

Assessing the utility of two- and three-dimensional behavioural metrics in habitat usage models

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ABSTRACT: For deep-diving, wide-ranging marine predators, foraging behaviour is often inferred from movement data. Various metrics are used to do this, and recently, metrics have been developed that consider both horizontal movement and vertical dive behaviour to better describe the use of the 3-dimensional environment these animals inhabit. However, the efficacy of these different metrics in predicting behavioural state is poorly understood. We used first passage time (2-dimensional) and first bottom time (3-dimensional) analyses on tracks derived from satellite-relayed data loggers to quantify and determine seal behavioural state while foraging at sea. Movement and dive data were collected from 38 southern elephant seals *Mirounga leonina* from Macquarie and Campbell Islands (in the Pacific sector of the Southern Ocean). Using a suite of environmental variables, linear mixed-effect models were derived for the 2 broad habitats visited by the seals: shelf and open ocean. The best-fitting models for each foraging metric in each habitat were then compared using a cross validation analysis to identify which foraging metric produced the best predictions of habitat use. In shelf habitats, the 3-dimensional foraging metric provided better predictions than the 2-dimensional metric, while the 2-dimensional foraging metric resulted in the best predictive capacity in the open ocean habitats. These findings highlight the importance of considering the appropriate foraging metrics when modelling foraging behaviour.

KEY WORDS: Foraging · Habitat · First passage time · *Mirounga leonina*

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INTRODUCTION

Oceans are dynamic and heterogeneous environments, where prey fields are distributed patchily in space and time (Steele 1978). To a degree, prey distribution is influenced by physical characteristics of the marine environment, such as temperature and

bathymetry (Bradshaw et al. 2004). Due to this environmental heterogeneity, predators do not move about randomly; rather, they focus their activities in regions where prey are concentrated or predictable (Hückstädt et al. 2012). A common option for developing a population-level assessment of the areas used by a species is to develop habitat models using

a suite of environmental co-variants (e.g. Arcos et al. 2012, Kusch & Schmitz 2013). By modelling the relationship between environmental factors and foraging behaviour for a subset of a population, areas of relative importance can be estimated across a population's entire spatial domain (Raymond et al. 2015). In addition, by incorporating projections of future environmental conditions into these models, the models become a valuable tool for examining which mechanisms underpin individual performance and ultimately population change (Guinet et al. 2001, Louzao et al. 2013, Deppe et al. 2014, O'Toole et al. 2014). However, predicting foraging behaviour from such models is not straightforward (Bradshaw et al. 2004, O'Toole et al. 2014).

There are numerous model frameworks that can be used to describe habitat usage and behaviour, including linear mixed-effect models (LMM), generalised additive models (GAM), and boosted regression trees (BRT) (Bradshaw et al. 2004, Deppe et al. 2014). The choice of model framework will influence the results and depends partly on data type and the nature of the question being asked. For example, LMM can account for non-independent observations, GAMs can consider non-linear relationships in data, and BRT optimise model predictive capacity (Elith et al. 2008) but may lack explanatory power. Despite their differences, all of the models consist of 3 common components that can influence their fit and subsequent predictive capacity: (1) the temporal and spatial scales considered, (2) the environmental variables selected, and (3) the metric used to identifying foraging behaviour. This study focuses on the third of these components.

As it is difficult to directly observe foraging behaviour in marine predators, foraging is often inferred from movement data. For example, reduced displacement speed and increased turning frequency are assumed to occur when a prey patch is encountered, a behaviour known as area restricted search (ARS), (Kareiva & Odell 1987, Fauchald & Tveraa 2003). A range of methods exist for estimating ARS, including first passage time analysis (passage-time; Fauchald & Tveraa 2003), fractal dimensions analysis (FD; Nams 1996), and state space models (SSMs; Jonsen et al. 2003, 2013). Developed for terrestrial animals, the traditional definition of ARS only considers animal movement in the horizontal dimension, as do all of these methods. For marine predators, including only horizontal movements ignores a significant component of their behaviour: diving in the vertical plane, often to considerable depths (Bailleul et al. 2008, Bestley et al. 2015). Methods have been devel-

oped that integrate the horizontal and vertical components of animal movement data to describe ARS behaviour in 3 dimensions, such as first bottom time analysis (bottom-time; Bailleul et al. 2008) and first hunting time analysis (hunting-time; Heerah et al. 2014).

To determine whether the use of 3-dimensional diving metrics improves habitat models, longitudinal data sets that include both horizontal and vertical movement data are required. Such data sets can be collected on southern elephant seals *Mirounga leonina*. Elephant seals exhibit extensive horizontal movements that include prolonged seasonal migrations of thousands of kilometres and foraging at a range of depths, diving to in excess of 2000 m (Hindell et al. 2016). While females generally favour pelagic foraging in the open ocean, males often forage demersally on shelf waters (Hindell et al. 2016). The well established divergence in foraging strategies further makes this species ideal as a model for investigating the veracity of appropriate foraging metric choice.

