LINKING MOVEMENT, DIVING, AND HABITAT TO FORAGING SUCCESS IN A LARGE MARINE PREDATOR

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Abstract. Establishing where and when predators forage is essential to understanding trophic interactions, yet foraging behavior remains poorly understood in large marine carnivores. We investigated the factors leading to foraging success in gray seals (*Halichoerus grypus*) in the Northwest Atlantic in the first study to use simultaneous deployments of satellite transmitters, time depth recorders, and stomach-temperature loggers on a free-ranging marine mammal. Thirty-two seals were each fitted with the three types of instrumentation; however, complete records from all three instruments were obtained from only 13 individuals, underscoring the difficulty of such a multi-instrument approach. Our goal was to determine the characteristics of diving, habitat, and movement that predict feeding. We linked diving behavior to foraging success at two temporal scales: trips (days) and bouts (hours) to test models of optimal diving, which indicate that feeding can be predicted by time spent at the bottom of a dive. Using an information-theoretic approach, a Generalized Linear Mixed Model with trip duration and accumulated bottom time per day best explained the number of feeding events per trip, whereas the best predictor of the number of feeding events per bout was accumulated bottom time. We then tested whether characteristics of movement were predictive of feeding. Significant predictors of the number of feeding events per trip were angular variance (i.e., path tortuosity) and distance traveled per day. Finally, we integrated measures of diving, movement, and habitat at four temporal scales to determine overall predictors of feeding. At the 3-h scale, mean bottom time and distance traveled were the most important predictors of feeding frequency, whereas at the 6-h and 24-h time scales, distance traveled alone was most important. Bathymetry was the most significant predictor of feeding at the 12-h interval, with feeding more likely to occur at deeper depths. Our findings indicate that several factors predict feeding in gray seals, but predictor variables differ across temporal scales such that environmental variation becomes important at some scales and not others. Overall, our results illustrate the value of simultaneously recording and integrating multiple types of information to better understand the circumstances leading to foraging success.

Key words: bathymetry; feeding probability; gray seals; Halichoerus grypus; *Northwest Atlantic; satellite tracking; stomach-temperature telemetry; wildlife telemetry.*

INTRODUCTION

Large predators do not feed all the time, nor are they always successful hunters. However, for many species the circumstances surrounding prey capture are largely unknown, particularly in the marine environment. Identifying the factors that lead to successful foraging in predators is important for a number of reasons. First, using empirical data to highlight the factors associated with successful foraging may help to improve existing optimization models designed to predict when and how feeding should occur (e.g., Charnov 1976, Krebs et al. 1983, Kramer 1988, Perry and Pianka 1997, Zollner and Lima 1999) or suggest new models which may lead to better predictions. Second, the spatial and temporal pattern of predation can introduce heterogeneity in prey mortality, which can have significant effects on ecosystem dynamics (Boyd 1996). Third, Lima (2002) argued that a greater emphasis on predator behavior is needed to change the way we generally think about predator–prey interactions. Upper-trophic-level predators are thought to negatively affect prey populations of commercial importance (Mohn and Bowen 1996) and those of conservation concern (Estes et al. 1998). In contrast, but equally important, a better understanding of predator foraging may provide insight into unintended changes in ecosystem structure and functioning brought about by the declines of upper-trophic-level predators in ecosystems worldwide (Baum et al. 2003, Lotze 2004).

Although prey capture is a central component of foraging, ecologists often study foraging tactics of predators in isolation, without information on foraging

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success. Foraging behavior of marine species can be broken down into four components: vertical movement (diving), horizontal movement or displacement, habitat use, and resultant prey capture. Our understanding of these individual components has increased substantially due to wildlife telemetry (e.g., Boyd et al. 2002, Charrassin et al. 2002, Harcourt et al. 2002, McConnell et al. 2002, Beck et al. 2003a, b, Laidre et al. 2004, Pütz and Cherel 2005), but lacking is the integration of these components in order to understand the consequences of foraging behavior on prey capture.

In air-breathing marine animals, individuals can increase their probability of feeding success by spending more time diving (Mori 1998, Mori and Boyd 2004). However, variation in the characteristics of prey distribution (e.g., uniform vs. patchy; Litzow and Piatt 2003), which in turn may be dependent upon the habitat (e.g., depth; Staniland et al. 2004), may influence diving patterns. By studying temporal variability in foraging success in tandem with diving behavior, it may be possible to determine how the probability of successful foraging varies with characteristics of the dive, which in turn can provide information about prey that may otherwise be difficult to measure (Mangel and Adler 1994). Alternatively, successful foraging and satiation may modify an individual's behavior (Saarikko and Hanski 1990, Wallin 1991), resulting in a change to diving patterns, thereby offering the potential opportunity to use this relationship to infer success from behavior.

Diving enables the predator to encounter prey, and thus we should expect diving behavior to reflect the depth and spatial distribution of prey and feeding success at fine scales. By contrast, horizontal movement should reflect predator behavior and prey distribution over a wider range of spatial scales (Hooker and Baird 2001) as an individual's movement will reflect its search tactics (Bell 1991). An individual can alter its movement by adjusting turning angles, move lengths, and travel speed (Bell 1991), but the success of search tactics will ultimately depend upon the abundance and distribution of prey (Zollner and Lima 1999). Clearly, the consequences of search tactics cannot be evaluated without knowing where feeding occurs.

A primary motivation for an individual to move is to locate prey and to find prey patches offering a higher reward (Charnov 1976). Given that it is often difficult to measure the quality of a patch (i.e., prey quantity or energetic content), particularly in the marine environment, characteristics of the habitat are often used as proxies. Prey availability is often correlated with physical and biological properties of the ocean, such as depth (Hastie et al. 2003), temperature (Charrassin and Bost 2001), and substrate type (Tollit et al. 1998). Therefore, habitat utilization by predators is assumed to reflect the quality and availability of resources in an area (Davoren et al. 2003, Laidre et al. 2004). Understanding habitat selection thus requires that we know both an individual's location and how the habitat is used (Kareiva and Wennergren 1995).

To survive, a predator must persistently track spatial and temporal distributions of prey patterns at varying scales (Benoit-Bird and Au 2003). Therefore, the spatial and temporal distribution of prey has a strong effect on the energetic costs of foraging, foraging success, and overall predator survival (Boyd 1996). The extent to which apex predators respond to prey variability will be an indication of the scales at which they can detect change (Swartzman and Hunt 2000). The relative mobility, home range, and size of an organism may affect the resolution at which an animal recognizes environmental heterogeneity (Kotliar and Wiens 1990, Rose and Leggett 1990, Russell et al. 1992). To understand the relationship of an organism to its environment, one must consider the scales of patchiness and the scales at which the organism can respond to this heterogeneity. Therefore it is important that we sample at several scales, necessarily scaling up when possible in order to effectively identify temporal scale inconsistencies that allow us to identify the processes affecting foraging success (Folt et al. 1998).

