

A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach

Leslie A. Cornick and Markus Horning

Abstract: The response of marine predators to changes in fine-scale prey distribution is poorly understood. Precipitous declines in marine apex predators necessitate a better understanding of the magnitude of fluctuations in prey availability that are within the compensatory behavioural plasticity of predators. We experimentally manipulated the fine-scale prey field for a marine carnivore in a controlled, captive setting and examined changes in behaviour and efficiency with changes in prey encounter rate. We hypothesized (i) a minimum prey encounter rate below which the cost of foraging always exceeds the benefit, (ii) foraging effort should increase with increasing prey encounter rates, and (iii) a maximum threshold prey encounter rate at which foraging efficiency is optimized. Dive duration, foraging time, and dive and foraging efficiency increased significantly with increasing prey encounter rate up to an asymptote of ~13 fish per dive cycle, supporting two of the three hypotheses. The results also support predicted responses to changing prey encounter rates derived from an optimal foraging model for diving animals and are the first experimental validation of optimal foraging model predictions in a marine mammal. We believe that these results provide new insight and suggest new experimental techniques for examining the foraging ecology of large marine predators.

Résumé : La réaction des prédateurs marins aux changements à petite échelle de la répartition de leurs proies reste mal comprise. Le déclin spectaculaire de certains prédateurs marins situés au sommet de la chaîne alimentaire montre la nécessité d'obtenir une meilleure compréhension de l'étendue des fluctuations de la disponibilité des proies, compte tenu de la plasticité compensatoire des comportements des prédateurs. Nous avons manipulé expérimentalement le champ des proies à petite échelle d'un carnivore marin dans un milieu contrôlé et fermé et nous avons noté les changements de comportement et d'efficacité associés aux variations de taux de rencontre des proies. Nous avons émis comme hypothèses que (i) il existe un taux minimal de rencontre des proies sous lequel la recherche de la proie est toujours plus coûteuse que le bénéfice obtenu, (ii) l'effort de quête de nourriture augmente avec l'accroissement du taux de rencontre des proies et (iii) il existe un seuil maximal du taux de rencontre des proies où l'efficacité de la recherche de nourriture est optimale. La durée des plongées, le temps consacré à la quête de nourriture, ainsi que l'efficacité de la plongée et de la recherche de nourriture, augmentent tous significativement avec un taux croissant de rencontre des proies jusqu'à une asymptote correspondant à ~13 poissons par cycle de plongée, ce qui appuie deux des trois hypothèses. Ces résultats confirment aussi les réactions à un changement des taux de rencontre des proies prédites par un modèle de quête optimale mis au point pour les animaux plongeurs. Il s'agit ici d'une première validation des prédictions d'un modèle de quête optimale chez un mammifère marin. Nous croyons que ces résultats apportent des perspectives nouvelles et ouvrent la voie à de nouvelles techniques expérimentales pour étudier l'écologie de la quête de nourriture chez les grands prédateurs marins.

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Introduction

Determining how natural and anthropogenic variability in prey availability affects predator foraging success is increasingly important as marine systems undergo significant declines in apex predators; however, the effects of changes in fine-scale prey distribution on predator performance are poorly understood. In the Gulf of Alaska and Bering Sea region, Steller sea lions (*Eumetopias jubatus*) and harbour seals

(*Phoca vitulina*), as well as several piscivorous bird species, have experienced declines in excess of 80% over the last three decades (Loughlin et al. 1984; Small 1998). Changes in food availability are widely believed to be at the crux of these declines, yet virtually no data exist describing the possible underlying mechanisms for such a response (Alaska Sea Grant College Program 1993; DeMaster and Atkinson 2002). Gross prey distribution and abundance surveys can track large-scale changes in a predator's general foraging

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L.A. Cornick^{1,2} and M. Horning. Laboratory for Applied Biotelemetry and Biotechnology, Texas A&M University, Galveston, TX 77551, U.S.A.

¹Corresponding author (e-mail: lacor@conncoll.edu).

²Present address: Department of Biology, Connecticut College 5348, 270 Mohegan Avenue, New London, CT 06320, U.S.A.

range, but they cannot determine how these changes manifest at the finer spatial and temporal scales that may impact the foraging efficiency of individual predators (Bowen 1997). Although recent advances in tracking technologies have vastly improved our ability to watch diving animals forage and enabled more detailed descriptions of three-dimensional movements and habitat use (Andrews 1998; Davis et al. 1999, 2001; Harcourt et al. 2000; Hindell et al. 2002), dive profiles of individual predators cannot be accurately correlated with mesoscale prey attributes, limiting the scope of their interpretation (McCafferty et al. 1998). Some recent investigations have examined changes in foraging strategy of pinnipeds in years of contrasting prey abundance (Costa et al. 1989; Boyd 1996; McCafferty et al. 1998; Boyd 1999; Staniland and Boyd 2003). However, these studies have primarily examined changes in foraging trip duration, attendance patterns, and energy budgets of lactating females during complete seasons of foraging. We currently do not know the magnitude of natural or anthropogenic prey removal for which marine apex predators can compensate by adjusting their foraging strategy on a dive-by-dive basis (e.g., dive duration, foraging time, foraging efficiency).

