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Animal Biotelemetry

TELEMETRY CASE REPORT

Behavior of satellite-tracked Antarctic minke whales (*Balaenoptera bonaerensis*) in relation to environmental factors around the western Antarctic Peninsula

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Abstract

Background: The Antarctic minke whale (*Balaenoptera bonaerensis*) is a relatively small baleen whale species and is well suited to life in the Antarctic pack ice. Information on their individual movement and distribution patterns is largely unknown due to their association with sea ice habitat where direct observations are limited. The primary objectives of this study are (1) to use satellite telemetry to quantify the movement patterns, distribution, and presumed foraging areas of Antarctic minke whales and (2) to assess the environmental conditions that are associated with areas used by minke whales along the western Antarctic Peninsula.

Results: Individual movement patterns from three Antarctic minke whales fitted with ARGOS-linked transmitters were analyzed with respect to environmental conditions. Behavioral states were identified using the Multi-Scale Straightness Index. Satellite telemetry revealed disparate behavioral patterns between these three individuals. Generalized additive model analysis demonstrated environmental variables, particularly sea ice, bathymetry, and sea surface temperature, are the best predictors of presumed foraging areas.

Conclusions: Satellite telemetry from three individuals revealed Antarctic minke whale summer foraging spaces are highly individualized but can generally be associated with pack ice habitat over the continental shelf. The coupled relationship between minke whales, krill, and sea ice suggests that these whales may be sensitive to changes in sea ice concentration, extent, and duration, making them particularly vulnerable to climate change.

Keywords: Antarctic minke whales, Satellite telemetry, Remote sensing, Sea ice

Background

Since 1950, dramatic physical changes have been observed and monitored in the Southern Ocean, including the warming of the atmosphere and deepwater circumpolar current, increased circumpolar flow, and regional loss in sea ice extent and duration [1–5]. The physical environment dictates the location and timing of algal blooms, which in turn influences the krill population and higher tropical order predators such as penguins, seals, and baleen whales [6, 7].

Little is known about the population distribution and individual movement patterns of Antarctic minke whales (*Balaenoptera bonaerensis*). Historic whaling records indicate that a proportion of the population is believed to migrate to winter breeding grounds in lower latitudes, such as northern Brazil, central South Pacific Ocean, and eastern and southern Indian Ocean [8–10]. Whaling records prior to the 1990s, however, classified all minke whales as one species (*Balaenoptera acutorostrata*), so the proportion of these catches that were actually *B. bonaerensis* (Antarctic minke whales) is unclear. Modern observations are scarce, and migration patterns are largely unknown for the Antarctic minke whale. Baleen whale occurrences and habitat conditions are typically

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mapped from observations made on ships unable to penetrate sea ice, so Antarctic minke whales were found in an association with the sea ice extent. Recent research, using icebreakers and helicopters, has shown that this species also occurs throughout the ice pack and within polynyas [11–13]. Antarctic minke whales have small, compact bodies, and short fins, making them well suited to life in the pack ice where they can easily maneuver in narrow spaces between ice floes [11]. Hard, pointed rostrums also allow minke whales to break through thin ice to breathe, creating holes, which in turn may provide an ecological service to other air-breathing marine predators such as seals and penguins [11, 14].

While many questions remain about the annual migration patterns of Antarctic minke whales, intra-seasonal movement patterns of the species have also not yet been studied. Modern advances in GPS and ARGOS satellite telemetry allow scientists to remotely acquire large quantities of animal movement data at fine spatiotemporal scales [15]. Greater computing power has also enabled researchers to describe and model individual movement patterns and identify behavioral information that is not directly observable [15, 16]. To better understand Antarctic minke whale habitat and movement patterns, we attached satellite tags to individual minke whales, tracked their daily movements, and related their behaviors to environmental conditions.