In this study, we compare the use of a 2- and a 3-dimensional foraging metric in habitat models for southern elephant seals in the Pacific sector of the Southern Ocean. Specifically, we (1) use tracking and dive data from southern elephant seals to derive a 2- and a 3-dimensional foraging metric, (2) use those metrics to develop statistical habitat models, (3) compare the fit and predictive ability of the resulting models, and (4) combine this knowledge into a predictive model to estimate those habitats most likely to be of greatest importance for southern elephant seals in the southern Pacific sector of the Southern Ocean.

MATERIALS AND METHODS

Study area and data collection

Satellite-relayed data loggers (SRDLs) (105 × 70 × 40 mm, ~545 g, cross section area 28 cm²) from the Sea Mammal Research Unit (University of St Andrews, Scotland) were deployed on 38 (female: n = 30, males: n = 8) southern elephant seals *Mirounga leonina* departing on post-moult foraging trips in the southern Pacific sector of the Southern Ocean between January 2004 and April 2013. Tags were ~0.3% of the weight of the smallest individual (~150 kg), and previous studies have demonstrated that seals carrying twice this load (instruments of up to 0.6% of their mass) were unaffected in either the short (growth rates) or the long term (survival) (McMahon et al. 2008).

The SRDLs collected data on depth (resolution: 5 m at 2000 m, 0.5 m at surface) at 5 s intervals and relayed this information in a summarised form of 6 depths and times per dive, corresponding with dive start and end points, plus an additional 4 within-dive major inflection points. Location estimates were made by the global ARGOS satellite system. Males were all tagged on Campbell Island (52° 33' S, 169° 08' E) with captures made between January and February 2012 ($n = 3$) and between March and April 2013 ($n = 5$). Individuals represented all age classes (juvenile, sub-adult and adult) and ranged in estimated weight from 150 to 1800 kg (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m562p181_supp.pdf). Females were tagged on Macquarie Island (54° 30' S, 158° 57' E) in January 2004 ($n = 4$), January 2005 ($n = 11$), and December 2009 ($n = 15$). All females were tagged in the isthmus region, and all were adults (Table S1). Individuals haul-out on both Campbell and Macquarie Island and are considered to be part of the same Macquarie Island stock (Slade et al. 1998).

Where possible, smaller animals were physically restrained using a head bag and anaesthetised via an injection of 1:1 tiletamine and zolazepam (Zoletil) into the extradural intra-vertebral vein (McMahon et al. 2000). Larger seals were given an intra-muscular injection of Zoletil using a remote injection (Ryding 1982). In both instances, injection volume was determined by pre-capture visual estimations of animal weight based on previous experience of weighing southern elephant seals, and injections were administered at 0.5 mg kg⁻¹ intravenously and 1.0 mg kg⁻¹ intra-muscularly. A SRDL was then glued to the head using epoxy resin (Field et al. 2012).

Data processing

All data processing and statistical analysis were undertaken using the statistical software R (v. 3.1.2; R Development Core Team 2014). Data from seals with <200 dives and all dives shallower than 20 m were not considered in the analysis. Regions visited by southern elephant seals during their foraging trips were classified as either shelf (ocean depth < 1500 m) or open ocean (ocean depth ≥ 1500 m) habitats. A cut-off value of 1500 m was selected because this is the maximum depth of the Campbell Plateau, the primary shelf habitat in the region (Adams 1962). In addition to areas associated with the Campbell Plateau, shelf habitats also included sections of the Antarctic continental shelf and regions of the Mac-

quarie ridge and Pacific-Antarctic ridge that rose above 1500 m.

Horizontal movement data

The most likely horizontal path taken by the seals was estimated from the ARGOS tracking satellite system data transmitted from the SRDLs with state space models (SSM) using the R package *bsam*. ARGOS positional data are grouped into 7 location classes based on quality (LC); 3, 2, 1, 0, A, B, and Z, which have a 68th percentile spatial error ranging from 0.5 km (LC 3) to 10 km (LC B) (Vincent et al. 2002). The use of SSM to process the location data accounts for error introduced by lower ARGOS location class data (Jonsen et al. 2005). Using *bsam*, each seal's location was estimated at 2 h intervals.

Vertical movement data

For each dive, the bottom-time was calculated as the amount of time that a seal spent below 80 % of the dives' maximum depth (Bailleul et al. 2008). Dive statistics were then averaged across 2 h intervals, coinciding with the 2 h location data ('dive locations').

2D and 3D foraging metrics

We used 2 metrics for inferring foraging behaviour from movement data: first passage time (passage-time) and first bottom time (bottom-time) (Fauchald & Tveraa 2003, Bailleul et al. 2008). These are based on the same underlying methodological framework (Fauchald & Tveraa 2003, Bailleul et al. 2008), making them directly comparable. Passage-time is a 2-dimensional metric considering just the horizontal component of the seals' movement, while bottom-time adds the third-dimension of dive behaviour into its identification of foraging behaviour.

