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Measurements of foraging success in a highly pelagic marine predator, the northern elephant seal

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Summary

1. Identification of foraging behaviour and the ability to assess foraging success is critical to understanding individual and between-species variation in habitat use and foraging ecology. For pelagic predators, behaviour-dependent foraging metrics are commonly used to identify important foraging areas, yet few of these metrics have been validated.

2. Using the northern elephant seal as a model species, we validated the use of a behaviour-independent measure of foraging success (changes in drift rate) at the scale of the entire foraging migration, and then used this to assess a variety of common foraging metrics that are based on movement patterns and dive behaviour. Transit rate consistently provided the best estimate of daily foraging success, although the addition of other metrics provides insight into different foraging behaviours or strategies.

3. While positive changes in buoyancy occurred throughout most of the migrations, implying successful feeding across much of the north Pacific, the areas of most rapid changes in buoyancy occurred along a latitudinal band (40–50° N) corresponding to a dynamic hydrographic region including Subarctic Gyre and Transition Zone waters.

4. These results support the use of transit rate as an index of foraging success: a metric that is easily derived from tracking measurements on a wide range of marine species.

Key-words: buoyancy, drift rate, marine mammal, marine predator, tracking, transit rate

Introduction

Spatio-temporal patterns of prey acquisition help define the foraging ecology of marine predators; however, direct measurements of the specific behaviours associated with successful foraging are limited to a few species where direct observation is possible (Tinker *et al*. 2007). Pelagic predators are among the widest ranging on the planet and exploit prey fields that are highly dynamic in both space and time (Polovina *et al*. 2001; Bakun 2006a, b; Hays *et al*. 2006; Sims *et al*. 2006). Advances in biologging have enhanced our ability to study their movements, foraging ecology and habitat utilization (Block 2005; Hooker *et al*. 2007; Rutz & Hays 2009; Bograd *et al*. 2010; Costa *et al*. 2010a, b). However, most of these techniques rely on indirect measures of foraging behaviour such as: surface transit and turning rates (Fauchald 1999; LeBoeuf *et al*. 2000), diving intensity or dive type (LeBoeuf *et al*. 1988; Bost *et al*. 2007), space-use metrics such as fractal dimension (Nams 1996; Laidre *et al*. 2004; Tremblay, Roberts & Costa 2007), first passage time (FPT) (Fauchald & Tveraa 2003; Pinaud & Weimerskirch 2007), or utilization distributions (Nelson *et al*. 2008), and inferential modelling approaches (Jonsen, Flenming & Myers 2005; Bailey *et al*. 2008; Schick *et al*. 2008; Gurarie, Andrews & Laidre 2009).

Following optimal foraging theory (Charnov 1976), most of these indirect measures assume prey are patchily distributed and are of similar composition in both size class and species. Unfortunately, it is quite difficult to characterize prey abundance and it is rarely done (Croll *et al*. 2005; Sims *et al*. 2006). An alternative is to use proxies of prey availability inferred from predator movement patterns (Austin, Bowen & McMillan 2004) and/or remotely sensed oceanographic parameters (Polovina *et al*. 2001; Hays *et al*. 2006; Pinaud & Weimerskirch 2007; Fossette *et al*. 2010). While these proxies yield useful insights into at-sea behaviour, few of these metrics have been validated or compared. As marine predators exhibit a complex suite of behaviours, it may be incorrect to assume particular behaviours correspond to successful

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*Correspondence author. E-mail: robinson@biology.ucsc.edu foraging. For example, area-restricted searching behaviour may not accurately reflect prey capture or foraging effort (Robinson *et al.* 2007; Weimerskirch *et al.* 2007).

Direct measures of foraging success such as jaw movement sensors, stomach temperature telemeters, acoustic recorders and accelerometers have been developed (Hooker *et al.* 2007; Soto *et al.* 2008). These tools, particularly stomach temperature telemetry, are attractive because they are quantitative and measure at the scale of individual capture events (Austin *et al.* 2006; Kuhn & Costa 2006). While these direct measures of foraging have been quite successful in laboratory trials, their success in the field has been limited to small sample sizes and short time periods, with few measurements of complete foraging trips (Simeone & Wilson 2003; Austin *et al.* 2006; Bost *et al.* 2007; Horsburgh *et al.* 2008; Kuhn *et al.* 2009). The wide-scale application of these tools remains elusive due to limited size/battery configurations, the need to recover instrumentation and the difficulty of working with some species (Myers & Hays 2006; Fossette *et al.* 2008).

A different approach to monitoring foraging behaviour is to develop metrics that are behaviour-independent and vary in response to the animals' body condition. Such a metric is available for elephant seals (*Mirounga* spp.), as they exhibit a unique drift-dive behaviour (Crocker, LeBoeuf & Costa 1997; Mitani *et al.* 2010). Briefly, the seals routinely exhibit dives in which they passively drift through the water column. The vertical rate of drift, which is easily measured using time-depth recorder data, is related to the animal's relative body composition (Crocker, LeBoeuf & Costa 1997; Webb *et al.* 1998; Biuw *et al.* 2003; Thums, Bradshaw & Hindell 2008a). As the animal feeds during a foraging migration, the relative proportion of adipose tissue will increase thereby increasing its buoyancy. Changes in buoyancy can be resolved to a few days to a week thus providing an integrated measure of foraging success in a given area (Biuw *et al.* 2003). While drift-dive analysis is an indirect measure, it is the only indirect measure that changes in response to the condition of the animal rather than its behaviour. Drift rates can be measured concurrently with tracking data and used to identify spatial patterns of feeding success (Biuw *et al.* 2007; Thums, Bradshaw & Hindell 2008a). While this approach has been used with Southern elephant seals (*Mirounga leonina*, Biuw *et al.* 2007; Bailleul *et al.* 2008; Thums, Bradshaw & Hindell 2008a), it has yet to be applied in a spatial context to northern elephant seals (*Mirounga angustirostris*) nor has it been used to assess the validity of other commonly used foraging metrics.