The primary objectives of this study are (1) to use satellite telemetry to quantify the movement patterns, distribution, and presumed foraging areas of Antarctic minke whales and (2) to assess the environmental conditions (sea ice, sea surface temperature, and bathymetry) that are associated with areas used by minke whales along the western Antarctic Peninsula (WAP).

Methods

Satellite telemetry

Three Antarctic minke whales were fitted with implantable smart position and temperature transmitting (SPOT-5) tags (Wildlife Computers, Redmond, WA, USA), using a similar method to [17], on February 9, 2013. The tags provided satellite-derived locations through the ARGOS system on a 4-h on, 8-h off duty cycle triggered by a conductivity switch. The present study uses only the tag's location data. The ARGOS system utilizes a multi-model Kalman filter algorithm to provide estimated location and error ellipses for all points [18].

Movement analysis

Locations were fit to a Bayesian state-space model in R [19, 20]. This model was used to account for error in ARGOS-derived location estimates and to normalize the data into regularly spaced locations with a 6-h time step. Tracks were modeled for 40,000 iterations, a 20,000 sample burn-in, and with a retention of every 20th sample to reduce sample autocorrelation. Model convergence and sample autocorrelation were visually assessed with autocorrelation and trace plots. Distance, speed, angle, and turning angle between time steps were estimated using the *move* package [21].

Track tortuosity, or the degree to which a track deviates from a straight line, can characterize different behavioral states, such as resting, migrating, or foraging [22]. Here we used the Multi-Scale Straightness Index (MSSI) to analyze the tortuosity and identify different behavioral states throughout each track [16]. The MSSI was chosen over the behavioral states produced by the Bayesian state-space model (SSM) for its ability to detect average behavioral states over different temporal scales as well as its simplicity in implementation and interpretation. The MSSI and SSM perform relatively equally in classifying behaviors for datasets with low to medium spatial noise, but the MSSI outperforms SSMs in the case of noisy data [16]. While it is difficult to assess the relative noise in our current dataset, we chose to use the MSSI as the conservative approach to maximize performance of our behavioral classifications, as even under low noise conditions the MSSI will perform equally as well as SSMs [16].

The MSSI is an adapted version of the Straightness Index, which is a simple ratio of distances [23]. Instead of evaluating the degree of straightness over the entire track, the MSSI computes track straightness multiple times and over a range of time scales, permitting the identification of distinct behavioral states throughout the track. To compute the MSSI, each track was analyzed at intervals equal to the fixed 6-h time step (s) between locations. These intervals are referred to as the granularity (g), or the temporal resolution at which the track was viewed. The observational sliding window (w) is the length of time over which we computed the MSSI. The MSSI is then defined as follows [16]:

$$S\left(t_j + \frac{w}{2}, g, w\right) = \frac{d_j(w)}{\sum_{k=0}^{s_2-1} d_{j+k_{s1}}\left(g\right)}$$

The first argument of S is the time at which the MSSI is defined and is shifted to be in the center of the window, the second argument is the granularity, and the third argument is the window. The numerator is the great circle distance between two locations at the time interval of w, and the denominator is the total distance traveled between the same two locations when viewed at the time interval of g.

The value of S is always between 0 and 1, where values close to 0 indicate more tortuous segments and values close to 1 indicate more straight-line movement.

Segments of the tracks with low MSSI values (≤ 0.4) were considered periods of area-restricted search (ARS) and segments with high MSSI values (≥ 0.6) were considered periods of transit. Dominant behavioral states could not be definitively determined with intermediate MSSI values (between 0.4 and 0.6) and were therefore considered a period of uncharacterized behavior.

The environment must also be considered when classifying behavioral states. The heterogeneity and dynamic aspect of dense pack ice will restrict movement between ice floes, causing their tracks to seem highly tortuous when it is unclear whether the individual is displaying ARS or transiting behavior. The purpose of this study is to quantify the movement patterns and behavior of Antarctic minke whales in relation to sea ice habitat, so the identification of ARS is critical to understanding their foraging behavior. These whales are known to consistently feed in this type of sea ice environment [24], so the present study will consider ARS as including all foraging behavior.