A diving animal's path can be described by a series of points, each with an associated time, location and set of dive statistics. Passage-time and bottom-time determine the relative behaviour at each location by centring a circle of a given radius around each point and then either calculating the time it would take for the animal to cross that circle (passage-time) or the residuals of the linear model ($\log[\text{dive bottom time}] \sim \text{maximum depth} + \text{dive duration}$) of all dives within that circle (bottom-time) (Fauchald & Tveraa 2003, Bailleul et al. 2008). Passage-time values increase for

sections of an animal's path where tortuosity is greatest, indicating ARS. Positive bottom-time residuals indicate an animal spent more time at the bottom of a dive than average for a dive of that duration, and this is summed for all dives made within the radius of the circle, providing a measure of relative dive effort (Bailleul et al. 2008). The scale at which ARS behaviour and dive effort occurred was then estimated by repeating these calculations for circle radii ranging from 5 to 500 km at 5 km intervals and plotting the log of the variances in passage-time and bottom-time values against circle radius, with the peak in variance corresponding to the optimal circle radius for that metric (Fauchald & Tveraa 2003, Bailleul et al. 2008). Both foraging metrics were used as a continuous variable.

Habitat models

A total of 5 environmental variables were used in the habitat models; sea surface temperature (SST, °C), sea surface height anomaly (SSHA, cm), chlorophyll *a* concentration (ChlA, mg m⁻³), wind speed (m s⁻¹) and current speed (m s⁻¹) (see Table S2 in the Supplement). Due to the high correlation between SST and latitude at a large scale, such as the open ocean habitat, this metric was only used in shelf habitat models. Each environmental variable was chosen based on previous findings showing that it influenced the at-sea behaviour of seals in some way (Table S2). Daily ChlA data were aggregated to 8 times the resolution to increase data coverage in these otherwise patchy data. All 5 variables were scaled using the R function *scale* to account for their different numeric scales and transformed where necessary (Table S2).

Candidate habitat models were developed for each foraging metric in each habitat type—shelf or open ocean—at a daily temporal scale, generated from the aggregation of the 2 h dive location data. Models were developed using only locations for which data for all environmental variables applicable to that habitat type were present.

LMMs were used to compare each response variable (first passage time [FPT] and first bottom time [FBT]) with the 5 environmental variables and individual seal included as a random term (function *lmer* in R package *lme4*). LMMs were chosen because they account for correlations between observations by including seal ID as a random effect, accounting for the fact that not every data point comes from a different seal (Bestley et al. 2010). These were then

compared to the null model (no environmental parameters but with the random term) using their conditional Akaike information criterion (AIC) values (cAIC) (Burnham & Anderson 2002, Yu 2016). All environmental variables that performed better than the null model were combined additively in every combination. Each of these were compared with the original 5 single variable models and null model using their cAIC. Top models for each foraging metric in each habitat type were identified as the most parsimonious model with a delta cAIC value less than 2.

A cross validation analysis was undertaken on the top model for each foraging metric (FPT and FBT) in each habitat (shelf and open ocean) to quantify the predictive ability for that model (James et al. 2013). A random location was extracted, and the model was run on the remaining data and then used to predict the foraging metric value of the withheld observation. This process was repeated for the number of observations in the data subset of interest (shelf habitats, *n* = 162; open ocean habitats, *n* = 1442).

The predictive performance of each model was determined by comparing the observed foraging metric values against the predicted values using linear regression. Models with greater predictive capacity were those where both the adjusted R² values and regression line gradients were closest to 1.

Estimated population-level habitat usage map

To demonstrate the performance of the models with the greatest predictive capacity for shelf and open ocean habitats, important foraging habitats were estimated for southern elephant seals across the temporal and spatial domain of the individuals in this study. Summer climatology and bathymetry rasters were sourced from Raymond (2012, updated 2014) to match the spatial and temporal range of the individuals in this study. All data were gridded at 0.1° × 0.1° south of 45° S (corresponding to the spatial extent of the tracking data set). The models were then used to assign a predicted foraging value to each 0.1° × 0.1° grid cell, based on the environmental data for that cell.

RESULTS

Dive and trip statistics

Individual seals *Mirounga leonina* from both sexes dispersed widely from their haul-out locations cover-