Here, we use 4 years of northern elephant seal diving and tracking data from two colonies to develop and assess 10 indirect measures of foraging behaviour and determine how well these correlate to changes in body condition as determined by changes in drift rate. Specifically, we address three questions:

1. Can changes in drift rate be used to infer foraging success (relative rate of energy gain) in the northern elephant seal?
2. Which tracking and/or diving metrics best estimate foraging success?
3. What is the spatial pattern of foraging success in northern elephant seals?

Materials and methods

FIELD SITES AND ANIMAL HANDLING

Satellite tracking and depth-logging electronic tags were attached to healthy adult female northern elephant seals at two breeding colonies: Año Nuevo state reserve, California, USA (37º5′ N, 122º16′ W) and Isla San Benito, Mexico (28º18′ N, 115º22′ W). Female northern elephant seals exhibit two foraging migrations per year: an 8-month post-moult migration and a 2-month post-breeding migration. The seals travel thousands of kilometres throughout the north Pacific, feeding largely in the meso-pelagic zone (LeBoeuf *et al.* 2000). A total of 107 complete migratory trips were recorded at the Año Nuevo colony from May 2004 through June 2008 and 15 were recorded from the Isla San Benito colony from May 2005 through May 2006. These sample sizes represent deployments for which a matched set of diving-behaviour data and tracking data were collected over the entire trip to sea.

Seals were chemically immobilized for instrument attachment and recovery using standard protocols (LeBoeuf *et al.* 1988, 2000). Each animal was equipped with a 0·5 W ARGOS satellite transmitter (Wildlife Computers, Redmond, WA, USA or Sea Mammal Research Unit, St. Andrews, Scotland), a time-depth recorder (Wildlife Computers) sampling at least once every 8 s and a VHF transmitter (ATS, Isanti, MN, USA).

BODY COMPOSITION

Body composition was measured at both deployment and recovery using the truncated cones method (Gales & Burton 1987; Webb *et al.* 1998). Girth and length measurements were taken at eight locations along the body. Blubber thickness was measured using a handheld ultrasound backfat meter (Scanoprobe, Ithaca, NY, USA) at 18 locations, three per girth measurement. Mass of the seal at instrument deployment and recovery was measured directly by suspending the seal in a canvas sling from a tripod using a Dyna-Link scale (1000 ± 1 kg). Instruments were attached 7·0 ± 5·0 days (mean ± SD) prior to departure from the colony and were removed 6·0 ± 4·4 days after return to the colony. These lags were of sufficient duration to warrant correction of mass and body composition estimates. Mass of females at departure and arrival was estimated from mass measured during deployment (or recovery) using equations derived from serial mass measurements of fasting female seals from previous studies [mass change (kg day^{-1}) = 0·51 + 0·0076*mass, $n = 27$, $r^2 = 0{\cdot}79$, $P < 0{\cdot}01$] (Simmons *et al.* 2010). For post-moult recoveries, the mass of the pup at recovery was added to that of the female. Adipose and lean tissue gain was estimated from mass change and body composition, assuming body composition at arrival (or departure) was similar to that during the recovery (or deployment) and that the pup at day-5 post-partum was 13% adipose tissue (Crocker *et al.* 2001). Energy gain was estimated assuming that adipose tissue was 90% lipid, lean tissue was 27% protein (Crocker *et al.* 2001) and an energy content of 37·33 kJ g^{-1} for lipids and 23·5 kJ g^{-1} for protein. These estimates of body composition have been validated against those from dilution of isotopically labelled water (Webb *et al.* 1998).

DATA PRE-PROCESSING

Raw ARGOS tracking data were filtered using a speed/angle filter to remove unlikely position estimates (thresholds: 12 km h^{-1} and 160°, respectively). The filter also investigated the secondary position calculations reported by ARGOS and replaced the primary positions as appropriate. The filtered tracks were then used in FPT (Fauchald & Tveraa 2003) and fractal landscape (Tremblay, Roberts & Costa 2007) calculations; both procedures output area-restricted search statistics in addition to a continuous time series of searching intensity. For the FPT analysis, we used a custom written programme to investigate spatial scales (circle radius) in 5-km increments from 5 to 200 km. Individuals that failed to exhibit area-restricted searching behaviour, as identified by the absence of a distinct peak in the Log[-var(FPT)] plot (see Fauchald & Tveraa 2003), were not included in this analysis.

The turning angle and transit rate estimates are both sensitive to the frequency of ARGOS position estimates, so we used a linear interpolation to normalize the tracking data. In the post-filtered ARGOS data set, the mean duration between positions was 6·67 h, so the tracks were linearly interpolated at an 8-h frequency. Turning angle and transit rate were then estimated from subsequent interpolated positions.

Diving data were collected at sampling frequencies between 1 and 8 s, but were subsampled to 8 s to facilitate comparison. The raw time series of depth measurements were analysed using purpose written software (IKNOS toolbox, Y. Tremblay, unpublished). Identified dives were retained only if they exceeded 32 s in duration and 15 m in depth. All dives were classified into one of four types (transit, foraging, drift and benthic) using a custom hierarchical classification programme. This classification was designed to detect the unique characteristics of dive types as previously described (LeBoeuf *et al.* 1988).