Careful consideration must be taken when defining the size of the window. It is recommended to choose the parameters after examining the MSSI over the entire track length [16]. Values should be chosen to represent the temporal scale of the desired behavioral states in order to identify changes in behavior. One major limitation of this dataset is the time step between locations. A temporal resolution of 6 h may be too coarse to identify each feeding bout during the day. A larger window, however, can compensate for this limitation by encompassing multiple bouts of the same behavior and providing an indication of the predominant behavior during that time. Therefore, we used a granularity of 1 (6 h) and a window size of 25 points, which equates to approximately 6 days. The results of our analysis will therefore provide behavioral state information on a multi-day to weekly scale rather than a fine scale, hourly analysis. The MSSI is well equipped for determining average behavioral states over a period of days and is therefore our chosen method for defining behaviors that will be associated with environmental covariates.

Environmental data

Remotely sensed data were used to determine potential covariates in the relationship between Antarctic minke whale movement and their environment. Daily sea ice concentrations were obtained from the National Snow and Ice Data Center (NSIDC), which were estimated from passive microwave data obtained by the special sensor microwave imager/sounder (SSMIS) onboard the defense meteorological satellite program (DMSP) satellite F17 using the NASA Team Sea Ice Algorithm, at a 25 km resolution [25]. This large spatial resolution was too coarse for our habitat prediction and was excluded from the generalized additive models. Sea ice extent (SIE) defines the ocean area covered by sea ice. A threshold of minimum sea ice concentration (15%) is used to identify the SIE. Daily SIE vector polygons were obtained from the National Ice Center, who use multiple satellite imagery sources including passive and active microwave, visible, and infrared sensors to create composite ice charts with a resolution down to 50 m (Courtesy of the U.S. National Ice Center). For sea surface temperature, NOAA's daily Optimally Interpolated Sea Surface Temperature (OISST) version 2 grids were used [26, 27]. These grids are constructed by blending observations from satellites, ships, and buoys to produce spatially complete ¼° by ¼° grids. NOAA uses comparisons with sea ice concentration grids to simulate and interpolate SSTs adjacent to and under sea ice cover. Gridded ocean depth was obtained by the International Bathymetric Chart of the Southern Ocean (IBCSO), a regional mapping project of the general bathymetric chart of the oceans (GEBCO), at a 500 m resolution [28]. The varied spatial resolutions of these data, although potentially affecting the model results, allowed us to incorporate daily environmental conditions into our habitat analysis. The primary goal of this study is to analyze Antarctic minke whale satellite telemetry to assess intra-seasonal movement patterns and environmental distribution.

Environmental analysis

Daily distance to the sea ice extent (SIE) was calculated using ArcGIS 10.3.1 ModelBuilder [29]. Whale location timestamps were iterated and matched with the corresponding SIE polygons. The geodesic distance between whale locations and SIE polygons was calculated with the *Near* tool, resulting in 4 distance calculations per day for each whale. Distances computed within the pack ice were multiplied by -1 to differentiate them from distances calculated in open water.

Gridded sea ice concentration (SIC), sea surface temperature (SST), and bathymetry were also evaluated using ArcGIS ModelBuilder. The SIC and SST models iterated through the timestamps in both the whale locations and raster grids to temporally and spatially match the corresponding data. Grid cell values were extracted at each whale location using the *Extract Multi Values to Points* tool. Since bathymetry is a temporally static dataset, the *Extract Multi Values to Points* tool was applied to the entire track without iterating through timestamps. We also calculated the environmental change between timestamps, which resulted in four additional variables: change in distance to the SIE (ΔSIE), change in SIC (ΔSIC), change in SST (ΔSST), and change in bathymetry (Δbath).