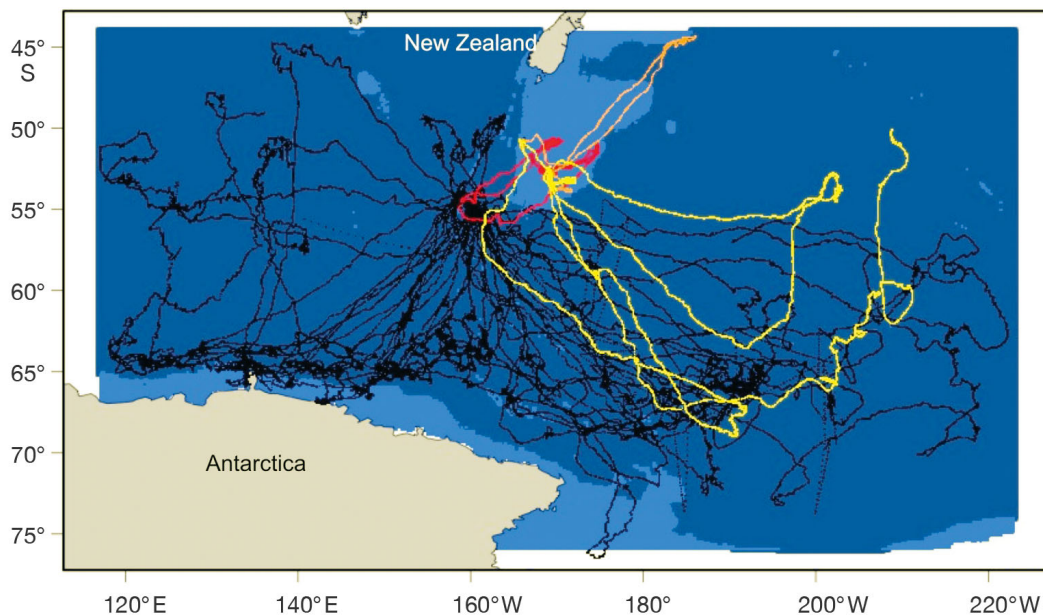


Fig. 1. Foraging tracks of male (red: adults, orange: sub-adults, yellow: juveniles) southern elephant seals departing from Campbell Island in 2012 and 2013 and female (black: all adults) southern elephant seals departing from Macquarie Island between 2004 and 2010. Light blue indicates shelf (≤ 1500 m) habitat, dark blue indicates open ocean (>1500 m) habitat, and grey indicates landmasses

ing a region of the Southern Ocean from 76.50° S to 44.36° S and 117.01° E to 223.31° E (Fig. 1).

Trip durations ranged from 21 to 249 d. The mean trip duration (\pm SD) was 80.3 ± 40.9 d for Campbell Island males and 183.6 ± 66.3 d for Macquarie Island females (see Table S1 in the Supplement). The total distances travelled from tagging locations were variable, with males having a mean maximum of 775.0 ± 935.6 km, while females travelled a mean maximum distance of 2233.0 ± 695.1 km, with some females reaching >3500 km (Fig. 1, Table S1). Mean dive duration for a trip ranged from 13.0 to 36.3 min, with a mean of 22.1 ± 0.4 min for males and 27.7 ± 4.95 min for females. The longest recorded dive was 92.3 min by a female seal (SES-9919_04). Mean maximum dive depths ranged from 625.0 to 1388.8 m, with females having a mean maximum dive depth of 1002.9 ± 182.5 m and males of 826.9 ± 210.5 m and an overall maximum of 1388.8 m by a female (SES-M053-09).

Females spent 90.2% of their time in open ocean habitats, a total of 5159 d across all females. Of these, 3506 d (61.3% of the total time) were spent in Antarctic waters south of 60° S. Females spent just 563 d (9.8% of total time) in shelf habitats, 463 d of these (8.1% of the total time) associated with the Antarctic continental shelf, with the remaining 100 d (1.8% of total time) associated with the southern tip of the Campbell Island Plateau and the Macquarie Ridge

(Fig. 1). Males spent a total of 674 d (63.8% of the total time) in shelf habitats and 382 d (36.2% of the total time) in open ocean habitats. Of the total 382 d that the males spent in open ocean habitats, 362 d (94.8%) were attributed to just 2 juvenile individuals (SES-238 and SES-301), these 2 juvenile being the only males to spend the majority of their trips in the open ocean (93.1 and 98.4% of their foraging trips, respectively). These individuals were also the only males to travel into Antarctic waters south of 60° S, although neither reached the Antarctic continental shelf (Fig. 1). The remaining 6 males spent an average of just $3.7 \pm 4.6\%$ of their trips in the open ocean, spending the majority of their time in shelf habitats associated with the Campbell Plateau (Fig. 1).

2D and 3D foraging metrics

Each dive location was assigned a passage-time (2-dimensional) and bottom-time (3-dimensional) value (Fig. 2). The optimal scale for ARS detection differed between seals and methods. On average, bottom-time identified ARS at a larger spatial scale (72.0 ± 80.6 km) than passage-time (38.2 ± 60.0 km); however, the appropriate scale for each method differed substantially between seals.

Broad similarities existed between the 2 metrics, with 3 key areas identified as intensive foraging areas