A number of theoretical models that predict the optimal foraging strategy for breath-hold divers have been developed (Kramer 1988; Ydenberg and Clark 1989; Houston and Carbone 1992; Thompson et al. 1993; Carbone and Houston 1996; Mori 1998a, 1998b). However, they are based primarily on concepts of diminishing returns during reoxygenation following a dive rather than diminishing capture rates during foraging. Where patch depth or quality was examined (Ydenberg and Clark 1989; Mori 1998b), the models suggest that these factors only become important in determining the time budget within a dive cycle when dive duration approaches the aerobic dive limit (Kooyman et al. 1980; Thompson and Fedak 2001). There have been efforts to correlate these models with observed dive behaviour of free-ranging animals (Costa et al. 1989; Nolet et al. 1993; Boyd et al. 1995; Baird and Dill 1996; Boyd 1999; Horning and Trillmich 1999; Harcourt et al. 2001; Acevedo-Gutierrez et al. 2002), but with mixed success, and controlled experiments are lacking. Boyd et al. (1997) demonstrated that increasing the cost of transport during diving, thereby increasing the energetic cost of foraging, produced a change in dive behaviour of lactating female Antarctic fur seals (*Arctocephalus gazella*). These data are consistent with predictions made by Houston and Carbone (1992) and with observed responses of fur seals to acute food reductions (Croxall et al. 1988; Trillmich and Ono 1991). However, this previous study (Boyd et al. 1997) did not attempt to correlate observed dive behaviour directly with fine-scale prey availability.

Thompson and Fedak (2001) developed the first model that explicitly examines how patch quality may influence dive duration and foraging time decisions by seals foraging in a patchy environment, within the constraints imposed by breath-hold diving. Based on a probability distribution that defines the probability of encountering a prey item in a given dive as a function of prey density (Fig. 1 in Thompson and Fedak 2001), they determined that the use of a simple giving-up rule based on the initial prey encounter rate in-

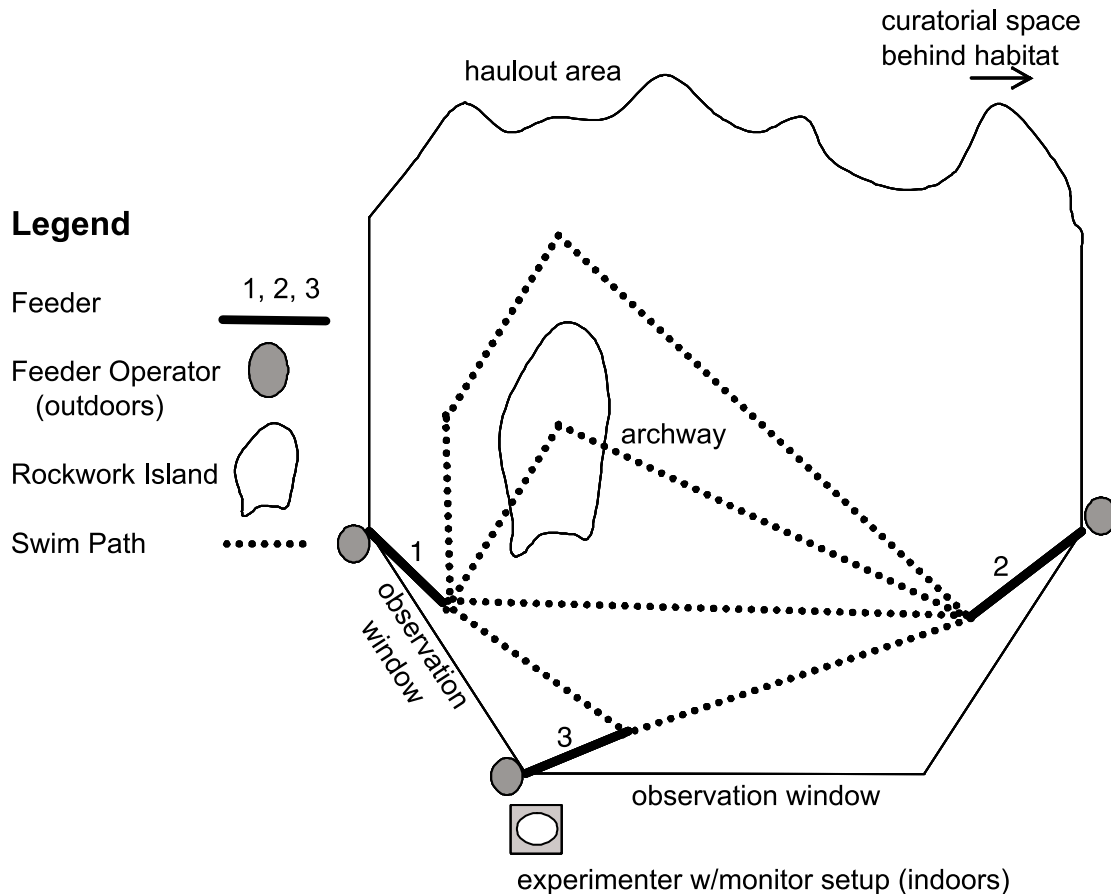
creased the overall rate of prey encounters over a series of dives. They concluded that in shallow dives, seals should terminate a dive prior to fully depleting their oxygen stores if patch density is low. The benefit of giving up early in a dive was reduced as travel time (or search time) increased and as patch density increased. In other words, the seal benefits from varying dive duration and foraging time according to the perceived prey density in a given dive, based on its initial prey encounter rate, by giving up sooner when the prey encounter rate is low and foraging longer when the prey encounter rate is high. Thompson and Fedak (2001) provided a plausible model for optimal foraging behaviour in seals that considers both the physiological constraints on maximal performance and the ecological constraints of prey availability within a given dive cycle.