To test for significant changes in habitat, change-point analysis and Mann–Whitney *U* Tests were performed using the *changepoint* [32] package in R. Change-point analysis estimates the point at which the statistics of a series significantly changes. We used the mean as our statistical property of change. Therefore, we identified the point at which each whale's average environmental condition significantly shifted. Mann–Whitney *U* tests were chosen because the data were not normally distributed.

Generalized additive models (GAMs) determined nonlinear relationships between environmental covariates and the MSSI, identifying which environmental conditions are most associated with presumed Antarctic minke whale foraging spaces. The end of the foraging season was individually defined based on the distance to the SIE and MSSI. Each trajectory was truncated at the point at which their distance to the SIE progressively increased and their behavior switched from primarily area-restricted (foraging) to primarily transient (migrating). The remaining portions of the tracks were disregarded for the remainder of the present study, but will be incorporated in future work analyzing migratory behavior.

For each track, GAMs were fit with the *gamm4* package [31] in R with a Gaussian error distribution. Models were built using varying combinations of environmental variables with correlations less than 0.7 to reduce multicollinearity. Two GAMs were generated for each whale: including all uncorrelated variables and extracting only the distance to SIE variables to evaluate whether ice extent alone can influence the MSSI. The Akaike information criteria (AIC) provided a measure to identify the most parsimonious model that explains the most variance using the least number of variables. To compare the two GAMs generated for each whale, the model with the minimum AIC value was chosen [32]. Finally, we performed a fivefold cross-validation resampling procedure to validate our models with the area under the curve (AUC), an estimation of the receiver operating characteristics. The AUC provides a measure of model accuracy that is independent of a particular threshold and assesses the true and false positive error fraction [33]. An AUC of 1 demonstrates ideal model performance, whereas AUCs < 0.5 indicate the models are performing no better than random.

Results

Distribution and movement

Tag IDs 112745, 112747, and 112750 will hereafter be referred to as Whales 1, 2, and 3, respectively. The tags reported locations for 109, 111, and 180 days (Table 1). During the first few weeks of February, the whales remained in Wilhelmina and the adjacent bays, after which they traveled in different directions (Fig. 1). Whale 1 traveled northeast into the Scotia Sea, Whale 2 traveled west along the coast before migrating north into the Pacific Ocean, and Whale 3 remained in the bays for much of its tag's lifetime until June when it migrated north.

Approximately constant azimuth frequencies and heavily right-tailed distance frequencies indicated these whales demonstrated two behavioral states: switching between periods of long distance, relatively straight travel and periods of short distance, highly tortuous movement. Individually, each whale in this study exhibited different patterns of behavioral states throughout the lifetime of each satellite tag (Fig. 2). All three whales, however, demonstrated increasing average MSSI values as the season progressed (Table 2), indicating a gradual transition into more straight movement and migratory behavior.

Foraging habitat

The whales' tracks were truncated before their northward migration to isolate the foraging season on 22 May, 25 April, and 8 June for Whales 1, 2, and 3, respectively. During the foraging season, environmental conditions were evaluated to characterize foraging habitat.

Each individual was associated with different sea ice conditions throughout the study period (Fig. 3, Table 3). For the majority of the foraging season, Whale 1 remained in pack ice concentrations greater than 50%. Whale 2 followed the coastline and SIE as it traveled through the Bellinghausen and Amundsen seas, predominantly within 50 km of the SIE. This whale remained in low ice concentrations, less than 50%, for its entire foraging season. Whale 3 remained in the bays of the WAP, close to the SIE and in low SIC.