Whereas time–depth recorders (TDRs) and satellite tags have provided the opportunity to study diving and movement, stomach-temperature telemetry (Carey et al. 1984, Wilson et al. 1992) has been used to measure feeding in free-ranging marine predators (Wilson et al. 1992, Pütz and Bost 1994, Garthe et al. 1999, Austin et al. 2006). When simultaneously deployed with TDRs, it has been possible to identify the diving behavior associated with feeding and the depths of prey capture by diving seabirds (Kato et al. 1996, Ropert-Coudert et al. 2001). In surface-feeding seabirds, stomach-temperature telemetry has been used in tandem with satellite telemetry, resulting in the ability to highlight key feeding locations (Catry et al. 2004) and movement tactics (Weimerskirch et al. 1997). Thus, the simultaneous recording of multiple types of data results in a better understanding of behavior that leads to prey capture and this, in turn, may allow prediction of feeding based on predator behavior. Using multiple data types, we can also test hypotheses about habitat use, movement tactics and predictions from optimal dive models.

Gray seals (Halichoerus grypus) are large, size-dimorphic, marine carnivores, and they are the most abundant pinniped inhabiting the Scotian Shelf and adjacent areas of eastern Canada. Females are capital breeders, fasting during a 16-d lactation period during which they provision a single offspring (Iverson et al. 1993, Mellish et al. 1999). Males also fast or substantially reduce feeding during the breeding season such that they, too, can be regarded as capital breeders (Lidgard et al. 2004). Thus, during the 3–4 months leading up to the breeding season in January, adults exhibit increased diving frequency and energy storage (Beck et al. 2003a, b, c) in preparation for reproduction. Gray seals are generalist predators of demersal and

pelagic fishes, but typically a small number of prey species dominate the diet at any one time or place (Bowen et al. 1993, Bowen and Harrison 1994), likely reflecting local prey abundance.

In this study, we simultaneously measured diving, movement, habitat use, and feeding in free-ranging gray seals to better understand the consequences of behavior on the foraging success of upper-trophic-level marine predators. We did this by measuring diving characteristics in relation to foraging success at two temporal scales relevant to the predator: diving bouts and foraging trips. We examined whether movement behavior could predict foraging success at the scale of foraging trips. Finally, we combined diving behavior, movement and habitat use into a single model to test which factors might predict foraging success at four temporal scales.

METHODS

Instrument deployment

The study was conducted from September 1999 to January 2002 on Sable Island (44°53′ N, 60°00′ W), a vegetated sand bar ~300 km southeast of Halifax, Nova Scotia, Canada. Known-aged adult gray seals were captured in September of 1999, 2000, and 2001 using hand-held nets (Bowen et al. 1992) and weighed to the nearest 0.5 kg prior to being anaesthetized with Telazol (equal parts of Tiletamine and Zolazepam; Fort Dodge Laboratories, Fort Dodge, Iowa, USA). Males and females received an average dose of 0.45 mg/kg body mass and 0.90 mg/kg body mass, respectively (Bowen et al. 1999).

To study movement paths during foraging, animals were instrumented with satellite-relay data loggers (SRDLs from Wildlife Computers, Redmond, Washington, USA or ST-18s from Telonics, Mesa, Arizona, USA) as described in Austin et al. (2004). SRDLs weighed <0.6% of body mass of the smallest individual. For the purposes of battery conservation, SRDLs were programmed to transmit for 8 h each day. To record diving behavior, each animal was also instrumented with a time–depth recorder (TDR) which weighed between 65 g and 300 g (<0.3% of an animal's body mass at deployment), depending on the model used (Mk3e, Mk5, Mk6, or Mk7; Wildlife Computers; Austin et al. 2006). TDRs were secured to the pelage between the shoulders using 5-min epoxy and were programmed to record depth every 20 s. A conductivity sensor was used to determine when the animal was at sea or hauled out on land.

We used stomach-temperature telemetry to detect feeding (Austin et al. 2006). Briefly, the stomach-temperature telemetry system consisted of two separate instruments (both from Wildlife Computers): (1) a stomach-temperature radio transmitter (STT; 32 g) placed in the stomach of the seal and (2) a radio receiver with an integrated microprocessor data logger (60 g) attached to the seal's pelage along the dorsal midline (next to the TDR) over the stomach using 5-min epoxy.

The receiver was programmed to record stomach temperature every 3 s in 1999 and 2000 and every 10 s in 2001. Details of modifications to the STT to maintain the device in the stomach are given in Austin et al. (2006). Study animals were reweighed and their instruments removed four months later when they returned to Sable Island during the breeding season in December/January.

Data processing

Locations of gray seals were determined from data collected by polar orbiting satellites operated by Service Argos. To remove erroneous data, locations were filtered using a three-stage algorithm (Austin et al. 2003) and the retained locations used to calculate a mean daily location.

Upon recovery, TDR data were processed using software supplied by the manufacturer (Wildlife Computers). Zero-offset correction software (Wildlife Computers) was used to account for shifts in the calibration of the pressure transducer of the instrument over the data collection period. Transducer drift and sea surface conditions introduce noise in depth measurements that cannot be completely removed by the Zero-offset correction program. Hence, we excluded dives <5 m in depth from the analysis. Dive analysis software was then used to analyze the corrected records and provide numerical descriptions of each individual dive (see Boness et al. 1994 for details).

The two-dimensional time–depth profile or shape has been used to infer the behavior associated with individual dives (e.g., Le Boeuf et al. 1988, Baechler et al. 2002). We used a discriminant function analysis developed for gray seals (Beck et al. 2003a) to identify five dive shapes: square, wiggle, v, left-skewed square, and right-skewed square. Depth, duration, bottom time, bottom time/depth, descent rate, ascent rate, skew (ascent/descent), and the presence or absence of wiggles (alternating vertical directions at depth) yielded discriminant functions that correctly classified 96.1% of the manually classified dives with a cross-validation error rate of 4.0%.

Individuals can modify their diving in response to prey abundance and distribution at multiple temporal scales (Boyd et al. 1994). Consequently, we examined diving behavior at two temporal scales: foraging trips and bouts of diving. A foraging trip was operationally defined as the period between entering the sea and returning to land. Duration of foraging trips was estimated as follows: a trip started when a period of haulout (i.e., extended dry time) was followed by ≥5 dives and ended when >20 min of accumulated dry time was recorded by the TDR between successive dives. Nested within each foraging trip, we examined clusters of continuous diving, defined as bouts. To determine the temporal organization of diving into bouts, we used a modification of an iterative statistical method presented in Boyd et al. (1994) and used by Beck et al. (2003b).

Bouts of diving by gray seals were classified into four putative functional types using the discriminant functions developed by Beck et al. (2003b). This method uses both the characteristics of individual dives within a bout (dive duration, surface interval, and depth) and characteristics of the bout itself (number of dives, bout duration, percentage of the bout spent at depth, and the percentages of square and v-shaped dives per bout). 97.5% of dive bouts were classified correctly with a cross-validation error rate of 2.5%.