Based on Thompson and Fedak's (2001) simple giving-up rule and the probability distribution for prey encounter rate (Fig. 1 in Thompson and Fedak 2001), we tested prey availability – foraging behaviour and efficiency relationships in a controlled experimental setting for the first time in a marine mammal. Specifically, we tested three hypotheses directly derived from their Fig. 1 (Thompson and Fedak 2001) predicting changes in diving behaviour with changes in prey encounter rate: (i) there should be a minimum prey encounter rate below which the cost of foraging always exceeds the benefit, whereby the animal ceases to forage, (ii) foraging effort (e.g., dive duration) should increase with increasing prey encounter rates, and (iii) there should be a maximum threshold prey encounter rate beyond which the overall foraging efficiency can no longer be improved (is optimized) within the limits of its physiological and (or) behavioural plasticity. By experimentally manipulating the prey encounter rate in a controlled setting and observing the dive behaviour associated with a range of encounter rates, we quantified the relationships between fine-scale, individual prey availability and observed foraging behaviour. To determine these relationships, we examined how dive duration, foraging time, dive efficiency, and relative foraging efficiency varied with changes in prey encounter rate in experiments performed with captive Steller sea lions.

Materials and methods

Experiments were conducted in the sea lion habitat tank (600 000 L, maximum depth 5 m, surface area 145 m²) at the Alaska SeaLife Center (ASLC) in Seward, Alaska, during two summer seasons (June–September) (Fig. 1). Three ABS plastic tubes (12 cm in diameter, 5 m long) served as fish feeders and were mounted on the observation glass at the top of the enclosure, extending into the tank to approximately 1 m from the bottom. Each feeder was mounted with a remotely controlled light target and trap door at its terminal end. Swimming distances between the feeder tube outlets ranged from 6 to 13 m. The light targets were controlled by the experimenter, positioned inside the ASLC near the front of the large underwater viewing window. Light targets were initially used with standard operant conditioning methods during training sessions to habituate the sea lions to the release of thawed prey items common in the diet of wild Steller sea lions (walleye pollock (*Theragra chalcogramma*)).

Fig. 1. Overhead schematic of experimental setup in Stellar sea lion (*Eumetopias jubatus*) habitat. Experimental animals entered the habitat from the curatorial space and initially entered the water from the haulout area. Targets were lit at random to cue the animal to “search” for a potential prey release. Swim paths were chosen by the animal. Swimming distances between feeders: 1–2 (under arch), 11.6 m; 1–2 (around arch), 13.1 m; 1–3, 6 m; 2–3, 7.3 m. Mean depth = 4.5 m.



and Pacific herring (*Clupea pallasii*) from the feeder tubes. Given that pinnipeds are opportunistic feeders, prey preferences were not of concern, and both species were assumed to be equally palatable. During the experimental sessions, the light targets cued the sea lions to swim between targets for simulated dive descent phases during which no prey items were released. The trap doors were operated by research assistants posted at the top of each feeder via radio instructions from the experimenter. Four real-time video cameras were mounted around the enclosure, one recording each feeder opening and one recording at the water's surface.

The ASLC's three 7-year-old trained sea lions (one male, two females) were used during the study. At the time of the experiments, the male weighed ~300 kg and the females weighed ~150 kg. Each animal was instrumented with a swim speed data logger (Ultramarine Instruments, Galveston, Tex.) and a time–depth recorder (MK7; Wildlife Computers, Redmond, Wash.).

Experimental sessions were performed as frequently as twice daily (morning and (or) afternoon) a minimum of 5 days per week. Sessions lasted between 3 and 26 min (mean = 9 min) and contained from 1 to 21 simulated foraging dives. Session duration was random depending on the quantity of fish allotted, the frequency of fish release, and

the behaviour of the experimental animal. Dive duration was controlled by the experimental animal. Over the course of 61 sessions, 442 simulated foraging dives were recorded and analyzed. Approximately 50%–60%, or 6–11 kg, of daily food consumption was used during experimental sessions, and all sessions were performed at least 4 h after the animal's last feeding. Thawed prey items were weighed and allotted randomly to one of the three feeders prior to each experimental session. Allotment of prey items was also randomized between sessions.