Bathymetric and sea surface temperature conditions were less varied among these individuals (Fig. 3). Whales

Table 1 Summary of satellite tracking data from 3 Antarctic minke whales tagged in Wilhelmina Bay on February 9, 2013

Tag ID	Deploy location	Last transmission	Days active	Total points	Modeled points	Track length (km)
112745 (Whale 1)	62°14′50″S 64°41′09″W	May 29, 2013	109	2662	436	6401
112747 (Whale 2)	62°14′30″S 64°41′22″W	May 31, 2013	111	1738	443	12,543
112750 (Whale 3)	62°15′09″S 64°38′11″W	August 8, 2013	180	3001	719	13,152

Total points indicate all locations determined by the ARGOS satellite tags, whereas modeled points show locations that were modeled using a first-difference correlated random walk model generating locations every 6 h

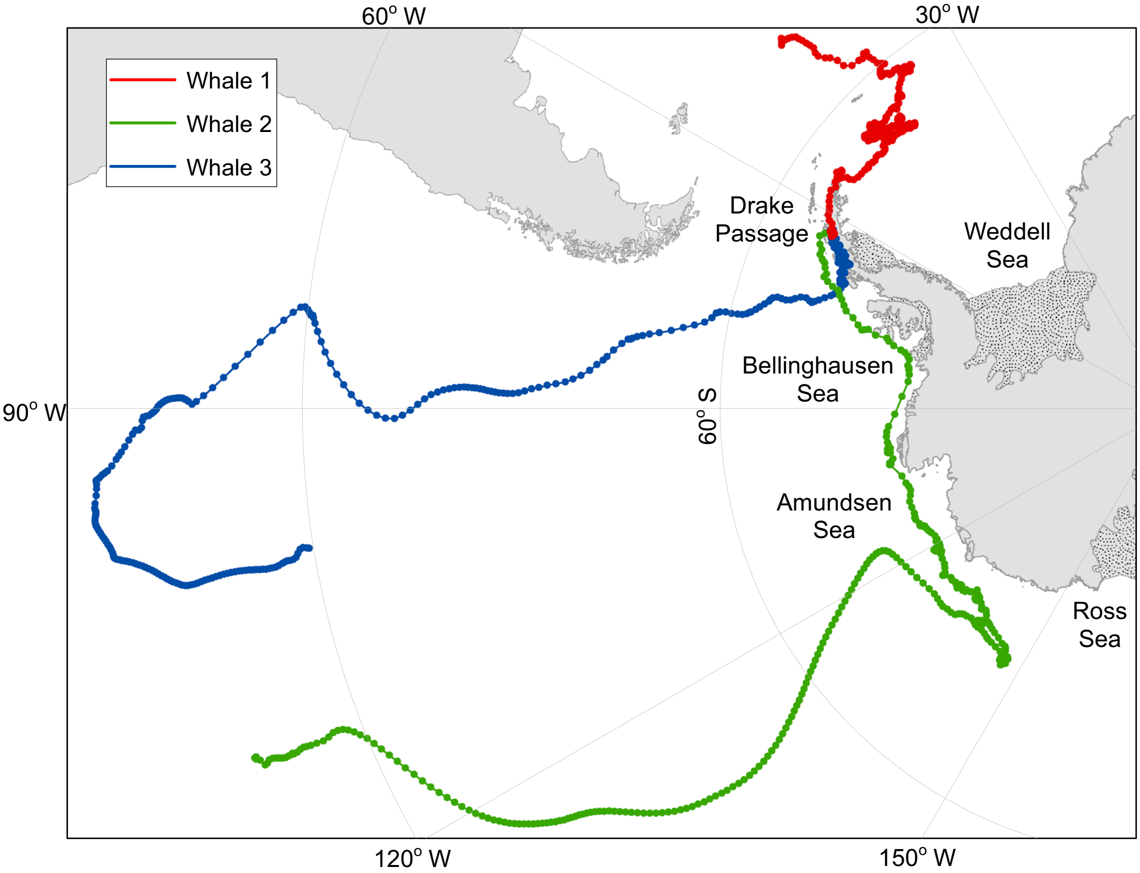

Fig. 1 Trajectories of 3 Antarctic minke whales tagged on February 9, 2013, in Wilhelmina Bay. Tracks show results of the first-difference correlated random walk model with a step interval of 6 h. Antarctic ice shelves are shown in stippled gray, and continental boundaries are shown in gray

1 and 2 demonstrated bimodal distributions in bathymetry, remaining in the shallow waters of the continental shelf early in the season and moving into deeper water as the season progressed. Whale 3, however, remained in shallow water, less than 500 m deep, for the duration of its foraging season. Each individual was predominantly associated with negative SSTs, coinciding with their use of sea ice habitat.