Stomach-temperature measurements were downloaded using software provided by the manufacturer, Wildlife Computers. The resulting data file was then processed using a custom-made program (written in Visual Basic within Microsoft Access) designed to identify the timing of individual feeding events (Austin et al. 2006).

To link an individual's dives with its movement path derived from the filtered Argos data, a custom-built Visual Basic program assigned a geographic location to each dive using the interpolated distance traveled between satellite-derived locations based on calculated speed of travel between pairs of locations. Finally, we matched feeding events with the corresponding dive, such that all dives and feeding were geo-referenced along the animal's movement path.

Given that gray seals are thought to be primarily benthic feeders (Beck et al. 2003a), we examined three habitat characteristics that are associated with the seafloor and thought to influence differences in benthic prey assemblages. Bottom seawater temperature and predominant sediment type were obtained from the Department of Fisheries and Oceans, Canada (K. Drinkwater and G. Fader, *personal communication*). Annual bottom temperature measurements, taken on a 0.2°C grid during yearly groundfish surveys in July/August, were converted to Thiessen Polygons using ArcInfo (ESRI, Redlands, California, USA) and then converted into individual raster coverages for each year of the study. Polygons of sediment type were converted to raster coverage using Spatial Analyst in ArcView (ESRI, Redlands, California, USA). Bathymetry was obtained from Etopo2 coverage (Smith and Sandwell 1997; *available online*).[4] Habitat measures were matched to each dive location by extracting values from the raster surface and writing them into a point-shapefile attribute table in ArcView.

Data analysis

Persistent directionality in movement paths may indicate travel, while a more tortuous trajectory (Zollner and Lima 1999) is generally assumed to be associated with foraging behavior (Bovet and Benhamou 1991). To assess whether significant directionality occurred in the distribution of turning angles between successive moves, mean turning angles were calculated for each seal (ranging from $-180°$ to $180°$) for each trip, throughout the stomach-temperature transmitter deployment period, using circular statistics (Batschelet 1981). Angular variance of turning angles was calculated using the CircStats module (version 2.0, *available online*)[5] in SPlus version 6.2 (Insightful Corporation, Seattle, Washington, USA; Lund 2004). Mean distance traveled, total distance traveled, and rate of travel were measured using the Animal Movement Extension (Hooge and Eichenlaub 2000) in ArcView. An index of linearity (LI) of each trajectory was calculated as the distance between the first and last point divided by the total distance traveled.

Several indices have been used to summarize diving effort in relation to foraging (Beck et al. 2003a). Two such indices are cumulative time spent diving per day and accumulated bottom time per day (bottom time was calculated as time spent within 85% of the maximum depth obtained during the dive). As these measures of effort are highly correlated, we present only the results of accumulated bottom time.

To test whether behavior and habitat characteristics could be used to predict the total number of feeding events, we used Generalized Linear Mixed Models (GLMM) to account for the repeated-measures nature of the data with Penalized Quasi-Likelihood (PQL) parameter estimation to account for the nonnormal error distributions. In these models, seals are treated as a random effect and the behavioral and habitat variables as fixed effects. An autoregressive variance–covariance matrix (corAR1) representing an autocorrelation structure of order 1 was used to model the serial correlation among observations within seals unless otherwise stated, but different error distributions were used depending on the nature of the variables in the models. GLMM results are given in the following format: $\beta \pm$ SD, t_{df}, P, where β is a measure of the slope of the relationship.

We tested the effects of diving behavior on the total number of feeding events at two temporal scales (bouts and trips) using a GLMM with a Poisson error distribution. At each scale, the predictor variables used were mean dive duration, mean bottom time per hour, mean depth, percentage of square-shaped dives, percentage of v-shaped dives, bout duration, and post-bout interval (i.e., time between successive bouts).

If longer trips resulted in some level of fatigue or time required for digestion, we expected that post-trip haulout duration (i.e., periods of rest) would be significantly associated with trip duration. To determine whether characteristics of the trip itself provided insight into the post-trip haulout duration, we constructed a GLMM with a lognormal error distribution with number of feeding events, trip duration, and accumulated bottom time per day as fixed effects. In addition, we hypothesized that time-to-first-feeding within a trip would be positively related to trip duration, assuming that longer trips meant

TABLE 1. Sex (M, male; F, female), age, mass at deployment, deployment length, number of feeding events/d for 19 adults with stomach telemetry data, and presence (x) of TDR and satellite data.

Sex	Age (yr)	Mass at deployment (kg)	STT deployment length (d)	Mean no. feeding events/d	TDR data	Satellite data
M	15	248.5	0.7	2.9	x	x
M	15	187.0	17.4	1.6	x	x
M	21	194.0	14.4	2.8	x	
M	21	208.0	30.5	2.7	x	x
M	21	235.0	2.3	0.0	x	x
M	23	215.0	7.2	2.7	x	x
M	23	286.5	7.5	1.1	x	x
M	26	222.0	17.4	0.9	x	
M	27	226.5	14.8	1.3	x	x
M	27	255.0	5.4	2.0	x	x
M	27	216.0	31.4	2.2	x	x
F	13	195.0	24.5	1.0	x	x
F	13	158.0	13.5	1.2	x	x
F	14	155.5	32.5	0.3	x	x
F	14	143.0	4.0	0.5		x
F	16	161.0	5.0	0.0		x
F	27	194.5	29.5	1.3	x	x
F	28	155.5	3.0	0.3		x
F	30	178.0	6.3	1.1	x	

Note: Abbreviations are STT, stomach-temperature radio transmitter; TDR, time–depth recorder.

that prey was located farther away. To test this, we constructed a GLMM with a lognormal error distribution.

Feeding is more likely to occur during extended periods of searching for prey. Therefore, we used a GLMM with a Poisson error distribution to test whether movement characteristics (distance traveled per day, angular variation, rate of travel, and the linearity index) within a trip predicted the number of feeding events.

Finally, to examine the temporal scale dependence of feeding on diving, movement, and habitat, we divided each seal's data record into 3-, 6-, 12-, and 24-h time blocks from start to finish, given that feeding events are more likely to occur in longer bouts simply because of an increased chance of prey encounter. In each time block, we calculated the number of feeding events and fit a GLMM with a Poisson error distribution to the data based on the following behavioral and habitat variables: mean depth, mean bottom time, mean dive duration, the number of each dive shape, distance traveled, angular dispersion, sediment type, bottom temperature, and bathymetry. Given equal time steps, we assumed a continuous autoregressive correlation structure (cor-CAR1) for the within-subject error term. To control for the varying number of dives in each time block across all seals, each GLMM was standardized using an offset to account for the number of dives per bin.