DRIFT-DIVE CLASSIFICATION

Drift dives have been identified visually (LeBoeuf *et al.* 1988), using inflection points (Biuw *et al.* 2003), velocity (Thums, Bradshaw & Hindell 2008a), as well as several statistical approaches (Robinson *et al.* 2007; Thums, Bradshaw & Hindell 2008b). We opted for an automated approach to ensure consistency and efficiency. This approach differed from the method employed by Biuw *et al.* (2003) as their dive data were summarized prior to transmission to accommodate the narrow data throughput of the ARGOS system (Fedak *et al.* 2002). Further, as our instruments did not measure swim velocity we could not identify drift dives as periods where forward surge was negligible (Crocker, LeBoeuf & Costa 1997; Thums, Bradshaw & Hindell 2008a). We developed a new approach in which the first derivative (vertical component of velocity) of the time-depth profile was calculated from a single dive. Then, a kernel density estimation was used to find both the drift rate (position of the peak) and the relative proportion of the dive spent drifting at the dominant drift rate (height of the peak). The peak was found by estimating the density from −1 to +1 m s^{-1} with intervals of 0·005 m s^{-1} and a bandwidth of 0·1 (Fig. 1). As previously observed in northern and southern elephant seals, a switch to positive buoyancy was observed during the post-moult migration (Crocker, LeBoeuf & Costa 1997; Thums, Bradshaw & Hindell 2008a). The transition from −0·1 to +0·1 m s^{-1} was abrupt, representing a rate of change that was an order of magnitude larger than any other part of the record, possibly due to the increased influence of drag as the animal approaches neutral buoyancy (Crocker, LeBoeuf & Costa 1997). Therefore, periods near neutral buoyancy are likely to provide erroneously elevated rates of lipid gain or loss. To reduce the impact of this effect, a correction was applied to the entire data set. Specifically, 0·1 m s^{-1} was added to all drift values $<$ −0·1 m s^{-1}, 0·1 m s^{-1} subtracted from all drift rates $>$ +0·1 m s^{-1}, and values near neutral buoyancy were assigned a rate of 0 m s^{-1}. Functionally, this corrected the rates when switching to or from positive buoyancy to a range consistent with the remainder of the record and did not impact the other parts of the record.

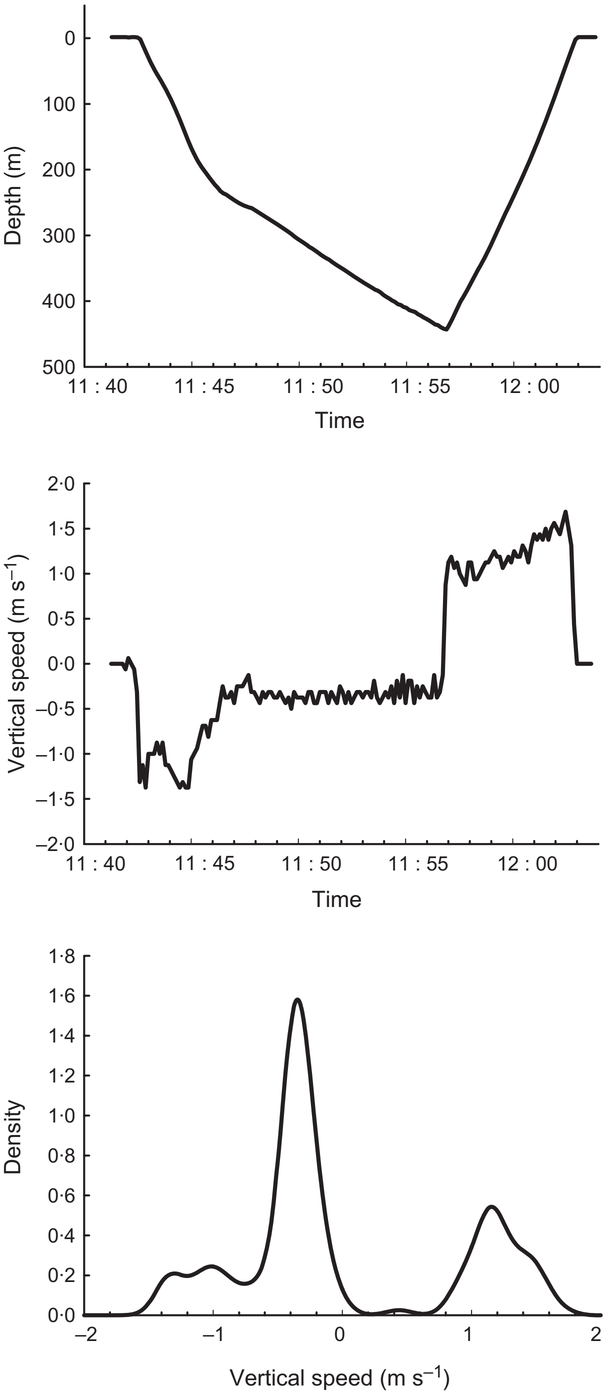

Fig. 1. Procedure used to analyse individual drift dives. The raw depth values (top panel) were used to calculate vertical speed throughout the dive (middle panel). A kernel density estimation was used to find the dominant drift rate (lower panel).

DRIFT RATE VALIDATION

Drift rate has been used as a relative measure of body composition in both the northern elephant seal (Crocker, LeBoeuf & Costa 1997; Webb *et al.* 1998) and southern elephant seal (Biuw *et al.* 2003). This is possible because the drift phase of drift dives is completely passive (Mitani *et al.* 2010); thus, the rate of drift should correspond to the buoyancy of the animal and this, in turn, should correspond to the adipose: lean tissue ratio (Webb *et al.* 1998). To validate the use of drift rate as a measure of foraging success in the northern elephant seal, body composition was measured at the beginning and end of the migration to estimate total energy gain and these values were compared to the range in drift rate values estimated from the drift dives. Measurements were excluded if the estimated mass (from the truncated cones analysis) differed from the actual mass by more than 5% or if the drift rate estimates were obscured by a relatively large proportion of benthic dives.

COMPARISON OF FORAGING METRICS

Daily estimates of 10 indirect foraging metrics were calculated from the tracking and diving data (Table 1). The track-based metrics were: FPT, fractal dimension, transit rate and turn angle. The diving-based metrics were: number of foraging dives, activity during foraging dives, bottom duration of foraging dives, number of wiggles during the bottom phase of foraging dives, number of drift dives and the mean relative proportion of the drift-dive spent drifting. The daily rate of change in drift rate was also calculated providing a behaviour-independent basis for comparison.