Change-point analysis revealed the same change in environmental habitat with regard to the direction of habitat change, yet the magnitude and timing differed (Fig. 3, Table 3). Each of these habitat shifts was statistically significant at an alpha level of 0.01. The majority of these habitat shifts took place from late February to mid-March, with two exceptions: Whale 3 experienced the most significant change in SIC on 1 June and did not significantly change its bathymetric conditions throughout its foraging season. Each whale's distance to the SIE decreased to negative values in early March, indicating a shift into pack ice habitat. This association with pack ice is also evident in their shift to higher ice concentrations. Whales 1 and 2 remained in the shallow waters of the continental shelf until mid-March when they moved into significantly deeper waters (Table 3). Each whale experienced a negative shift in sea surface temperature. For Whales 1 and 2, the temperature shift coincided with their changes in ice conditions. Whale 3's shift into cooler waters, however, occurred earlier than significant changes in sea ice conditions, which may be a result of remaining in the bays of the WAP for the majority of the study period. The significant change in Whale 3's distance to the SIE is a result of the unusually low ice extent between 4 and 8 March. Instead of traveling into open water, this individual remained in Andvord Bay during this fluctuation in ice conditions.

Significant differences were also detected between transiting and foraging behaviors (Table 4). Whale 1 demonstrated a greater negative distance to the SIE (indicating the whale was farther inside the pack ice) during ARS. This individual was also associated with shallower depths and slightly warmer waters while exhibiting foraging behavior. Whale 2 demonstrated foraging behavior