A range of prey encounter rates (0–16 fish per dive) was simulated by releasing either one or two fish from a given feeder, with releases occurring sequentially (fish released upon every visit to a feeder) or intermittently throughout a dive. Dive duration, initial search time (time between the start of a dive and release of the first prey item), foraging time (time from first to last prey release in a single dive), surface interval duration (time between successive dives), dive efficiency, and relative foraging efficiency were calculated from dive recorder and videotape data. Dive efficiency is defined as the ratio of bottom time to the duration of the dive cycle (dive duration plus postdive surface recovery time), where bottom time is assumed to be effective foraging time. Relative foraging efficiency was calculated as catch per unit effort by total mass (grams) of prey items consumed

per dive cycle duration, as a proxy for the instantaneous rate of energy gained versus energy expended during a given dive cycle. Owing to the inability of the animals to encounter prey items while swimming between feeders within a dive, each bout was assumed to occur within a single patch. Additionally, given the limitations of working in a limited depth tank, all dives were assumed to be shallow.

To remain consistent with previous studies, we examined these relationships in terms of large versus small body mass and long versus short search time. An initial analysis of variance was performed on all variable means across sessions to determine differences between individual sea lions and between small versus large relative body mass, and to detect any interactions between the variables tested. Where no significant effects were detected, the data were pooled, either by body mass or for all three sea lions, for all subsequent analyses. Each dive was categorized according to its prey encounter rate and medians calculated for all five variables at each prey encounter rate across sessions. To avoid pseudo-replication, no prey encounter rate value was repeated within a single session (Hurlbert 1984). Given that there was a minimum of 6–24 h between sessions and that the animals were not fed prior to each session, each session was assumed to be an independent treatment. Medians were considered the appropriate measure of central tendency for subsequent analyses because of the lack of normal distributions in the variables measured (Zar 1999). Total simulated search time for each dive was categorized into short (<15 s) and long (>15 s) relative search times based on the median from all dives. To identify trends in behaviour and efficiency with increased prey encounter rate and to determine the best fit curve, each variable was then regressed on prey encounter rate using forward stepwise polynomial regression. All analyses were performed using SPSS 10.0 for Windows (SPSS Inc. 1999).

To test for training and reward effects, three additional trial sessions, covering 45 dives, were performed with experimentally increased locomotor costs through the use of a drag harness on the two female sea lions. The harness raised the hydrodynamic drag experienced by the animal, thus increasing the energetic cost of swimming and, by extension, of foraging. Cost-increased dives were matched to randomly selected standard dives of the same prey encounter rate and search time and the individual dive durations, foraging times, and relative foraging efficiencies compared using Student's *t* test (Zar 1999).

Results

Overall dive durations (9–119 s) and postdive surface intervals (1–79 s, with 90% <15 s) were comparable with those observed for free-ranging Steller sea lions (Merrick and Loughlin 1997; Loughlin et al. 1998). Dive duration ($F_{[1,60]} = 14.262$, $p < 0.01$), foraging time ($F_{[1,60]} = 4.202$, $p = 0.041$), surface interval ($F_{[1,60]} = 9.429$, $p = 0.002$), and relative foraging efficiency ($F_{[1,60]} = 7.774$, $p = 0.006$) differed significantly with relative body mass. No differences were observed between the two females or between the two types of prey items released. Energy density (kilocalories per gram) did not differ significantly between the two prey species (Bando 2002).

Dive duration ($R^2 = 0.70$, $F_{[2,6]} = 6.90$, $p = 0.03$ and $R^2 = 0.80$, $F_{[2,5]} = 9.50$, $p = 0.02$ for large and small body mass, respectively), foraging time ($R^2 = 0.58$, $F_{[1,7]} = 9.53$, $p = 0.02$ and $R^2 = 0.75$, $F_{[2,5]} = 7.50$, $p = 0.03$ for large and small body mass, respectively), and foraging efficiency ($R^2 = 0.94$, $F_{[3,5]} = 25.14$, $p < 0.01$ and $R^2 = 0.97$, $F_{[3,5]} = 37.85$, $p < 0.01$ for large and small body mass, respectively) increased significantly with increased prey encounter rate (Fig. 2). Dive efficiency also increased significantly with increased prey encounter rate ($R^2 = 0.62$, $F_{[2,9]} = 7.08$, $p = 0.01$) but did not differ with body mass.