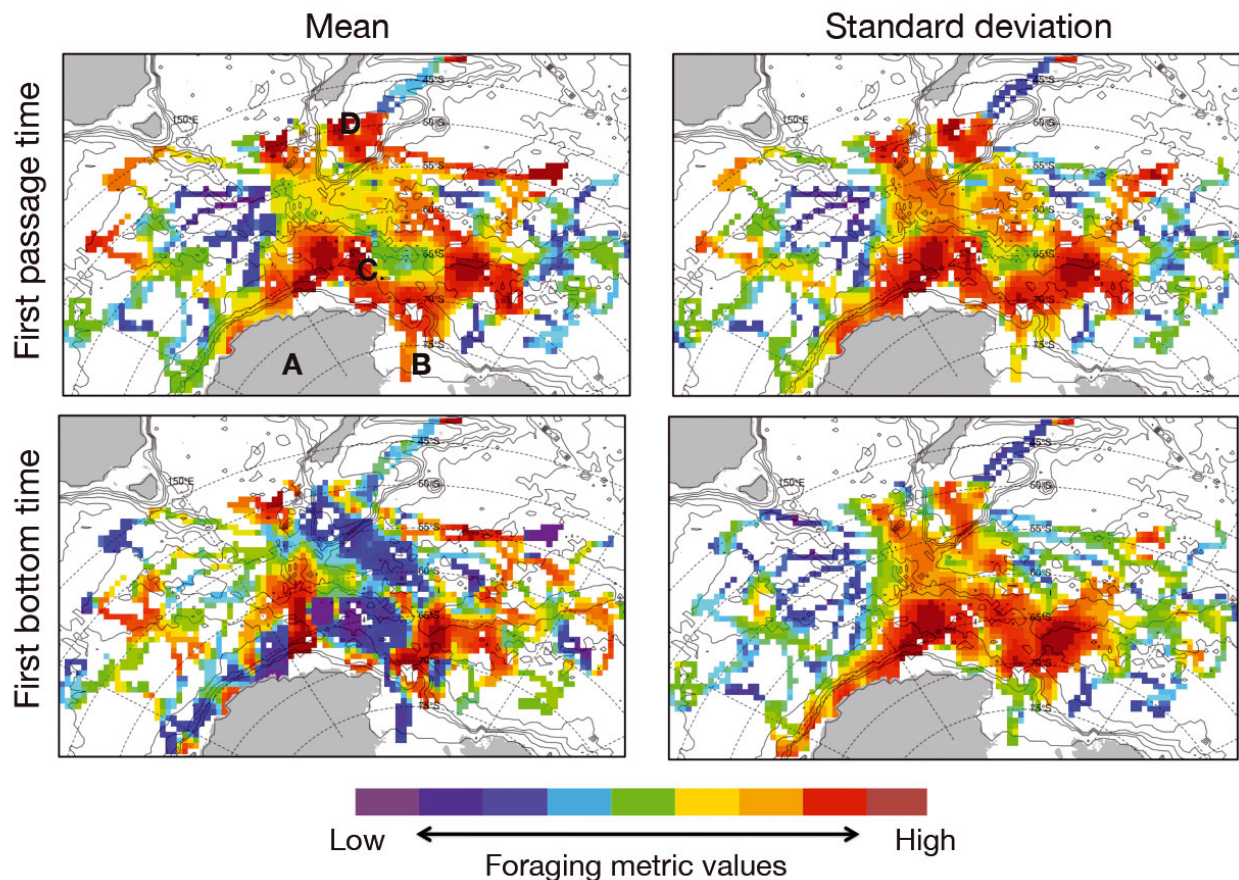


Fig. 2. Mean and standard deviation of each foraging metric calculated for all dive locations falling within a 60 × 60 km grid cell. Grid cell foraging metric values were aggregated by a factor of 3, before re-sampling each cell to return the grid to its original dimensions. Finally, the smoothed data were again re-sampled to only include grid cells that originally contained data. (A) continental eastern Antarctica, (B) the Ross Sea, (C) the Balleny Islands and (D) the Campbell Plateau

by each metric: (1) north of the Ross Sea, (2) close to the eastern Antarctic coast (~150° E to 165° E), and (3) west of the Campbell Plateau. Two of the most notable differences between the metrics were over the Campbell Plateau and north of the Balleny Islands where passage-time but not bottom-time identified intensive foraging activity (Fig. 2).

Seals exhibited considerable variability in terms of the foraging index allocated to them by each metric. A large standard deviation value was associated with many grid cells, particularly when mean foraging metric values were high (Fig. 2).

Table 1. Top models for each foraging metric in shelf and open ocean habitats. Model choice was based on the most parsimonious model with a delta cAIC value <2. For each top model, the slope of the linear model of predicted versus observed foraging metric values, plus or minus the standard deviation is listed, along with the adjusted R² value and the p-value. The direction of the effect of each environmental variable is indicated in parentheses. The model with the greatest predictive capacity, identified as the model with both an adjusted R² value and regression line slope closest to 1 in each habitat type, is in **bold**. ChlA: chlorophyll a concentration, SSHa: sea surface height anomaly, SST: sea surface temperature

	Bottom-time	Passage-time
Open ocean		
Top model	ChlA ⁽⁻⁾ + current speed ⁽⁺⁾ + SSHa ⁽⁺⁾	SSHa⁽⁻⁾ + current speed⁽⁻⁾
Slope	0.472850 × 10 ⁻² ± 1.3793 × 10 ⁻²	0.70842 × 10 ⁻² ± 1.196 × 10 ⁻²
R ²	0.4621	0.7188
p	<2.2 × 10 ⁻¹⁶	<2.2 × 10 ⁻¹⁶
Shelf		
Top model	Current speed⁽⁻⁾ + SST⁽⁻⁾ + SSHa⁽⁺⁾ + wind speed⁽⁻⁾	Current speed ⁽⁺⁾
Slope	0.82025 × 10 ⁻² ± 3.395 × 10 ⁻²	0.62479 × 10 ⁻² ± 4.046 × 10 ⁻²
R ²	0.8281	0.6624
p	<2.2 × 10 ⁻¹⁶	<2.2 × 10 ⁻¹⁶