The 11 foraging metrics (10 behavioural metrics plus change in drift rate) were determined at different temporal scales and had different signal to noise ratios. For example, changes in the intensity of foraging dives can be measured hourly and scale by more than an order of magnitude whereas changes in drift rate can be observed on time-scales of several days and typically vary by < *c*. 20% over this period. To facilitate comparison, all indices were smoothed using a cubic spline interpolation (split function, MatLab, The Math Works, Natick, MA, USA), following Biuw *et al.* (2003). The settings for all interpolations were identical and based on the properties of the drift rate data set. To determine the most appropriate setting for the interpolation (i.e. frequency of interpolant nodes), we estimated the intra-day variability in drift rate measurements by calculating the range in drift rates observed each day. We then compared this value to the mean inter-day change in drift rate. The grand mean intra-day range in drift rate values across all animals was 0·0488 m s^{-1} and the grand mean inter-day rate of change was 0·0035 m s^{-1} day^{-1}, thus an average of 6·97 days would be necessary to detect a change in drift rate equivalent to 50% of the daily spread in values. For the interpolation, we placed knots at a slightly more conservative 9-day interval to extract daily estimates of the parameter; visual inspection revealed this to be a satisfactory compromise between smoothness and overfitting and represents an appropriate spatial scale relative to the error of Argos data (Bradshaw, Sims & Hays 2007). The smoothing procedure for the drift data are presented in Fig. 2.

Table 1. Tracking and diving-behavioural metrics used to predict foraging success

Metric	Description
ΔDrift	Daily rate of change in drift rate (m s^{-1} day^{-1})
FPT	First passage time at dominant spatial scale (days)
FracD	Daily estimate of fractal dimension (unit-less)
Trans	Transit rate (km h^{-1})
Angle	Mean daily turn angle (degrees)
ForagN	Daily rate of foraging type dives (dives per day)
ForagINT	Mean activity of foraging type dives (unit-less)
ForagBOT	Mean duration of bottom phase of foraging dives (s)
ForagWIG	Mean number of bottom depth wiggles in foraging dives (wiggles per dive)
DriftN	Mean rate of drift type dives (dives per day)
DriftINT	Mean relative proportion of drift dive at dominant drift rate (unit-less) calculated from the peak kernel density (see Fig. 1)

We used linear mixed effects models (SAS Institute, Inc.) to assess each of the foraging metrics relative to foraging success as measured by change in drift rate with individual as the random factor. All variables were inspected for clear deviations from normality and transformed as appropriate. For each migration (post-breeding and post-moulting), a suite of 14 candidate models were selected *a priori* to assess the relative importance of track- and diving-based metrics as predictors of changes in drift rate (Table 2). Weighted AIC_c scores were used to rank candidate models and assess the importance of individual and groups of predictor variables.

Results

Of the 171 sets of instruments deployed from 2004 through 2008, a total of 122 had a complete time-depth record and a complete satellite track. The seals migrated to foraging areas across the northeast Pacific (Fig. 3), most frequently along the subarctic frontal zone, and exploited all of the major hydrographic regions described previously (Simmons *et al.* 2010). Sample sizes by year from 2004 through 2008 were 15, 37, 29, 23 and 18, respectively. Post-breeding migrations were limited in both duration and spatial extent relative to the post-moult migration (Fig. 3). Several individuals from both Año Nuevo and San Benito remained near the coast for either extended periods or the entire migration, but the vast majority of seals fed predominantly in the oceanic zone.

DRIFT RATE VALIDATION

Fifty of the 122 data sets met the criteria for inclusion in the drift rate validation (i.e. frequent drift diving throughout the migration and accurate body composition estimates). These 50 data sets are representative of the entire data set, encompassing individuals from all years of study, both annual migrations, and all major hydrographic regions (Fig. 3). The range in drift rates measured for each individual was a significant predictor of total energy gain, as estimated from the body composition measured at the beginning and end of the migrations (Fig. 4; $R^2 = 0{\cdot}71$, $P < 0{\cdot}001$).

Estimates of the change in drift rate throughout the migrations were consistent with expected values (Crocker, LeBoeuf & Costa 1997; Biuw *et al.* 2003; Thums, Bradshaw & Hindell 2008a), mean 0·0012 ± 0·0030 m s^{-1} day^{-1}. Generally, the rate of change in drift rate was lowest at the beginning and end of the migration. Distinct variations were measured throughout the records and were consistent with visual

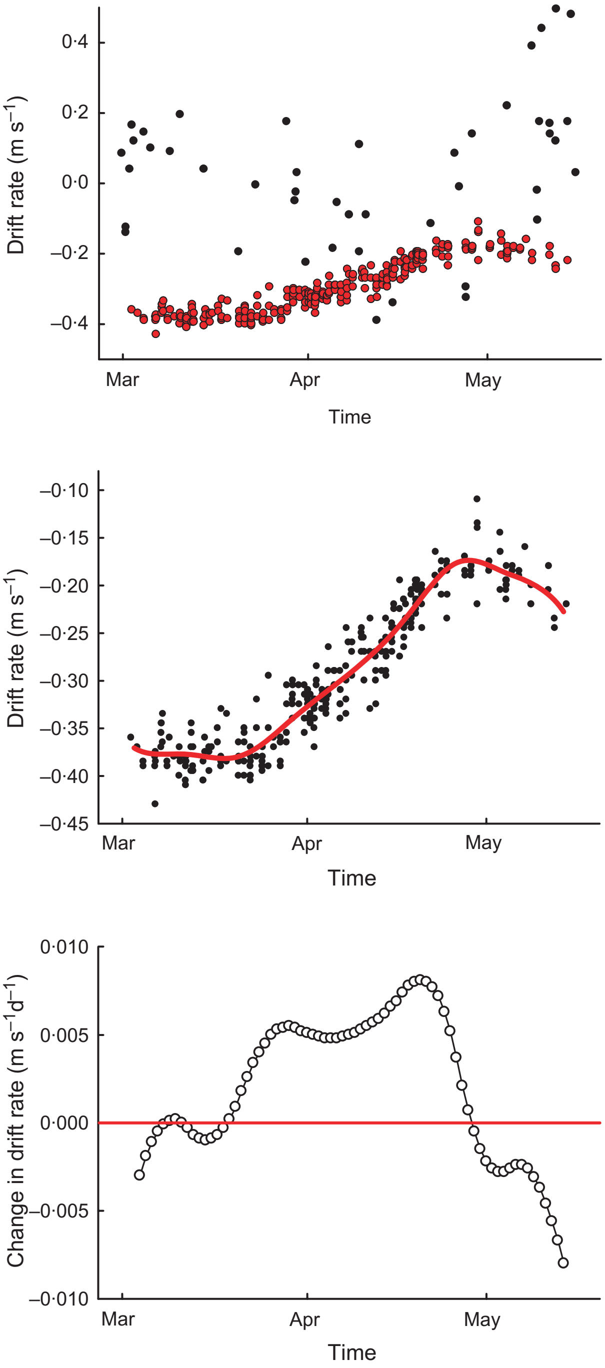

Fig. 2. Procedure used to analyse a time series of drift dives. Raw drift values were manually filtered (top panel). Red points were retained for the subsequent analysis. A cubic spline interpolation was used to fit the data (middle panel). The first derivative of the spline was calculated to determine the daily rate of change in drift rate (lower panel). Values below zero imply a reduction in relative lipid content, while positive values imply an increase in relative lipid content.

