the reoxygenation phase is completed within the first 1–2 respirations ($\sim 25\%$ of the surface interval duration), while the remainder of the recovery period is devoted to purging CO_2 (Boutilier et al., 2001). This is likely a result of the high buffering capacity of marine mammal blood (Boutilier et al., 1992), as well as their higher tolerance for metabolic byproducts, such as lactate. These adaptations allow the animals to suspend their recovery period as soon as they have replenished O_2 stores, continue diving, and process any residual byproducts during longer surface intervals following an entire dive bout. This has also been demonstrated in Weddell seals (*Leptonychotes weddellii*, Lesson), which continue processing high concentrations of lactate after an anaerobic dive during a subsequent series of aerobic dives (Castellini et al., 1988). When dives are well within the aerobic dive limit (ADL, Kooyman et al., 1980), as in this study, shortening the recovery phase of the dive is an easy, cost-effective means of adding to the total foraging time in a bout, simply because during aerobic diving they are not having to manage accumulation of lactate, and need only to buffer any accumulated CO_2 . Understanding how these animals manage the byproducts of breath-hold diving is a question that needs to be addressed experimentally in order to gain a complete picture of how they exploit their physiological adaptations as part of an optimal foraging strategy, particularly during the post-dive recovery. For example, we did not detect any trends in surface interval duration over the course of a bout, which might suggest increasing CO_2 loads. Unfortunately we were not able to measure post-

bout recovery periods in this study because the animals were removed from the enclosure after each session for feeder removal.

When dive behavior and efficiency are examined as a function of prey encounter rate for both standard and cost-increased dives, the importance of ecological, rather than physiological, constraints becomes apparent. On a dive-by-dive and bout-by-bout basis dive effort and efficiency increase as prey encounter rate increases, and the minor reduction in mean foraging efficiency is no longer evident (Fig. 2). These results are also comparable to the previous optimal foraging experiments conducted with the same animals, providing further support to the hypothesis that foraging effort should increase with increasing prey encounter rates (Cornick and Horning, 2003). When prey encounter rate is very low (< 3 fish per dive), dives are abandoned early regardless of the cost of locomotion (Fig. 2a). This suggests that the low potential energy gain rate of these dives overrides the need to overcome the increased cost of locomotion. In other words, at very low prey encounter rates, it is not worth continuing the dive even when locomotor costs are at 'normal' levels. Additionally, foraging efficiency begins to decelerate at prey encounter rates of approximately 5–6 fish per dive cycle (Fig. 2d,f), which supports Cornick and Horning's (2003) third hypothesis: that there should be a maximum threshold prey encounter rate at which efficiency is optimized, such that further dive effort does not increase energetic gain. These results are consistent with Thompson and Fedak's (2001) model of foraging for seals in a patchy environment, which predicts shorter dive durations at the lowest prey encounter rates.

On a dive-by-dive basis, dive duration and foraging time decelerate at a significantly greater rate during cost-increased dives as prey encounter rate increases, reflecting the increased cost of locomotion (Fig. 2a–b). However, across prey encounter rates dive efficiency and foraging efficiency are comparable between standard and cost-increased dives, both within individual dives (Fig. 2c–d) and across bouts (Fig. 2d–e). This not only reflects the animals' ability to compensate for the increased work required by the increased locomotor costs, but also illustrates that foraging strategy is more sensitive to changes in prey availability than to changes in the cost of locomotion when the animal is working within its physiological constraints (i.e., within the ADL). These results are comparable to field studies of Antarctic fur seal females, which compensated for changes in prey availability by increasing effort in order to meet the energetic demands of lactation, even when fitted with high-profile data loggers and in years of reduced krill abundance (McCafferty et al., 1998).

An understanding of how marine apex predators are able to meet their energetic demands by adjusting their foraging strategy in the face of increased foraging costs, whether in the form of reduced prey availability or increased metabolic costs, is critical to our ability to predict the effects of natural and anthropogenic changes in the distribution, abundance, and community structure of their prey suite. This is particularly important for threatened and endangered species, whose ability to adapt to these changes may be a determining factor in their survival. These results provide additional validation of the use of locomotor cost manipulation as an experimental approach to examine the effects of differential foraging costs on behavior and efficiency. By further elucidating the functional relationships between prey availability, the cost of swimming, and dive behavior and efficiency, this study also suggests that the responses of free-ranging animals to reductions in prey availability may be indirectly examined by monitoring their responses to cost manipulations, and provides additional data to inform the continued improvement of models of the complex interplay between the physiological and behavioral ecology of foraging in diving mammals.

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