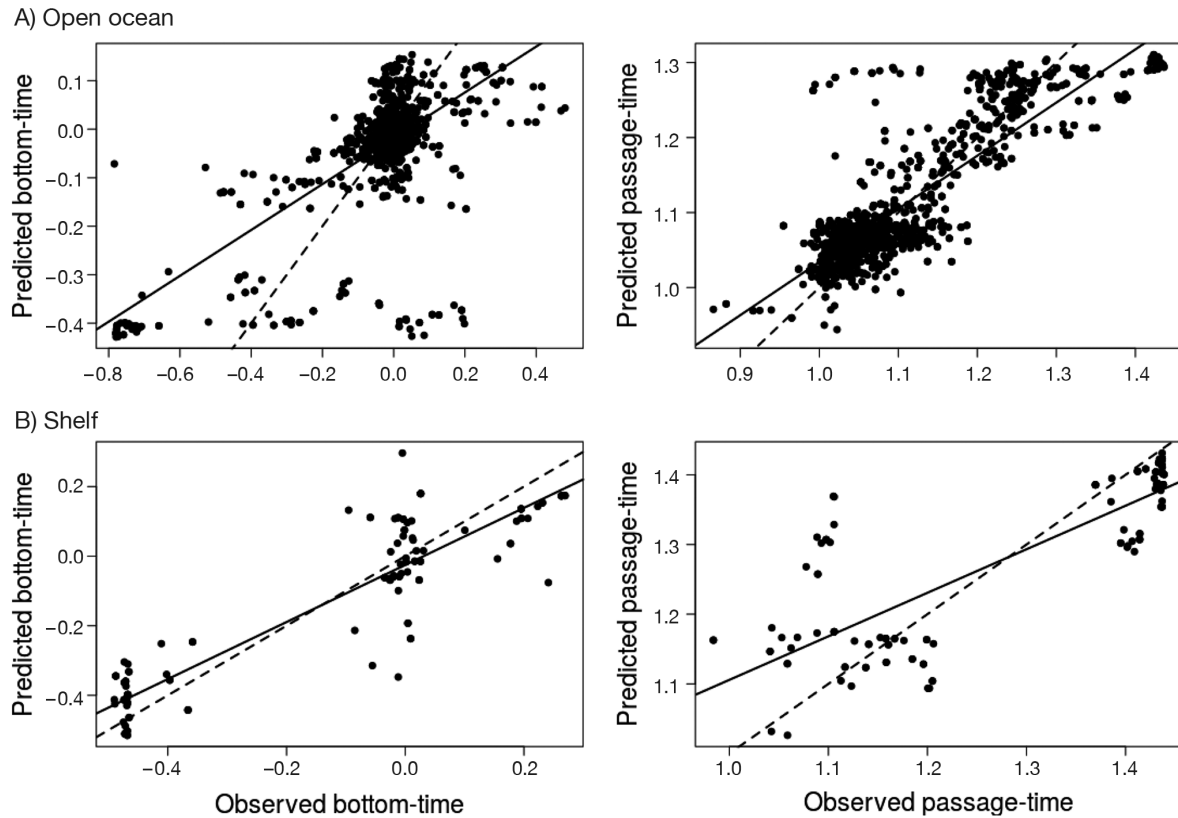


Fig. 3. Observed and predicted values from a bootstrap analysis of each foraging metric environmental model in (A) open ocean habitats and (B) shelf habitats. The solid line represents a linear model between the observed and predicted values. The broken line is the line of equivalence where the slope equals 1 and intercepts both axes at zero

Habitat models

Of the 746 and 3684 d spent by seals in shelf and open ocean habitats, respectively, only 164 d and 1442 d were used to model important foraging habitats for the population due to the lack of environmental data, primarily chlorophyll *a*, when satellite coverage was poor due to cloud or ice cover.

Based on cAIC values (see Table S3 in the Supplement), the most descriptive models for each foraging metric in the open ocean habitat were bottom-time related negatively to Chl*a* and positively to current speed and SSHA, and passage-time related negatively to SSHA and current speed (Table 1). In shelf habitats, bottom-time was related negatively to SST, current speed, and wind speed and positively to SSHA, while passage-time was related to singularly positive current speed values (Table 1, see Table S3).

Comparison of the observed and predicted model outputs from the cross validation indicated that for shelf habitats, bottom-time was the best metric. The bottom-time based habitat model displayed greater accuracy in its predictions compared to passage-

time, with a linear regression gradient between observed and predicted values of 0.82 ± 0.03 and an adjusted R^2 of 0.83. In contrast, for open ocean, passage-time was the best-performing model, with a regression slope and adjusted R^2 value closer to 1.00 (Fig. 3, Table 1).

Estimated population-level foraging habitat

Using the best model for each habitat type, potentially important southern elephant seal ARS regions were mapped throughout the range covered by individuals in this study based on regional environmental summer climatologies (Fig. 4).

In the open ocean, elevated passage-time values were predicted around the Antarctic ice edge, with extended regions north of the Ross Sea and off the eastern Antarctic coastline. Additional regions of elevated passage-time values were also predicted in much of the northern extent of the prediction region.