Table 2. Candidate models to predict change in drift rate from tracking-based and diving-behaviour-based metrics of foraging behaviour

Candidate models	Hypothesized mechanism
FPT	Higher search effort, time in area
FracD	Higher search effort, plane coverage
Trans	Decreased transit speed
Angle	Increased turning angle
ForagN	More frequent putative foraging dives
ForagINT	More active putative foraging dives
ForagBOT	Increased time at depth
ForagWIG	More vertical excursions at depth
DriftN	More frequent drift dives (food processing)
DriftINT	Longer relative duration of drift dives (food processing)
FPT + FracD + Trans + Angle	Tracking metrics
ForagN + ForagINT + ForagBOT + ForagWIG	Putative foraging dive metrics
DriftN + DriftINT	Drift dive metrics
FPT + FracD + Trans + Angle + ForagN + ForagINT + ForagBOT + ForagWIG + DriftN + DriftINT	All diving and tracking metrics

inspection of the raw data. The post-breeding migration yielded slightly faster changes in drift rate compared to the post-moult migration (t = 5·858; d.f. = 3,717; P < 0·001). The mean rate of change in drift rate was 0·0015 ± 0·0033 m s^{-1} day^{-1} (mean ± SD) during the post-breeding migration and 0·0011 ± 0·0030 m s^{-1} day^{-1} during the post-moult migration.

COMPARISON OF FORAGING METRICS

To assess the ability of track- and diving-based foraging metrics to predict foraging success as estimated from changes in drift rate, we used linear mixed-effects models for post-breeding and post-moulting data separately. Auto-regressive covariance structures did not improve the fit of the models. AIC$_c$ weighted model rankings indicated a better fit for models containing drift-dive information (frequency or intensity) and transit rate (Table 3). A separate ranking analysis, exclusive of models with drift diving parameters, identified transit rate as the most important single parameter for predicting changes in drift rate in both the post-breeding and post-moulting migrations (Table 4). FPT, frequency of foraging dives (ForagN), intensity of foraging dives (ForagINT) and foraging dive bottom time (ForagBOT) were all significant parameters in at least one of the global models. Although these parameters are not part of the most parsimonious models, they are significant predictors of changes in drift rate.

To inspect the individual variation in the relationship of transit rate against changes in drift rate, least-squares linear regressions for each animal were conducted. Seventy four of the 79 seals showed a negative relationship; fifty of these were significant at the 0·05 level. Although the regression lines from both seasons were similar, regression lines for the post-moult migration had a strong convergence between 0·000