GLMM models were fitted in SPlus version 6.2 (Insightful Corporation). All plausible models with two-way interactions were examined and residuals were checked for lack of fit. To determine the best fit to a GLMM, models having the lowest Akaike's Information Criterion (AIC_c) were selected (and the highest Akaike weight, w_i; see Appendices). AIC_c was used over typical AIC to avoid overfitting and to account for small sample sizes (second-order bias correction; Burnham

and Anderson 2004). All GLMMs having a delta AIC_c value (Δ_i) < 2 were considered as having substantial support. Where multiple hypothesis testing (i.e., numerous *t* tests) was carried out, all *P* values were Bonferroni-corrected within groups of tests.

RESULTS

Thirty-two seals were equipped with all three instruments (time–depth recorder [TDR], satellite transmitter, and stomach-temperature radio transmitter [STT]), but stomach-temperature data loggers functioned in only 19 of those 32 (Table 1). Satellite data were received from 26 animals, but only 16 of those also had concurrent stomach-temperature data (Table 1). Similarly, although 23 animals had valid TDR records, only 16 of those also had stomach-temperature data. Thus, all three types of data were simultaneously measured in only 13 of the 32 seals. Although TDRs and satellite transmitters recorded data from September to January, the STT remained in the stomach of those individuals for an average of 15.9 ± 2.7 d (means with standard errors are given throughout; Table 1). We recorded a total of 517 feeding events for an average of 30.4 ± 7.0 events per seal, although there was a great deal of individual variability (cv = 95.3). For the purpose of examining the distribution of foraging success, both TDR and satellite records were truncated to match the period of time for which the STT collected data in each individual.

Mean body mass at initial capture was 226.7 ± 8.6 kg for males ($n = 11$) and 167.6 ± 6.8 kg for females ($n = 8$; Table 1). Despite known differences in foraging behavior of males and females (Beck et al. 2003*a*, *b*, *c*), our sample size was too small to investigate sex differences. Similarly, due to small sample sizes, month and year were not treated as explanatory factors.

TABLE 2. Characteristics (mean ± SE) of four bout types among 16 adults.

Bout characteristic	Type 1	Type 2	Type 3	Type 4
Mean depth (m)	51.2 ± 1.4	57.3 ± 1.4	21.1 ± 1.2	18.0 ± 1.6
Mean dive duration (min)	6.7 ± 0.1	5.6 ± 0.1	5.1 ± 0.2	3.6 ± 0.2
Mean bottom time (min)	4.2 ± 0.1	3.0 ± 0.1	3.1 ± 0.2	1.2 ± 0.1
Mean number of dives	63.6 ± 2.8	10.2 ± 0.4	13.4 ± 1.0	6.0 ± 0.4
Square-shaped dives (%)	68.0 ± 1.4	78.7 ± 1.3	36.0 ± 1.9	20.5 ± 2.5
V-shaped dives (%)	5.1 ± 0.6	22.5 ± 2.0	25.9 ± 2.6	46.5 ± 3.0
Mean bout duration (h)	7.9 ± 0.4	8.2 ± 0.1	1.3 ± 0.1	0.4 ± 0.0
Mean post-bout interval (h)	4.3 ± 0.8	0.6 ± 0.1	9.4 ± 1.9	9.6 ± 0.1

Diving behavior and foraging trips

Sixteen gray seals performed an average of 82.1 ± 10.0 dives per day for a total of 20 568 dives during the period of SST data collection. Mean dive depth and duration were 38.9 ± 5.0 m and 6.1 ± 0.5 min, respectively. Of all dives, 58% were classified as square shaped, followed by right-skewed square dives (16%), wiggle dives (11%), v-shaped dives (8%), and finally left-skewed square dives (7%). Mean depth was greatest for square-shaped dives (54.9 ± 0.2 m), and least for the left-skewed square dives (25.1 ± 0.8 m). Wiggle dives had both the longest duration (7.8 ± 0.07 min) and the greatest bottom time (5.1 ± 0.1 min), while v-shaped dives, involving no bottom time, were the shortest (4.2 ± 0.1 min). Beck et al. (2003a) provide more detail on the characteristics of diving behavior in this population.

We studied 79 trips among the 16 adults that had satellite and SST data, averaging 4.9 ± 1.1 trips per seal and lasting an average of 3.2 ± 0.9 d. Overall, seals spent 60.7% ± 6.2% of their time at sea. Post-trip duration, during which the seals hauled out on land, was on average 2.7 ± 0.5 d. Each trip averaged 5.4 ± 0.8 dive bouts and 364.4 ± 268.2 dives, for an average of 140.0 ± 16.2 dives per day during a trip. As expected, 98.6% ± 0.6% of dives occurred within bouts. Individual bouts averaged 3.4 ± 0.5 h with an average of 29.6 ± 3.5 dives per bout. Seals exhibited an average of 3.3 ± 0.6 bouts per day and a mean post-bout interval of 8.6 ± 1.7 h. The four bout types differed primarily in depth, bottom time, and number of dives (see Table 2 for details of type differences). Type 1 bouts were most common, followed by the other three types, which occurred in similar frequency to each other. Most feeding occurred during bout types 1 and 2, the deepest bouts and those with the greatest amount of bottom time.

Movement

In total, 808 locations were logged from the 16 animals with SRDLs and STTs, an average of 3.8 ± 0.4 locations per seal per day. The filtering algorithm removed 160 erroneous locations (18.9% ± 3.7%), leaving 648 locations, or 3.1 ± 0.3 locations per seal per day for analysis. Most mean daily locations were distributed over the Sable/Western Banks, within an area ~100 km from Sable Island where the seals had been tagged (Fig. 1). Movement tracks were highly variable among seals (Table 3). However, the mean turning angles of most seals were centered near 90° or 270°, indicating frequent reversals in direction. Turning angles were moderately dispersed with mean angular dispersion of 0.55 ± 0.073 (random = 1, concentrated = 0; Table 3).

Habitat

Bathymetry associated with gray seal satellite locations ranged from 1 m to 937 m, and 80% of locations were in water <100 m deep with an overall mean depth of 69.7 ± 0.66 m. Mean bottom temperature associated with satellite locations was 7.2° ± 0.04°C, and ranged from 0° to 17°C. Almost all locations were over sandy type sediments: 85% over clean, well-sorted sand or gravel, 8% over muddy sand with gravel, 2% over clay and sandy silt, and 1% over silty clay.

Feeding and diving behavior

We recorded 375 feeding events (84% of the total) within bouts of diving from 16 adults. The remaining 71 events were associated with dives either not belonging to a bout ($n = 64$), or dives that were <5 m or longer than 30 min and had been deleted in initial data processing ($n = 6$). Feeding occurred in 200 or 27.2% of bouts. Bouts in which feeding occurred were longer and had more accumulated bottom time than non-feeding bouts and the dives within feeding bouts were longer and had greater bottom time individually (Table 4). Generally, the proportion of dive shapes was similar between feeding and non-feeding bouts, but the percentage of v-shaped dives was significantly less in non-feeding bouts (Table 4). Most feeding occurred during type 1 bouts (78.1%), followed by type 2 bouts (13.9%), type 3 bouts (6.4%), and type 4 bouts (1.6%). The percentage of time associated with feeding was greater in type 2 bouts, followed by types 1, 3, and 4, after accounting for differences in bout duration (Table 2). The best predictor of the number of feeding events within a bout was mean bottom time ($0.40 ± 0.046$, $t_{726} = 8.59$, $P < 0.001$; all results are given β ± SD, t_{df}, P, where β is a measure of the slope of the relationship). Mean dive duration, mean depth, percentage of square-shaped and v-shaped dives, and bout duration did not improve model fit (Appendix A).