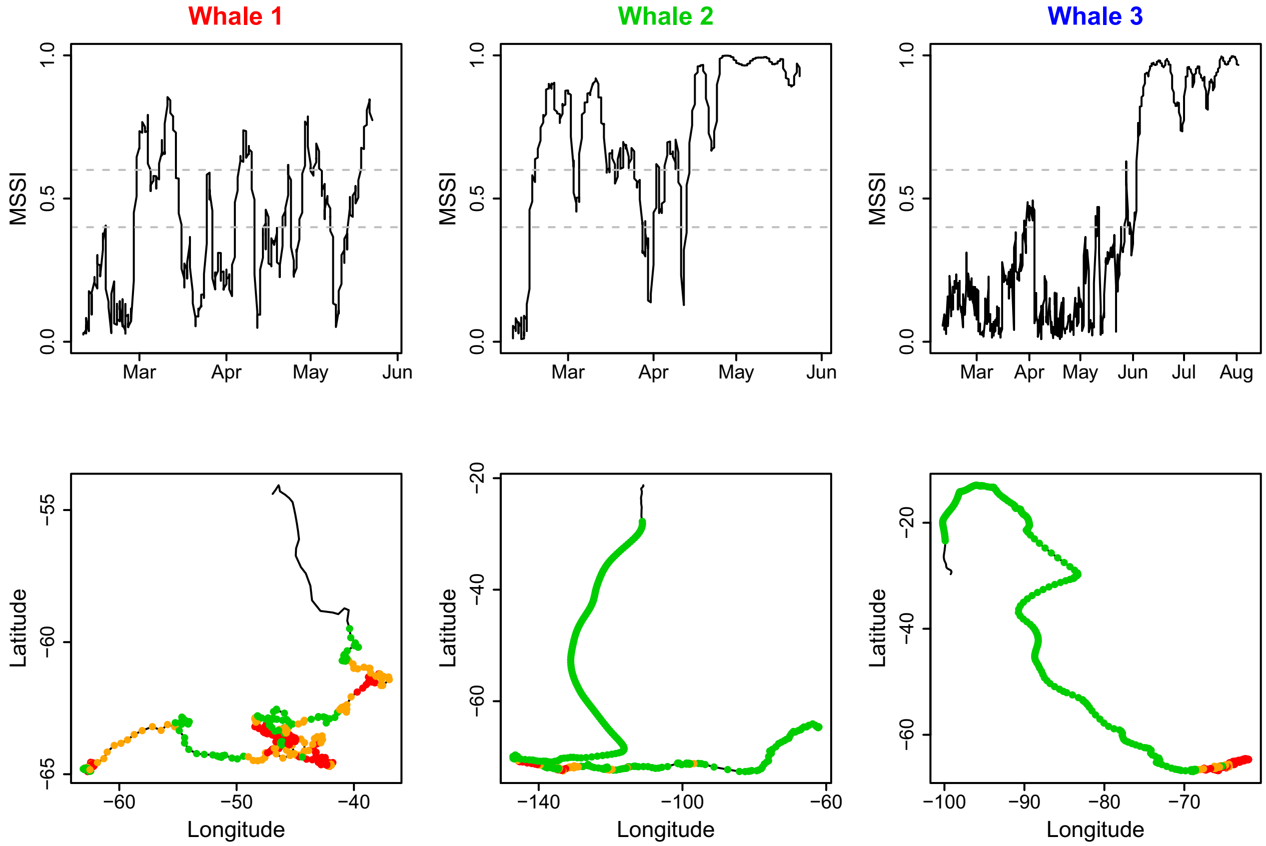

Fig. 2 Results of the MSSI computation over each track length. The top row shows the MSSI for the trajectory data with a fixed granularity and window size, $g = 1$ and $w = 25$. The second row shows the trajectory data in spatial coordinates with points colored according to approximate behavioral states, where green points represent MSSI values ≥ 0.6 (transiting), red points represent MSSI values ≤ 0.4 (ARS), and orange points represent uncharacterized behavioral states (MSSI values in the 0.4–0.6 buffer). Colored points are absent from the terminus of each track due to the window size restrictions

Table 2 Monthly MSSI values for each track (mean ± standard deviation), where MSSI ≥ 0.6 indicates transiting behavior and MSSI ≤ 0.4 indicates ARS

	Whale 1	Whale 2	Whale 3
Total track	0.40 ± 0.23	0.72 ± 0.26	0.44 ± 0.37
February	0.18 ± 0.14	0.55 ± 0.34	0.15 ± 0.06
March	0.46 ± 0.24	0.65 ± 0.19	0.18 ± 0.12
April	0.42 ± 0.18	0.73 ± 0.22	0.13 ± 0.13
May	0.49 ± 0.20	0.97 ± 0.03	0.26 ± 0.13
June	–	–	0.86 ± 0.16
July	–	–	0.94 ± 0.05
August	–	–	0.97 ± 0.01

The tags on the first two whales discontinued transmission in May, whereas the third whale's tag remained transmitting until August

within pack ice habitat as seen by a greater negative distance from the SIE and a greater sea ice concentration. Whale 3, however, exhibited foraging behavior in less dense pack ice, shallower depths, and warmer waters.