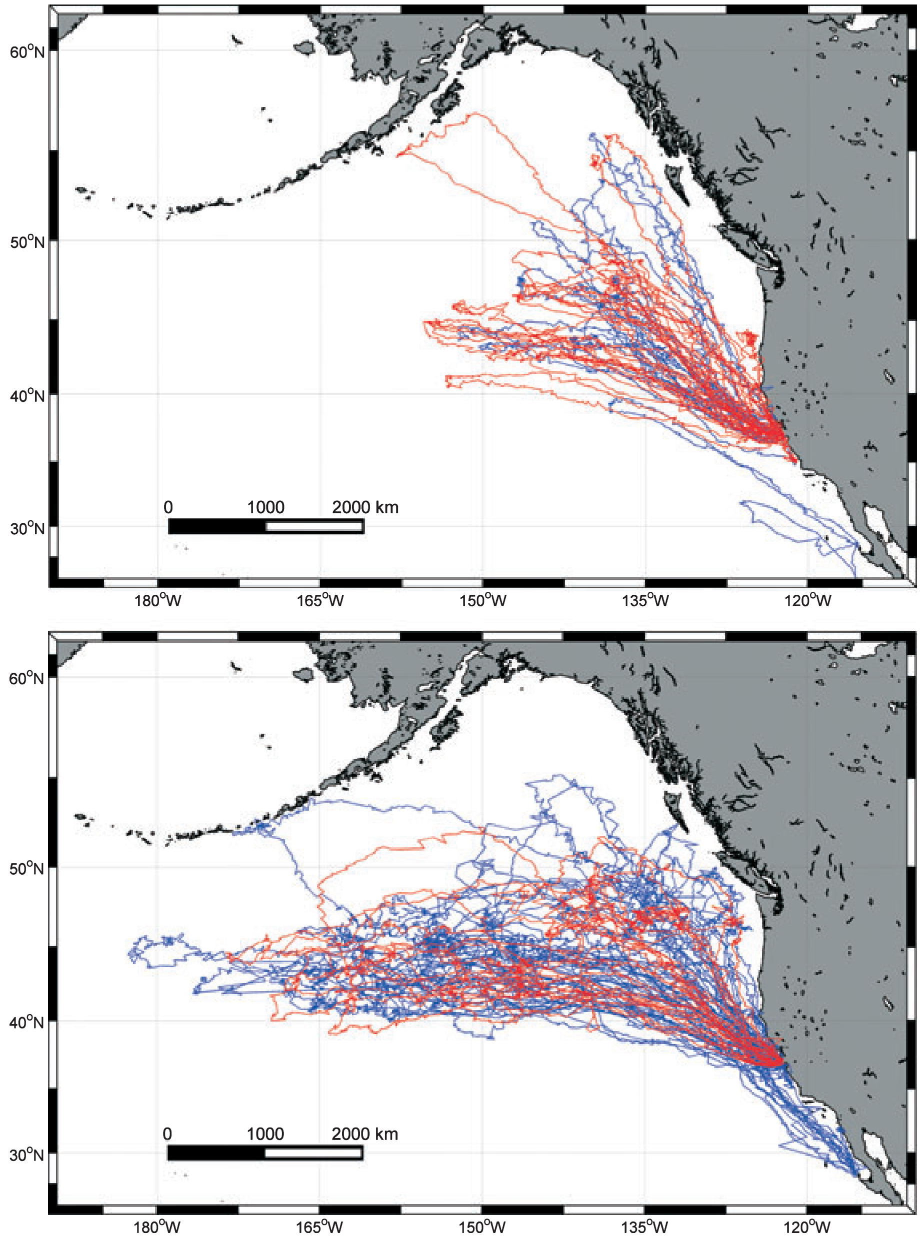

Fig. 3. Filtered ARGOS satellite tracks from 37 post-breeding (top panel) and 42 post-moult (lower panel) migrations with a matched and complete ARGOS satellite track and time-depth recorder record. Red tracks indicate migrations that were used in the drift rate validation.

and 0·005 m s^{-1} day^{-1} at 2 km h^{-1}. On average, transit rate explained 26% of the variation in drift rate. Plots of each foraging metric from a representative example are available online as supporting information.

POPULATION-LEVEL FORAGING BEHAVIOUR

Daily estimated changes in drift rate for each animal were combined across all seasons and years to create a population-level map of foraging success (Fig. 5). Although the most rapid positive changes in drift rate occurred at the distal region of each track, positive changes in drift rate were observed throughout the distribution, implying broadly distributed prey sources. The most rapid positive changes in drift rate occurred within a latitudinal band (40–45° N) corresponding to a dynamic hydrographic region consisting of Subarctic Gyre and Transition Zone waters (Roden 1991; Longhurst 1998). The only region of consistent negative change in drift rate occurred in animals migrating from Isla San Benito northward through the 30°–37° N latitudinal band, possibly indicating a less productive area. This pattern was consistent for both outbound and inbound migrations.

Discussion

We used diving and tracking data from northern elephant seals to address three questions related to at-sea foraging success of a marine predator: (i) Can changes in drift rate be used

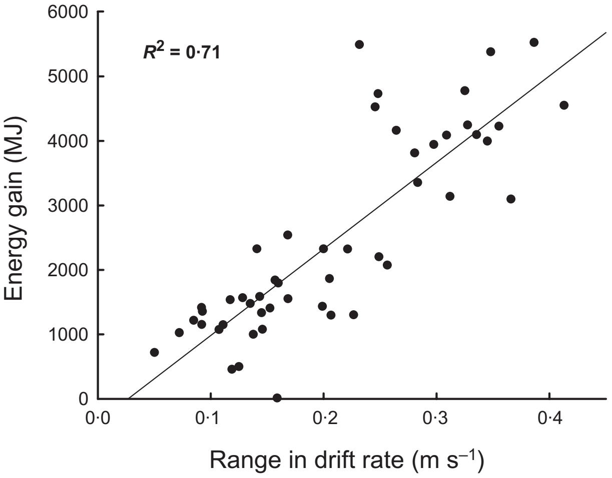

Fig. 4. Change in drift rate values for 50 seals vs. total energy gain, standardized by seal standard length (top panel). Least-squares linear regression, $R^2 = 0·71, P < 0·001$.

to infer foraging success (relative rate of energy gain) in the northern elephant seal? (ii) Which tracking and/or diving metrics best estimate foraging success? (iii) What is the spatial pattern of foraging success in the northern elephant seal?

To address our first question, we compared absolute energy gain over a complete foraging migration to the change in buoyancy and found a strong relationship. At the scale of the entire foraging migration, change in drift rate is a strong predictor of energy gain. This result is consistent with previous studies of both northern and southern elephant seals (Crocker, LeBoeuf & Costa 1997; Biuw *et al.* 2003, 2007; Thums, Bradshaw & Hindell 2008a). It is likely that changes in drift rate are reflective of energy gain/foraging success at smaller temporal scales as well, but this remains untested due to the difficulty of acquiring direct measures of foraging success at sea.

DRIFT RATE ANALYSIS CONSIDERATIONS

The measure of foraging success via changes in drift rate of elephant seals is appealing because it requires only time-depth recorders and, as a measure of animal condition, should be more reliable than metrics based purely on behaviour. However, there are potential errors associated with the use of drift rate data to estimate foraging success (Crocker, LeBoeuf & Costa 1997; Webb *et al.* 1998; Biuw *et al.* 2003; Thums, Bradshaw & Hindell 2008a). For example, energy gain could occur without a change in buoyancy if there were equivalent increases in lipid and lean tissue. Lean tissue could also be preferentially deposited, as might be the case after a long fast, decreasing the animal's buoyancy; this could be interpreted erroneously as negative energy balance (Crocker *et al.* 2001). Both situations result in an underestimate of energy gain.

The growth of a fetus in many females during the post-moult migration will also cause errors in estimates of foraging success (Crocker, LeBoeuf & Costa 1997); in this study, pup mass represented an average of 17% of the total mass gain. Lean tissue has approximately twice the impact on buoyancy relative to adipose tissue (Webb *et al.* 1998) and if the seal maintains constant buoyancy throughout the later stages of gestation, 34% of the total mass gained during a migration would be adipose deposition that merely offsets the change in buoyancy caused by a fetus. While it is difficult to differentiate between energy gain or loss when an animal is becoming negatively buoyant, an increase in buoyancy should only be associated with energy gain. This is because the preferential use of protein stores is not likely to occur in a well-insulated animal and has never been observed in elephant seals (Pernia, Hill & Ortiz 1980; Adams & Costa 1993). Therefore, while changes in drift rate may not always accurately characterize foraging success; they do provide a conservative estimate of it. This

Table 3. Akaike information criteria (AIC) ranking results for linear mixed-effects modelling of tracking-based and diving-behaviour-based foraging indices on changes in drift rate. Ranking includes all candidate models. Bold values indicate the most significant parameters