Feeding occurred during 46 of 79 trips (58%). Trip duration ($0.28 ± 0.02$, $t_{58} = 14.12$, $P < 0.0001$) and accumulated bottom time per day ($0.001 ± 0.0004$, $t_{58} =$
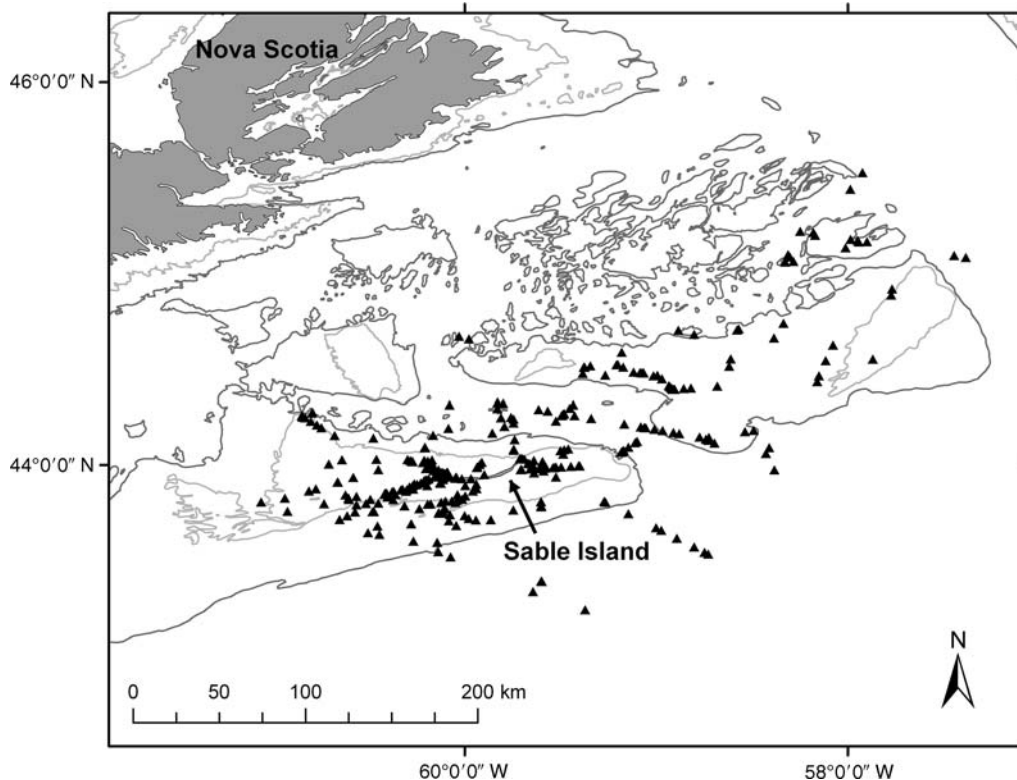
FIG. 1. Estimated locations (black triangles) of feeding from combined data for 13 adult gray seals. The 100-m isobath (dark gray line) and 50-m isobath (light gray line) are also shown.

3.66, $P = 0.005$) best explained the variation in the number of feeding events per trip (Appendix B). Time to the first feeding event did not predict trip duration (0.42 ± 0.31, $t_{25} = 1.31$, $P = 0.2$). However, variation in post-trip haulout duration was significantly affected by trip duration (-0.22 ± 0.049, $t_{58} = -0.54$, $P < 0.0001$) and accumulated bottom time per day (-0.001 ± 0.0005, $t_{58} = -1.95$, $P = 0.05$), with longer trips resulting in shorter post-trip haulouts, suggesting that fatigue is not an important factor affecting trip duration (Appendix C).

Movement and the spatial distribution of feeding

Among 16 adults, angular variance was greater in feeding trips (0.52 ± 0.04) compared to non-feeding trips (0.17 ± 0.52; $t_{77} = 5.01$, $P = 0.04$), indicating greater tortuosity during trips in which feeding occurred. The mean speed of travel was significantly greater in feeding trips (0.3 ± 0.08 m/s) vs. non-feeding trips (0.07 ± 0.02 m/s; $t_{77} = -2.7$, $P = 0.023$). This, combined with the longer duration of feeding trips, resulted in significantly greater distance traveled per day (24.5 ± 4.8 km) compared to non-feeding trips (11.1 ± 1.3 km; $t_{77} = -3.4$, $P = 0.015$). Significant predictors of the number of feeding events per trip were angular variance (0.47 ± 0.08, $t_{16} = 5.98$, $P < 0.001$) and distance traveled per day (0.02 ± 0.008, $t_{16} = 2.51$, $P = 0.023$; Appendix D).

Most feeding occurred within ~100 km of Sable Island, on Sable/Western Banks and Banquereau Bank (Fig. 1). Individual locations tended to be clustered between the 50-m and 100-m isobaths on the offshore bank areas (Fig. 2). Search tactics varied among seals, ranging from rather tortuous paths, often reversing direction (Fig. 2a), to directed movement to a presumed prey patch and then from the patch to Sable Island (Fig. 2b). Despite having lengthy stomach-temperature records, some animals traveled only short distances from Sable Island (Fig. 2d). Feeding occurred mostly over offshore banks (Fig. 2b, c), with the exception of a few off the continental shelf (Fig. 2a). 53.3% of feeding events were clustered along portions of the track that were tortuous (Fig. 2d), but 47.7% of feeding was also indicated along relatively straight sections of track (Fig. 2a, c).

There was no significant difference in mean bottom temperature where feeding occurred ($7.2° \pm 1.1°C$) vs.

TABLE 3. Mean, standard error, and coefficient of variation of movement characteristics of 16 adults.

Movement characteristic	Mean	SE	CV (%)
Total distance traveled (km)	191.3	48.5	91.4
Distance traveled/d (km)	12.3	2.7	79.1
Travel rate (km/h)	1.4	0.3	67.7
Linearity index	0.40	0.069	59.6
Angular variance	0.55	0.073	46.5

TABLE 4. Comparison (paired *t* test) of dive bout characteristics (mean ± SE) for dives in which feeding occurred and did not occur.