When examined for the effect of relative search time, dive duration ($R^2 = 0.80$, $F_{[2,8]} = 14.38$, $p < 0.01$ and $R^2 = 0.98$, $F_{[2,7]} = 10.97$, $p < 0.01$ for long and short search time, respectively), foraging time ($R^2 = 0.68$, $F_{[2,7]} = 7.57$, $p = 0.02$ and $R^2 = 0.89$, $F_{[2,7]} = 28.54$, $p < 0.01$ for long and short search time, respectively), dive efficiency ($R^2 = 0.64$, $F_{[2,7]} = 6.20$, $p = 0.03$ and $R^2 = 0.62$, $F_{[2,7]} = 5.70$, $p = 0.03$ for long and short search time, respectively), and relative foraging efficiency ($R^2 = 0.97$, $F_{[1,8]} = 236.48$, $p < 0.01$ and $R^2 = 0.76$, $F_{[3,6]} = 6.43$, $p = 0.03$ for long and short search time, respectively) were all significantly positively correlated with prey encounter rate (Fig. 3).

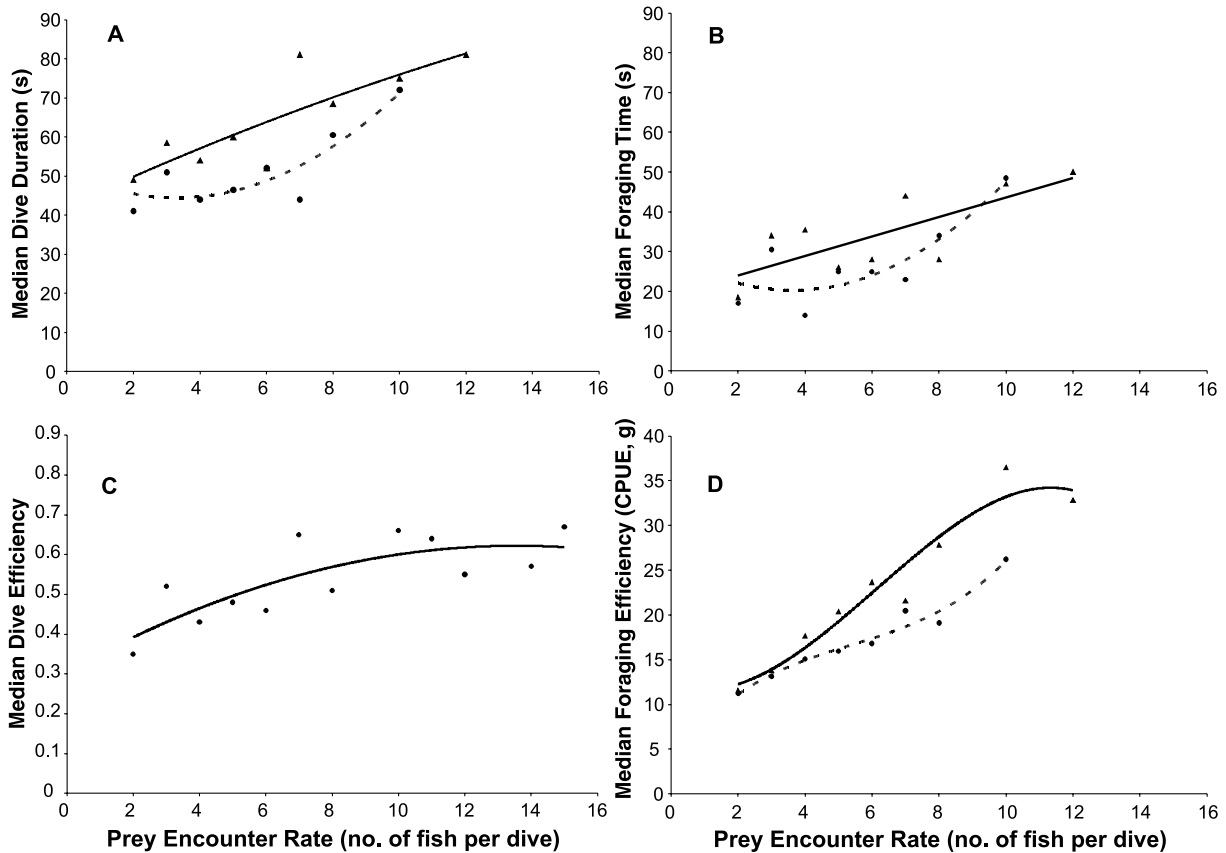
Median dive duration, foraging time, and relative foraging efficiency were markedly reduced during cost-increased dives but not statistically significant (Fig. 4).

Discussion

Increased prey encounter rate led to increased dive duration, foraging time, dive efficiency, and foraging efficiency under all conditions, supporting our hypothesis that foraging effort should increase with increasing prey encounter rate. This demonstrates the importance of fine-scale prey availability in determining foraging strategy and provides support for Thompson and Fedak's (2001) simple rule of thumb approach. It also emphasizes the importance of assessing microscale prey distribution in addition to mesoscale prey biomass determinations, particularly when considering potential impacts of natural or anthropogenic changes in prey on predator foraging.