Over the Campbell Plateau, where the males in this study were primarily recorded, the shelf habitat

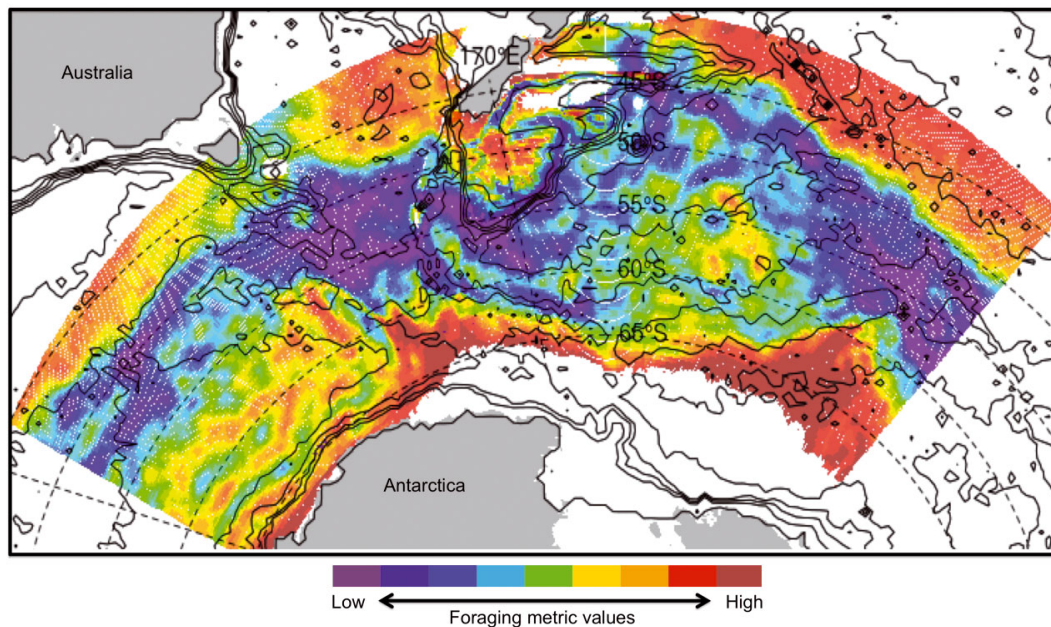


Fig. 4. Estimated regions of relative habitat quality based on the best shelf (bottom-time related to current speed + SST + SSHA + wind speed) and open ocean (passage-time related to SSHA + current speed) habitat models in sea ice-free regions of the Southern Ocean

model predicted regions of elevated bottom-time values, indicating above-average time spent at the bottom of a dive, around Campbell Island and Auckland Island. High bottom-time values were also predicted off the southern tip of New Zealand's south island (Fig. 4).

DISCUSSION

Given that elephant seals *Mirounga leonina* spend most of their time at sea diving, often to great depths, it is likely that behavioural metrics derived purely from surface-based movement data will provide only a coarse representation of their true behaviour (Bestley et al. 2015). Further, the very different foraging behaviours used by this species, with benthic feeding in shelf waters and mid-water foraging in open water, suggests that a single model is unlikely to adequately capture the complexity of habitat use. Habitat models and species distribution models are being increasingly used to understand which areas are important for marine predators (Raymond et al. 2015) and to predict how distributions are likely to change in the future (Hazen et al. 2013). With continuing environmental change, the ability to accurately predict a species current and future distribution and habitat use is becoming increasingly important.

Comparison of foraging metrics

Three concurrent regions of elevated passage-time and bottom-time values were identified (north of the Ross Sea, west of the Campbell Plateau, and off the eastern Antarctic coastline). However, the metrics differed in other regions, most notably over the Campbell Plateau and around the Balleny Islands (Fig. 2, locations C and D). While elevated passage-time values were detected, indicating reduced horizontal displacement speed and consequentially probable ARS behaviour, bottom-time values were low, indicating a below-average time spent at the bottom of dives.

The differences seen between these metrics highlight the need for careful consideration of movement metric choice in habitat modelling. First passage time and first bottom time use fundamentally different behavioural characteristics to calculate their values: time taken to cross a circle compared to the cumulative time spent in the bottom 20% of a dive. Because elephant seals are known to display different foraging behaviours depending on habitat and target prey species type, the related behavioural changes will be expressed differently in the various foraging metrics. Consequentially, caution must be taken in interpreting the results of such models. While it is generally assumed, based on the definition of ARS, that elevated passage-time and bottom-time values indicate foraging-like behaviour (Bailleul et al. 2008, Fauch-

ald & Tveraa 2003), we have shown that this is not always the case for southern elephant seals. In some circumstances, southern elephant seals may display a reduction in average bottom time in correlation with more profitable foraging grounds (Thums et al. 2013). Likewise, certain bathymetric features may compel a seal to move more linearly while foraging on prey, reducing the associated passage-time. Correct model interpretation therefore requires prior knowledge of a species foraging ecology.