Bout characteristics	Feeding bouts (*n* = 200)	Non-feeding bouts (*n* = 536)	*t*	*P*
Mean depth (m)	39.3 ± 5.1	31.8 ± 4.0	1.5	0.3
Mean dive duration (min)	6.3 ± 0.3	5.2 ± 0.4	2.1	0.04
Mean bottom time (min)	4.0 ± 0.3	3.0 ± 0.3	2.3	0.03
Accumulated bottom time (min)	260.2 ± 43.0	73.5 ± 14.7	4.2	<0.001†
Number of dives	58.1 ± 7.9	18.8 ± 2.3	4.8	<0.001†
Bout length (h)	7.4 ± 1.2	2.1 ± 0.3	4.6	<0.001†
Accumulated bottom time (min/h)	33.9 ± 1.8	29.5 ± 1.8	2.2	0.04
Number of dives/h	9.5 ± 0.9	12.5 ± 0.9	5.7	<0.001†
Post-bout interval (h)	9.9 ± 5.0	8.2 ± 1.7	0.3	0.7
Square-shaped dives (%)	53.8 ± 6.0	41.7 ± 5.2	1.5	0.1
Wiggle dives (%)	10.2 ± 3.4	10.2 ± 3.3	0.002	0.9
V-shaped dives (%)†	4.6 ± 1.1	15.2 ± 2.8	3.6	0.002†
Left-skewed square (%)	8.8 ± 3.0	9.2 ± 2.6	0.1	0.9
Right-skewed square (%)	20.6 ± 5.9	18.1 ± 2.3	0.4	0.7

† Significant at *P* < 0.004 (Bonferroni-corrected *P* value).

locations where feeding did not occur (8.5° ± 1.1°C; paired *t* test, $t_{12} = -0.98$, $P = 0.35$). Similarly, underlying bathymetry did not differ significantly between feeding (−51.1 ± 10.9 m) and non-feeding locations (−52.12 ± 10.27 m, $t_{12} = 0.31$, $P = 0.76$). Sediment type also did not differ between feeding and non-feeding locations (82.0% vs. 85.0% clean, well-sorted sand, 10.2% vs. 8.1% muddy sand, 1.3% vs. 1.7% clay, sandy silt, and 0.9% vs. 1.1% silty clay, respectively).

Temporal scale and factors affecting feeding frequency

At the 3-h scale, mean bottom time and distance traveled were the most important predictors of feeding frequency among the 13 seals with simultaneous movement, diving, and STT data (Appendix E, Table 5). At the 6-h and 24-h time scales, the total distance traveled was the most important predictor of feeding (Table 5, Appendices F and H), such that as distance increased, so did the frequency of feeding. By contrast, bathymetry was the most significant predictor of feeding at the 12-h interval, with feeding more likely to occur at deeper depths (Appendix G). Percentage of v-shaped dives was also a significant predictor of feeding at the 12-h and 24-h scales, whereas longer dive duration also predicted feeding at the 12-h scale (Table 5).

DISCUSSION

We believe this is the first study to have simultaneously recorded movement, diving, and feeding frequency in a free-ranging pinniped with a sample of individuals large enough to permit testing of hypotheses. Our findings indicate that several factors are significantly associated with feeding in gray seals. The single most important predictor of feeding was bottom time, but estimated total distance traveled, angular variance, and bathymetry were also significant factors. Our results further indicate that features of the animal's behavior associated with feeding differ across temporal scales and that environmental variation becomes important at some scales and not others.

Despite the value of simultaneously collecting multiple types of data, this approach is difficult in practice. Instrument failures reduced our sample size from an expected 32 seals to only 13 with all three types of data. Although we had greater success than previous researchers (e.g., Bjørge et al. 1995, Lesage et al. 1999), it nonetheless proved difficult to keep the STT from being passed from the seal's stomach prematurely, resulting in shorter records than planned. Comparisons of diving characteristics and mass gain of seals with and without the STT indicated that this procedure had no measurable negative instrument effects. Nevertheless, we cannot exclude the possibility that some of the variation in feeding frequency among seals might have been influenced by carrying the STT (Austin et al. 2006). Further research will be needed to better understand how feeding frequency changes over time and to test for the effects of both intrinsic (e.g., sex) and extrinsic factors (e.g., prey abundance) on foraging success.

The ability to detect feeding events in pinnipeds using stomach-temperature transmitters has been well established through captive studies (Gales and Renouf 1993, Hedd et al. 1995, Andrews 1998) and has been frequently used in free-ranging seabirds (Wilson et al. 1992, Pütz and Bost 1994, Garthe et al. 1999). In Steller sea lions (*Eumetopias jubatus*), the size of ingested prey that can be readily detected by the stomach-temperature transmitter has been shown to be as small as 100 g (Andrews 1998). However, there is evidence that gray seals regularly consume sand lance, *Ammodytes dubius* (Beck 2002), which can be as small as 30 g. Video evidence from harbor seals (*Phoca vitulina*) suggests that sand lance are often taken in succession, increasing the chances of detecting an ingestion event, as multiple prey items cumulatively decrease stomach temperature. Still, we cannot completely rule out the possible occurrence of false negatives due to the inability to detect very small prey items, a factor which may have contributed to the relatively low number of trips that contained feeding events (58%).
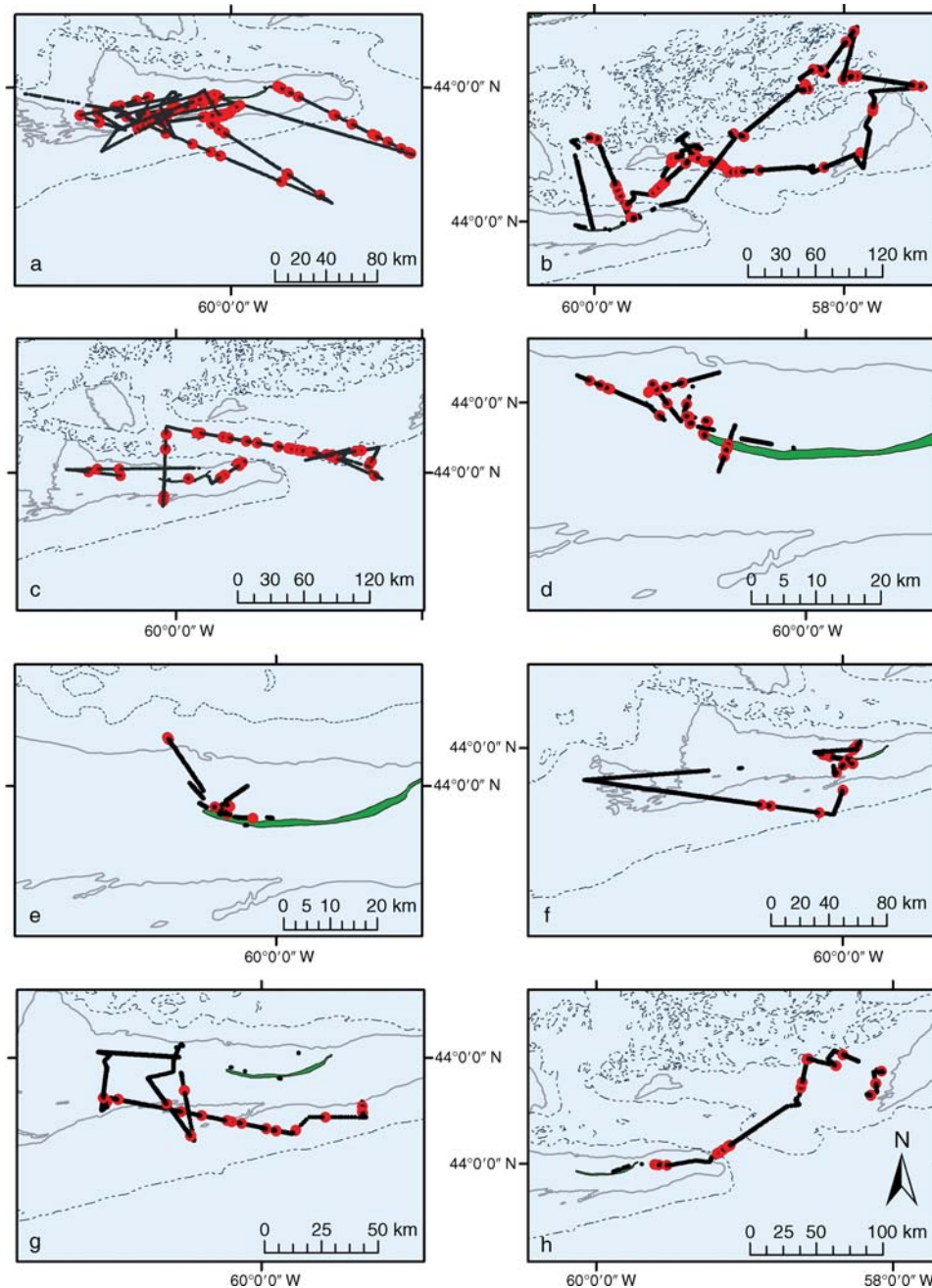
FIG. 2. Movement paths of gray seals, with feeding locations indicated by solid red circles; 100-m (dashed line) and 50-m (gray line) isobaths are also shown. (a) Seal 5114, duration = 30.5 d, $n = 87$; (b) seal 6124, duration = 31.4 d, $n = 69$; (c) seal 24, duration = 30 d, $n = 42$; (d) seal 5687, duration = 32.5, $n = 30$; (e) seal 6122, duration = 32, $n = 14$; (f) 5110, duration = 14 d, $n = 21$; (g) seal 5684, duration = 17, $n = 30$; (h) seal 6125, duration = 8.5, $n = 36$. Values of n are the numbers of observations for each seal.