Dive duration and foraging time were consistently greater for large body mass but increased at a slightly decelerating rate, whereas dive duration increased at an accelerating rate for small body mass. The general relationship between relative body mass and dive behaviour was expected based on a basic tenet of dive physiology: that because metabolic rate scales to body mass at 0.67 (White and Seymour 2003), whereas oxygen stores scale 1:1, maximum attainable dive performance increases with body mass. There are, however, fewer data points for small body mass, and this relationship is less well defined as prey encounter rate grows large. We would not expect smaller animals to exhibit nearly exponential increases in dive duration. However, because these dives are not approaching the maximum performance limits of the animals, there may be less likelihood of seeing some of the classic mass-related effects. Given the mass-related difference in foraging efficiency, we believe that additional data in the higher range of prey encounter rates for the smaller animals would result in a shift in those relationships, such that

Fig. 2. Dive behaviour and efficiency parameters as a function of prey encounter rate and predator relative body mass. Lines were fitted using forward stepwise polynomial regression (4). Solid lines represent large body mass and dashed lines represent small body mass. (A) Median dive duration. Large: $R^2 = 0.70$, $p = 0.03$; small: $R^2 = 0.80$, $p = 0.02$. (B) Median foraging time. Large: $R^2 = 0.58$, $p = 0.02$; small: $R^2 = 0.75$, $p = 0.03$. (C) Median dive efficiency defined as the ratio of the duration of foraging time to the duration of the dive cycle; $R^2 = 0.62$, $p = 0.01$ (dive efficiency did not differ significantly with predator body mass). (D) Median relative foraging efficiency measured as catch per unit effort (CPUE) in mass of fish per dive cycle. Large: $R^2 = 0.94$, $p < 0.01$; small: $R^2 = 0.97$, $p < 0.01$.



they would exhibit similar increasing but decelerating trends as the corresponding trends for large body mass.

The significant positive relationship between prey encounter rate and dive efficiency suggests that all animals were maximizing time spent foraging within a given dive cycle as prey encounter rate increased, continuing to forage longer when the expectation of continued success was high. While the lack of body mass effect on dive efficiency was unexpected, given that larger divers should be able to dive longer for the same metabolic cost, the effective difference between the two groups in the real proportion of time spent foraging may be masked by differences in prey processing. The smaller animals frequently brought very large prey items to the surface for consumption, resulting in significantly longer surface times that were unlikely to be caused by a need for oxygen replenishment. This offset the greater foraging times exhibited by the larger animal, which resulted in similar dive cycle durations, and therefore similar dive efficiency, for both groups. Bringing large prey items to the surface for processing has been observed in free-ranging pinnipeds as well (Roffe and Mate 1984). Thompson and Fedak (2001) pointed out that this strategy, although likely uncommon, may modify the observed behaviour associated with the sim-

ple giving-up rule by terminating a successful dive earlier than would be expected for small prey that can be consumed underwater.

The comparable foraging efficiency of both large and small animals when prey encounter rate was low is consistent with Mori's (1998a) conclusion that larger animals do not necessarily have increased foraging efficiency but is contrary to the standard perception that "bigger is better" for divers in terms of increased aerobic dive limit and maximal performance (Kooyman and Ponganis 1998). Our results suggest that increased body size confers no apparent advantage when prey is scarce but may become more important when prey encounter rate is high because larger animals can remain submerged longer without resorting to anaerobic metabolism (Kooyman and Ponganis 1998). This is an intriguing result that bears further investigation. Although maximal performance limits are not the sole determinant of foraging efficiency, the ability to remain submerged longer and remain within the aerobic dive limit, and the associated increase in search options, may be particularly important to the foraging efficiency of juveniles or of adults during the breeding season (Schreer and Kovacs 1997; Hindell et al. 1999; Horning and Trillmich 1999; Irvine et al. 2000; Beck

Fig. 3. Dive behaviour and efficiency parameters as a function of prey encounter rate and relative initial search time. Lines were fitted using forward stepwise polynomial regression (4). Solid lines represent short search time (<15 s) and dashed lines represent long search time (>15 s). (A) Median dive duration. Short: $R^2 = 0.98, p < 0.01$; long: $R^2 = 0.80, p < 0.01$. (B) Median foraging time. Short: $R^2 = 0.89, p < 0.01$; long: $R^2 = 0.68, p = 0.02$. (C) Median dive efficiency defined as the ratio of the duration of foraging time to the duration of the dive cycle. Short: $R^2 = 0.62, p = 0.03$; long: $R^2 = 0.64, p = 0.03$. (D) Median relative foraging efficiency measured as catch per unit effort (CPUE) in mass of fish per dive cycle. Short: $R^2 = 0.76, p = 0.03$; long: $R^2 = 0.97, p < 0.01$.