	Post-breeding			Post-moulting		
Candidate models	Rank	AIC$_c$	AIC weight	Rank	AIC$_c$	AIC weight
FPT + FracD + Trans + Angle + ForagN + ForagINT + ForagBOT + ForagWIG + DriftN + DriftINT	**1**	**−22 697·7**	**0·9999**	**1**	**−80 804·9**	**0·9999**
FPT + FracD + Trans + Angle	**2**	**−22 523·1**	**< 0·01**	**3**	**−79 850·3**	**< 0·01**
ForagN + ForagINT + ForagBOT + ForagWIG + DriftN + DriftInt	**3**	**−22 497·7**	**< 0·01**	**2**	**−80 090·2**	**< 0·01**
Trans	**4**	**−22 475·4**	**< 0·01**	**6**	**−79 372·5**	**< 0·01**
DriftN + DriftINT	**5**	**−22 386·2**	**< 0·01**	**4**	**−79 545·2**	**< 0·01**
DriftINT	**6**	**−22 140·9**	**< 0·01**	–	−78 512	< 0·01
DriftN	7	−22 130·3	< 0·01	**5**	**−79 464·2**	**< 0·01**
Angle	8	−21 991	< 0·01	–	−79 167	< 0·01
FPT	9	−21 840·2	< 0·01	–	−79 044·6	< 0·01
FracD	10	−21 724·2	< 0·01	–	−78 884·4	< 0·01
ForagBOT	11	−21 660·5	< 0·01	–	−78 389	< 0·01
ForagWIG	12	−21 644·3	< 0·01	–	−78 313·2	< 0·01
ForagINT	13	−21 572	< 0·01	–	−78 389·1	< 0·01
ForagN	14	−21 570·9	< 0·01	–	−78 357·9	< 0·01

Table 4. Akaike information criteria (AIC) ranking results for linear mixed-effects modelling of tracking-based and diving-behaviour-based foraging indices on changes in drift rate. Ranking excludes models specific to elephant seals (i.e. exclusive of models containing DriftN or DriftINT parameters). Bold values indicate the most significant parameters

	Post-breeding			Post-moulting		
Model	Rank	AIC$_c$	AIC weight	Rank	AIC$_c$	AIC weight
FPT + FracD + Trans + Angle + ForagN + ForagINT + ForagBOT + ForagWIG	**1**	**−22 628·4**	**0·9999999**	**1**	**−80 706·2**	**0·9999999**
FPT + FracD + Trans + Angle	**2**	**−22 523·1**	**< 0·01**	**2**	**−79 850·3**	**< 0·01**
Trans	**3**	**−22 475·4**	**< 0·01**	**3**	**−79 372·5**	**< 0·01**
Angle	4	−21 991·0	< 0·01	–	−79 167	< 0·01
FPT	5	−21 840·2	< 0·01	–	−79 044·6	< 0·01
ForagN + ForagINT + ForagBOT + ForagWIG	6	−21 805·9	< 0·01	–	−79 060·9	< 0·01
FracD	7	−21 724·2	< 0·01	–	−78 884·4	< 0·01
ForagBOT	8	−21 660·5	< 0·01	–	−78 389	< 0·01
ForagWIG	9	−21 644·3	< 0·01	–	−78 313·2	< 0·01
ForagINT	10	−21 572·0	< 0·01	–	−78 389·1	< 0·01
ForagN	11	−21 570·9	< 0·01	–	−78 357·9	< 0·01

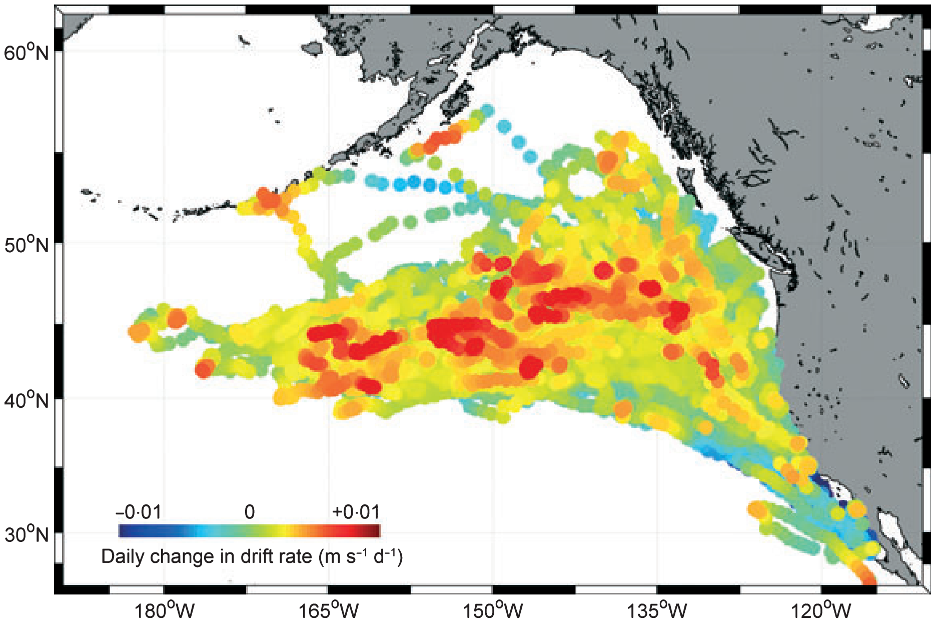

Fig. 5. Daily estimates of change in drift rate for 79 seals (11 395 seal-days) used in the foraging index comparison. Points are vertically sorted according to the 'change in drift rate' value (i.e. warm colours are plotted over cooler colours).

becomes increasingly important towards the end of the post-moult migration due to the exponential growth of the fetus (Robbins & Robbins 1979). The impact of gestation on drift rate values in this study was apparent: daily changes in drift rate typically exhibited a marked decline well before the return-phase of the migration. The effect of these errors is likely one of magnitude, as it is likely that pregnancy and variable tissue deposition impact only the relative importance of feeding areas while not greatly impacting the classification of regions as successful or unsuccessful. However, estimates of foraging success at the beginning and end of migrations, particularly those during the post-moulting migration when animals are pregnant, should be treated with caution.