Although dive shape analysis has become a widespread approach for inferring behavior associated with individual dives in pinnipeds (Le Boeuf et al. 1988, Hindell et al. 1991, Bengtson and Stewart 1992), cetaceans (Martin et al. 1998), seabirds (Wilson et al. 1996), and turtles (Hochscheid et al. 1999), direct evidence of this functionality remains limited (Lesage et al. 1999, Baechler et al. 2002). We did not attempt to link feeding events to single dives and their corresponding shape in this study given that there was some small discrepancy between the times recorded by the two instruments (data-logger and TDR) due to drift in the independent clocks. Instead, we examined how the characteristics of clusters of dives (i.e., bouts) influenced feeding frequency at a range of temporal scales.

TABLE 5. Predictors of feeding by time interval from the best-fit GLMM models ($n = 13$).

Time interval (h)	df	Predictor variables	$\beta \pm$ SE	P
3	840	Mean bottom time	0.173 ± 0.038	<0.0001
		Distance traveled	0.033 ± 0.014	0.01
6	462	Distance traveled	0.024 ± 0.009	0.009
		V-shaped dives	0.080 ± 0.563	0.887
		Distance $\times$ v-shaped dives	0.033 ± 0.027	0.222
12	285	Bathymetry	-0.003 ± 0.001	0.003
		V-shaped dives	1.44 ± 0.546	0.009
		Mean dive duration	0.090 ± 0.046	0.053
24	177	Distance traveled	0.0178 ± 0.002	<0.0001
		V-shaped dives	1.72 ± 0.52	0.001

Diving behavior of gray seals differed markedly when successfully foraging compared to periods when seals were presumed foraging but were unsuccessful. Diving bouts in which feeding occurred were three times longer, deeper, and had greater bottom time than those without evidence of feeding. There may be at least two reasons for this. First, if feeding occurred randomly over time, longer bouts would always have a higher probability of feeding. Second, bouts may be longer because an animal was successful, i.e., animals may modify their behavior to remain longer in a profitable patch. Bout duration should be related to patch quality (Mori 1998, Harcourt et al. 2002), since the duration of a dive bout may be an indication of the time a seal spends in a prey patch (Mori and Boyd 2004). Seals that were successful had longer bouts but did not dive more frequently; instead, they increased the duration and particularly the time spent at the bottom of each dive. For a given depth of dive, this effectively reduces travel time such that more time is spent at depth where prey is more likely to be encountered as predicted by optimal foraging theory (Mori and Boyd 2004). Providing that the predator remains within its aerobic dive limit, the duration of bottom time should depend upon the distance traveled in the vertical component of the dive (Kramer 1988). Thus, seals should opt to forage in as shallow water as possible to meet their energy requirements.

In most species of pinnipeds and diving seabirds, dives with long bottom times (so-called square-shaped dives) are thought to be associated with foraging (Schreer et al. 2001). In harbor seals, food intake is positively correlated with the proportion of dives with long bottom time (Lesage et al. 1999, Baechler et al. 2002). In our study, bottom time was a significant predictor of feeding, at all temporal scales of investigation, thereby providing further support for the use of bottom time as an index of foraging. From an optimal foraging perspective, dives with lengthy bottom times can enable predators to optimize time at a prey patch, as long as they remain within their aerobic dive limit; length of bottom time should depend upon the distance traveled in the vertical component of the dive (Kramer 1988; but see Costa and Gales 2000). As a result, Schreer et al. (2001) offer the caveat that relatively shallow divers, like the gray seal, are able to dive to the bottom while remaining within their physiological depth limit because of limited travel time to and from the bottom. Thus, if these animals are foraging optimally, they will spend more time at the bottom of the dive, resulting in dive profiles that appear to be square, therefore inflating the importance of bottom time as an indication of feeding.