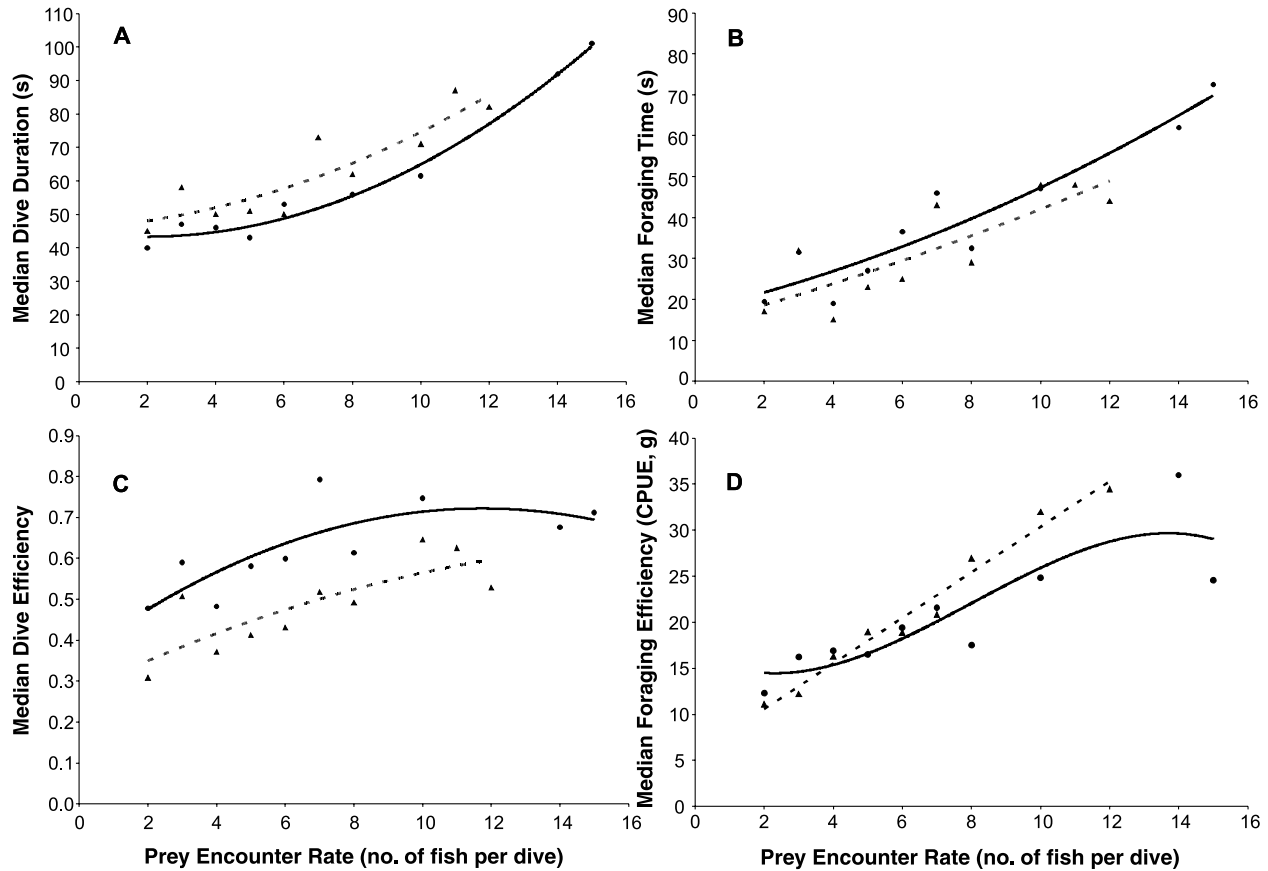
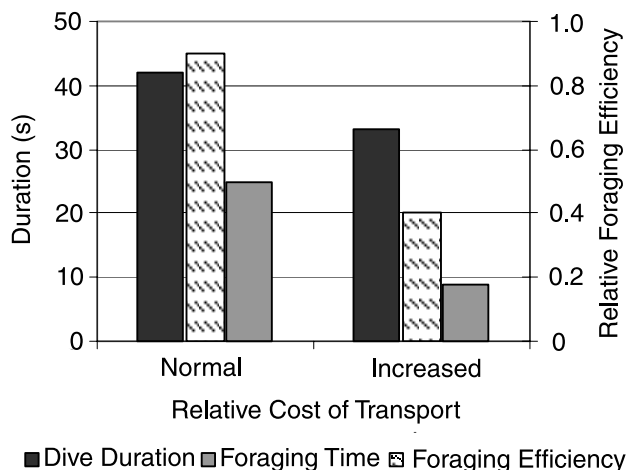


Fig. 4. Effect of increased cost of transport on dive behaviour and foraging efficiency. Dive duration, foraging time (s), and relative foraging efficiency (catch per unit effort (g)) decreased markedly with increased cost of transport via increased hydrodynamic drag.



et al. 2003). We should also note that in this study, all dives are assumed to be shallow, which effectively eliminates oxygen-related constraints on the choice to surface during a given experimental session, and these results may be a function of the limited depth of the captive environment. They may also be an artifact of small sample size, given the availability of only three animals, and only one of relatively large body mass.