Using 2- and 3-dimensional foraging metrics in habitat modelling

By employing different foraging metrics when seals were foraging pelagically in open ocean habitats and benthically in shelf habitats, we were able to reduce the common issue of poor model predictive capacity (e.g. Bradshaw et al. 2004, O'Toole et al. 2014), generating comparatively good predictive models for each habitat. While in open ocean habitats the use of a traditional 2-dimensional foraging metric produced the best predictive models, in shelf habitats the use of the 3-dimensional foraging metrics improved the model predictive capacity. The contrast in physical characteristics of open ocean and shelf habitats make different foraging techniques profitable in each. These results indicate that biophysical models that integrate animal behaviour and physical environmental variables may be necessary for making predications about habitat usage.

In comparison to the open ocean habitat, the area of shelf habitat used by seals in this study was relatively small. In the open ocean, the distance between foraging bouts may enable the 2-dimensional foraging metrics to detect behavioural change. In shelf habitats with less distance between patches, the additional information about diving behaviour may be required to distinguish separate foraging events.

Differing physical characteristics between shelf and open ocean habitats could also influence the relevance of the chosen environmental covariates for the models. For diving animals, ocean surface properties may not be the most appropriate indicators of foraging behaviour because these properties are not necessarily representative of the conditions encountered by the animal at depth (O'Toole et al. 2014). Despite weak water stratification over the Campbell Plateau in the summer months, the mixed layer depth becomes very shallow (<50 m) (Morris et al. 2001). Further, while in the open ocean physical features, such as eddies and prey distribution, have marked

surface expressions in terms of SSHa and ChlA, in shelf regions prey aggregations may be a response to finer-scale topographic related features not mirrored by an alteration in surface properties.

Estimated regional foraging habitat

Employing the best predictive models for each habitat to estimate regional habitat usage, the regions associated with the Antarctic ice edge, north of the Ross Sea, lower-latitude waters, and over the Campbell Island plateau were predicted to have high foraging metric values. The omission of sea ice locations, while necessary due to the unavailability of environmental data in conjunction with sea ice, restricted the spatial extent of our models, particularly for adult males. Male elephant seals forage in sea ice, with the marginal ice edge zone being a region of particularly high productivity (Bailleul et al. 2007). While adult females also sometimes make use of sea ice habitats, they tend to avoid it over winter (Bailleul et al. 2007, Muelbert et al. 2013).

A number of previous studies have identified the region north of the Ross Sea as a profitable foraging ground. Southern elephant seals from Macquarie Island have been found to display positive changes in drift rate, indicating increased body condition from foraging success, in the marginal ice zone of the Ross Sea (Biuw et al. 2007). Prey patch quality studies have also found the northern Ross Sea to be a high-quality prey region (Thums et al. 2013).

The open ocean model identified regions of high passage-time values based on low SSHa and current speed values (Table 1). Low SSHa values often indicate the presence of cyclonic cold-core eddies and can also be associated with frontal zones (Nel et al. 2001). Eddies exert a large effect on the local ecosystem. They can carry organisms between regions, produce favourable conditions for primary production through upwelling, and concentrate prey items near the surface within easy reach of predators (Nel et al. 2001, Godø et al. 2012, Bouchet et al. 2015). Eddies have previously been identified as important for a range of marine predators such as grey-headed albatross *Thalassarche chrysostoma* (Rodhouse et al. 1996, Nel et al. 2001) king penguins *Aptenodytes patagonicus* (Cotté et al. 2007), and southern elephant seals *M. leonina* (Cotté et al. 2015). Grey-headed albatross have been found to feed at the periphery of eddies, where fish and squid are attracted to the oceanographic feature by the presence of myctophids and crustaceans (Nel et al. 2001). Because

southern elephant seals also eat squid and myctophid fish (Bradshaw et al. 2003, Cherel et al. 2008, Banks et al. 2014), eddies may also provide them with profitable foraging grounds, and previous studies have found elephant seals target both cyclonic and anti-cyclonic eddy features during foraging (Campagna et al. 2006, Bailleul et al. 2010, Dragon et al. 2010).

The shelf model used low SST, weak current and wind speeds, and high SSHA as determinants of foraging habitats. The Campbell Plateau features these conditions, with cool sub-Antarctic mode water flowing up over the plateau and weak cyclonic and anti-cyclonic currents (Morris et al. 2001), the anti-cyclonic ones of which would result in higher SSHA values. Despite relatively low levels of primary production due to iron limitation, the Campbell Plateau supports a range of fish, bird and seal species (Bradford-Grieve et al. 2003). Other shelf habitats are favourable regions for elephant seals from a range of other populations, such as Kerguelen (O'Toole et al. 2014) and Peninsula Valdés (Campagna et al. 1999).

This study highlights the importance of metric choice when modelling elephant seal foraging habitats and of having a clear understanding of species foraging ecology when interpreting foraging metric results. By considering both horizontal and vertical movement data, we were able to produce robust predictive environmental models in both shelf and open ocean habitats. Identifying the variation in key environmental variables for habitat models in shelf and open ocean habitats is also important for accurately predicting how habitat usage may change in response to environmental change. The identification and application of the appropriate foraging and environmental metrics is an important step in understanding the fundamental relationship between environmental structure and animal performance, providing the basis for understanding how individuals and ultimately populations are affected by change.

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