By contrast, v-shaped dives have been attributed to non-foraging activities, including predator avoidance (Hindell et al. 1991), travel (Le Boeuf et al. 1992, Campagna et al. 1995), or exploration (Bengston and Stewart 1992, Schreer and Testa 1996). Therefore, the association of v-shaped dives with feeding, based on the temporal-scale analysis (Table 5), was somewhat unexpected. In pinnipeds, blood circulation to the stomach is restricted at depth to ensure adequate oxygen supply to essential tissues, known as peripheral vasoconstriction (Butler and Jones 1997). Therefore, it has been suggested that digestion may be delayed until deep diving has ended and perfusion of the stomach tissues can once again occur (Crocker et al. 1997, Page et al. 2005). Hence, it is possible that shallow (generally <15 m), v-shaped dives exhibited by gray seals may be associated with digestion. This finding would not have been evident at the scale of individual bouts where the percentage of v-shape dives was significantly less in feeding bouts than in non-feeding bouts (Table 4), but when we extend the scale of analysis from 6 h to 24 h, the association of v-shaped dives with the number of feeding events became evident.

At the longer temporal scale of foraging trips, trip duration was the most important predictor of feeding, followed by total distance traveled. Given that time at sea is positively correlated with number of dives (Robinson et al. 2002), increasing trip duration should increase the chances of encountering prey. Predators require time to find prey patches, and the time spent searching is presumably a function of patch characteristics (Stephens and Krebs 1986). Therefore, gray seals might extend foraging trip duration if they have found profitable prey patches. That total distance traveled during a trip explained significant variation in feeding frequency is consistent with simulation studies of foraging success in relation to search tactics (e.g., Zollner and Lima 1999). Variable directional changes are often associated with feeding (Smith 1974); as an animal's path increases in tortuosity, it is better able to

optimally sample a prey patch (Benhamou 1992, Turchin 1998). Indeed, increased angular variance was associated with successful foraging in this study. Optimal foraging movements are thought to consist of low-speed, sinuous searches in high-resource density areas, and high-speed directed steps between these areas, a strategy known as area restricted search (Nolet and Mooij 2002). Jaquet and Whitehead (1999) found that high foraging success (measured by rates of defecation) is related to convoluted track lines and increased directional changes while low foraging success is related to directed courses and large net displacements in the sperm whale (*Macrocephalus physeter*). We observed almost as many feeding events along relatively straight sections of track as in more tortuous sections which may indicate feeding while traveling, or alternatively this finding may simply be an artifact of the sampling resolution and the inability to detect fine-scale directional changes between satellite locations.

Large mobile animals may transit many habitats within the course of a day (Macdonald and Rushton 2003). Therefore, one of the main difficulties in understanding habitat associations is determining which habitats are particular to specific behaviors. By simultaneously recording behavior and location, we were able to largely overcome this problem. We found no evidence that bottom sediments or bottom temperature played a role in foraging success of gray seals. Colder bottom temperatures were a highly significant predictor of narwhal distribution (Laidre et al. 2004), and were strongly related to increased catch rates of Greenland halibut (*Reinhardtius hippoglossoides*), the narwhals' preferred prey. Likewise, sediment type has been related to both harbor seal (Tollit et al. 1998) and shag (*Phalacrocorax aristotelis*; Wanless et al. 1997) distribution, probably due to the presence of sand lance (*Ammodytes* spp.) in sandy sediments. Failure to find an effect of bottom temperature may have been due to the discrepancy in the sampling periods (temperatures in July/August vs. seals in September/October). Lack of association with sediment type was presumably related to the fact that a single sediment type dominated the areas used by gray seals.

However, bathymetry was an important predictor of feeding at a scale of 12 h, such that feeding was more likely when seals were diving to deeper depths (~70 m). Preferred prey of gray seals includes sandlance (Beck 2002, Beck et al. 2005) which are found at shallow depths, typically <90 m. However, sandlance can exhibit both benthic and pelagic behaviors and therefore can use a range of depths. Similarly, redfish (*Sebastes* spp.), another important prey item (Beck et al. 2005), inhabit deeper off-shelf areas (100–700 m), but migrate vertically at night (Scott and Scott 1988). Gray seals also prey on flatfish, (e.g., *Pleuronectidae*) which typically inhabit shallower depths, ranging from 90 to 250 m, and capelin (*Mallotus villosus*), 0 to 300 m (Scott and Scott 1988).

Our study underscores the importance of considering scale in the interpretation of foraging behavior and the distribution of feeding (Fauchald et al. 2000). Using temporal units defined by gray seals themselves (i.e., bouts and trips) allowed us to adopt a LaGrangian approach to investigating scale inconsistencies which increases our understanding of individual decision making leading to population level dynamics (Folt et al. 1998). Within bouts (i.e., hours and <10 km), characteristics of diving were important predictors of feeding, but, at the scale of trips (i.e., days and >100 km), movement characteristics such as speed, distance traveled, and angular variance were critical. Manipulating temporal scale by dividing data records into 3- to 24-h time blocks revealed dependencies that would not be evident at the scale of bouts or trips and provides further evidence in support of cross-scale research in studies of marine organisms and their environment (e.g., Rose and Leggett 1990, Whitehead 1996, Folt et al. 1998, Nams 2006). Only at the shortest temporal scale of 3 h was mean bottom time an important predictor, perhaps suggesting an estimate of patch residence time. At all longer time scales, distance traveled was the most important variable. As temporal scales increase, predators can increase their foraging success by increasing their distance traveled (Whitehead 1996). Bathymetry, a proxy for habitat, only became an important explanatory variable at the 12-h temporal scale, suggesting that seals searched different habitats perhaps several times per day.

Overall, our results illustrate the value of simultaneously recording and integrating multiple types of information to better understand the circumstances leading to foraging success. This study has both tested and generated new hypotheses about the characteristics of foraging that may be used to predict feeding; information that should be useful in understanding the foraging behavior of other marine predators exploiting large-scale and patchy prey resources. Also, using the results of this study, it should be possible to extend our findings (e.g., predictors such as angular variance, accumulated bottom time) to a much larger sample of gray seals for which both movement and diving behavior have been obtained in the past, and thereby predict where and when foraging might have occurred. Both habitat selection models and spatially explicit predator–prey models will benefit from the ability to predict where and when feeding occurs.

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APPENDIX A

Results from GLMM ($n = 16$) with dive parameters predictive of the number of feeding events per bout (*Ecological Archives* E087-187-A1).

APPENDIX B

Results from GLMM ($n = 16$) with dive parameters predictive of the number of feeding events per trip (*Ecological Archives* E087-187-A2).

APPENDIX C

Results from GLMM ($n = 13$) with parameters predictive of the length of the post-trip haulout (*Ecological Archives* E087-187-A3).

APPENDIX D

Results from GLMM ($n = 16$) with movement parameters predictive of the number of feeding events per bout (*Ecological Archives* E087-187-A4).

APPENDIX E

Results from GLMMs to predict number of feeding events per 3-hour time bin (*Ecological Archives* E087-187-A5).

APPENDIX F

Results from GLMMs to predict number of feeding events per 6-hour time bin (*Ecological Archives* E087-187-A6).

APPENDIX G

Results from GLMMs to predict number of feeding events per 12-hour time bin (*Ecological Archives* E087-187-A7).

APPENDIX H

Results from GLMMs to predict number of feeding events per 24-hour time bin (*Ecological Archives* E087-187-A8).