Dive duration was greater overall, and foraging time reduced, when initial search time was long, consistent with the Thompson and Fedak (2001) model. Although the scope of these experiments and the limitations of the captive setting did not allow us to make observations for deep dives or to examine the function of dive depth, this result is consistent with the generally observed trend in marine mammals of increased dive duration with increased depth, which may reflect the initial search for a prey patch at the onset of a dive (Kooyman 1989). These results are also consistent with a number of classical diving models that predict reduced foraging time with increased travel time (Kramer 1988; Ydenberg and Clark 1989; Houston and Carbone 1992). This is also reflected in the decreased dive efficiency when search time was long. It is important to note that both dive

duration and foraging time increased significantly for all prey encounter rates, regardless of initial search time, which demonstrates the importance of the perception of patch quality in determining the optimal strategy within a given dive cycle, which is reflected in the overall increase in foraging efficiency as prey encounter rate increased. These results support Thompson and Fedak's (2001) assertion that, within the aerobic dive limit, the decision to terminate a dive is more likely driven by prey considerations than by physiological constraints. Relative foraging efficiency increased for all values of prey encounter rate when search time was long, whereas it reached the hypothesized threshold at a prey encounter rate of about 14 when search time was short. There are insufficient data beyond a prey encounter rate of 12 for long search times to be able to extrapolate a similar deceleration in that relationship, although we believe it to be the case. The result that foraging efficiency was greater overall when search time was long for prey encounter rates greater than four was unexpected. This may also be confounded by the lack of samples for prey encounter rates greater than 12 or may be another artifact of the prey processing at the surface described previously.

Although not statistically significant, we believe that the consistent reductions in dive duration, foraging time, and relative foraging efficiency during cost-increased dives are indicative of true cost-related effects. This approach was used previously with a marine mammal, with an observed decrease in dive depth and duration of adult female Antarctic fur seals carrying a drag device, compared with separate control animals (Boyd et al. 1997). The approach is based on the premise that relative foraging efficiency is similarly affected by either decreased prey encounter rates with constant cost of foraging or increased cost of foraging with constant prey encounter rates (Stephens and Krebs 1986; Ydenberg and Clark 1989; Boyd et al. 1997; Horning and Trillmich 1999). This result suggests that the animals' performance during experimental sessions was not driven by reward expectations or other training effects, which validates the basic experimental design. Additional cost-increased experiments are necessary to determine the proportional increase in locomotor costs created by the drag harness and to adequately test the consequences of these costs to behaviour and efficiency. Experiments with free-ranging animals would provide a rigorous test of these relationships in situ. If similar results are obtained, this would be considered a validation of the applicability of this approach to the study of optimal foraging in free-ranging animals.

As a result of coordination with other concurrent diet studies at the ASLC that utilized the same sea lions, we were unable to feed ad libitum during our experimental trials, requiring further testing of the optimal prey encounter rate threshold hypothesis. However, the asymptotic behaviour of the relationships between prey encounter rate and dive and foraging efficiency provides preliminary support for this hypothesis, such that beyond a prey encounter rate of approximately 10–12 efficiency no longer increased. These data are also consistent with recent video observations of Antarctic fur seals feeding on krill, which showed increased dive bout duration with increased prey encounter rates (Hooker et al. 2002).

Sample sizes for completely unsuccessful dives were insufficient to confidently evaluate results at the lowest prey encounter rates. However, our results are consistent with the only existing study to date of foraging in otariid (eared) seals linking presumed reductions in prey availability to changes in dive behaviour in free-ranging Galapagos fur seals (*Arctocephalus galapagoensis*) (Horning and Trillmich 1999). They demonstrated that during full moon cycles, when prey in the deep scattering layer were concentrated at depths beyond the diving ability of juvenile fur seals, the percentage of time spent foraging dropped significantly, with some animals not foraging at all until the full moon phase passed. This supports our concept of a minimum threshold prey encounter rate below which the most efficient strategy is to conserve energy and wait to forage until conditions improve.

The technology, experimental paradigm, and theoretical models do not exist to conduct controlled experiments under natural foraging conditions with large carnivores. Nor can fine-scale prey availability be measured directly for individual animals foraging in the wild. This study provides a first approximation of the plasticity of dive-by-dive foraging behaviour as it relates to variable prey encounter rates in a diving predator and provides the first controlled, experimental examination of published foraging theory model predictions in a large carnivore. We believe that these results encourage a new direction in the study of optimal foraging in carnivores and suggest new interpretations of long-held assumptions. They demonstrate that controlled experiments can be devised, even with large, deep-diving animals, to simulate a wide range of foraging scenarios using manipulation of the fine-scale prey field. They also suggest possibilities for studies of free-ranging animals that may facilitate a more meaningful interpretation of telemetered dive behaviour and the development of more refined models quantifying the effects of natural and anthropogenic changes in prey distribution and abundance on the foraging efficiency of predators.

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