Another aspect of drift dive analysis that requires further refinement is the drift behaviour around neutral buoyancy. Similar to Crocker, LeBoeuf & Costa (1997), we observed a nearly instantaneous transition in drift rates from −0·1 to +0·1 m s^{-1} for nearly all of the individuals reaching positive buoyancy during the post-moult migration. This pattern was also observed in nearly all of the individuals switching from positive to negative buoyancy. Theoretical calculations of buoyancy suggest a nonlinear response near neutral buoyancy (Crocker, LeBoeuf & Costa 1997), but the observed transition clearly exceeds the expected rate of change in drift rate and is inconsistent with the time series of drift rates published on southern elephant seals (Biuw *et al.* 2003; Thums, Bradshaw & Hindell 2008a). Measurements of stroke pattern and body position during drift dives could be obtained with accelerometers and would help to elucidate this process and provide an appropriate correction.

In addition to northern and southern elephant seals, drift diving has been recorded in New Zealand fur seals (*Arctocephalus forsteri*; Page *et al.* 2005) and sperm whales (*Physeter macrocephalus*; Miller *et al.* 2008). After validations against empirical measurement of mass or energy gain, drift rate analyses in these species may prove to be equally informative.

TRANSIT RATE

In our second question, we asked which diving or tracking metrics best estimate foraging success. We calculated 10 diving and tracking metrics that are considered to be indicative of foraging activity, and feeding success. Results of the linear mixed-effects model indicate that transit rate is the best single predictor of changes in buoyancy; that is, periods of slow horizontal transit tend to coincide with periods of positive buoyancy change. This result is consistent with previous studies that have also demonstrated the importance of transit rate as a predictor of foraging success. LeBoeuf *et al.* (2000) and Crocker *et al.* (2006) found that mean daily transit rate was significantly related to mass gain over a complete foraging migration, except during ENSO events. Kuhn *et al.* (2009) found transit rate to be a significant predictor of feeding rate, as measured by stomach temperature telemetry, during the initial transit phase of the migration.

Estimates of transit rate for pelagic predators are typically derived from light-level geolocation or satellite telemetry, both providing relatively coarse-scale movement information (in both space and time). Recent advances in GPS technology, most notably Fast-Loc GPS, enable collection of higher quality tracking data, which improves the accuracy of transit rate estimates. Indeed, GPS tags have already been used to track a variety of taxa (Sims *et al.* 2009; Costa *et al.* 2010a, b; Hays *et al.* 2010).

While this study confirmed the power of transit rate to predict foraging success, it was variable across individuals; transit rate was a good predictor of foraging success in most individuals but not in all individuals. This is expected as the foraging behaviour of individuals can vary (Tinker *et al.* 2007; Villegas-Amtmann *et al.* 2008) and different foraging metrics may be more appropriate for some individuals and not for others. In addition, the environment may impact the ability to record accurately transit rates. Strong ocean currents may be capable of altering the perceived transit rate of some species, thus biasing the track segments identified as putative foraging areas (Gaspar *et al.* 2006; Girard, Tucker & Calmettes 2009). Studies of slow-moving species (e.g. sea turtles) may benefit from correction of movement trajectories based on surface-current data by revealing additional periods of slow transit.

While transit rate had the greatest predictive power of any single metric, greater predictive power was achieved when multiple metrics were used. A combination of foraging metrics could be used to identify different foraging patterns over the various phases of the track or to identify different foraging behaviours amongst individuals (Tinker *et al.* 2007; Villegas-Amtmann & Costa 2010; Weise, Harvey & Costa 2010).

The presence of multiple foraging strategies and prey types may cloud analyses, which assume that specific behaviours are associated with successful foraging. In this study, we show that among 10 tracking and diving metrics, transit rate is the single best predictor of foraging success. The other foraging metrics may provide insight into when and where different feeding strategies are used rather than identify foraging success *per se*. This has important implications for studies with other pelagic predators where direct feeding data are difficult to acquire, and also highlights the need for a better understanding of the potentially diverse foraging strategies employed by individuals and how these may relate to the distribution and composition of their prey.

POPULATION-LEVEL FORAGING SUCCESS

To address our third question, we combined the daily change in drift rate for all animals across seasons, years and colonies to generate a comprehensive map of foraging success in the North Pacific Ocean. Positive changes in drift rate were observed throughout the migration, implying widely distributed and abundant prey. However, the most rapid positive changes in drift rate occurred within a latitudinal band (40–50° N, extending to the international dateline) corresponding to a dynamic hydrographic region between the Subarctic Gyre and the North Pacific Transition Zone (Roden 1991; Longhurst 1998). Previous studies have suggested that this region is important for foraging elephant seals (LeBoeuf *et al.* 2000; Simmons *et al.* 2010). The seals foraged successfully in this region during both of their semi-annual foraging migrations, despite experiencing dramatically different oceanographic conditions. This region is also important habitat for a variety of other marine vertebrates, including northern fur seals (*Callorhinus ursinus*; Ream, Sterling & Loughlin 2005; Lea *et al.* 2009), bluefin tuna (*Thunnus thynnus*; Boustany *et al.* 2009), albacore (*Thunnus alalunga*), loggerhead turtles (*Caretta caretta*; Polovina *et al.* 2001) and albatrosses (*Phoebastria* spp.; Kappes *et al.* 2010).

SUMMARY

We validated the use of drift rate analysis in the northern elephant seal at the scale of the entire foraging migration, then used the rate of change in drift rate to compare several of the most commonly used foraging metrics. Behaviour-independent measures of foraging success at sea, such as buoyancy change, are difficult to record in most species. However, it is possible to estimate the locations of foraging success at both the individual and population level from behaviour-dependent metrics. Of the behaviour-dependent metrics used in this study, transit rate provided the best estimate of at-sea foraging success. This has broad implications, as the foraging metrics examined here can be derived from tracking data that can be obtained using electronic tags from a wide array of marine vertebrates (Block 2005). By mapping transit rate onto animal tracking data, it may be possible to identify and compare important foraging regions across large spatial extents and diverse taxa. Such studies are already being published (Fossette *et al.* 2010) and will facilitate a more comprehensive understanding of how migratory predators exploit pelagic ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Colour-coded track maps and time-series plots of the 11 foraging metrics for one individual during the post-moult migration.