Model predictions

Each model run is documented in Table 5 with dependent variables: R^2, ΔAIC, and AUC before and after k-fold cross-validation. Little change was observed in the AUC before and after cross-validation, demonstrating sufficient model performance. Model selection was based on the ΔAIC, AUC, and R^2. The models that included all uncorrelated covariates, instead of distance to the SIE variables only, were the most parsimonious. Variables representing the change in environmental condition

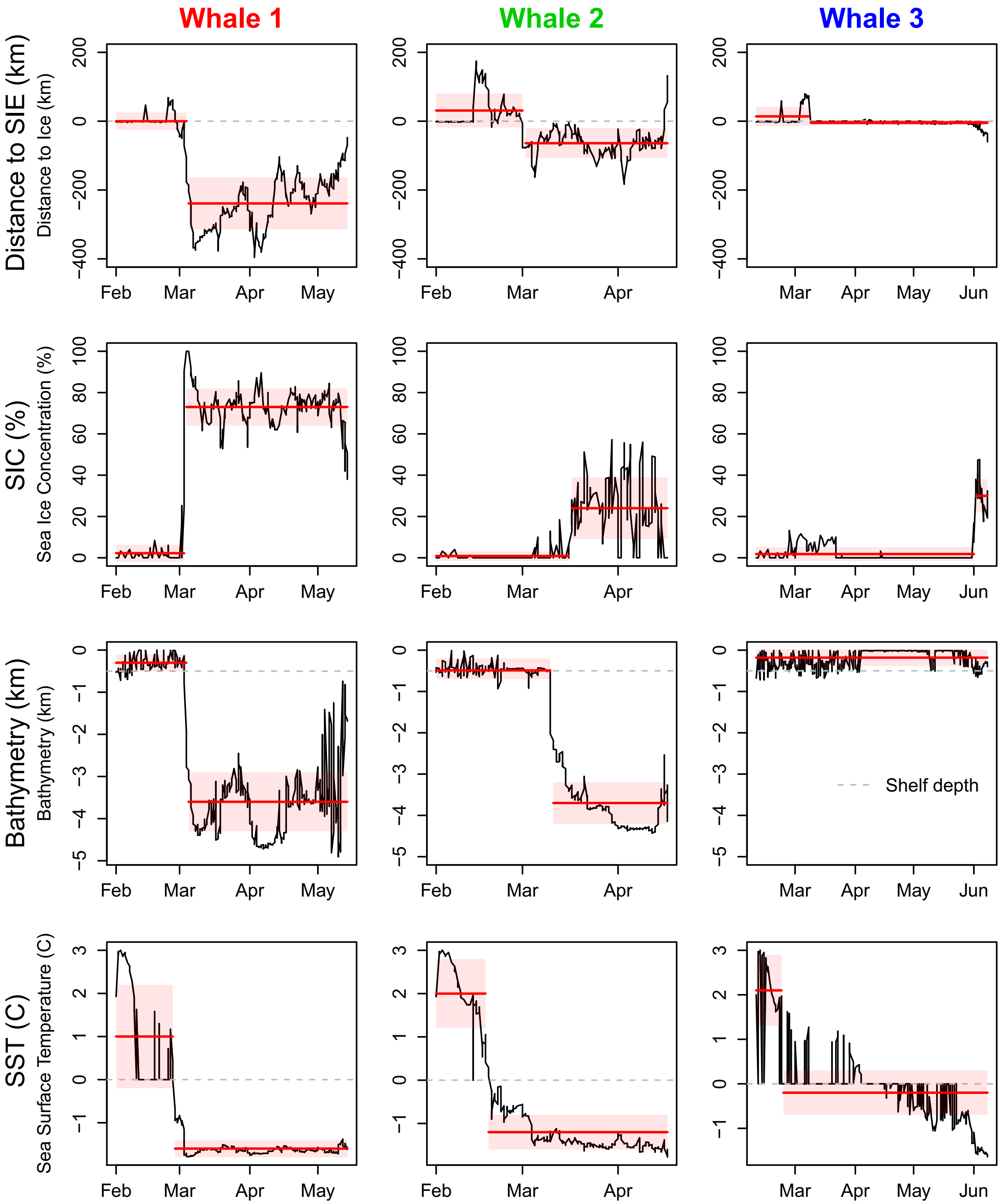

Fig. 3 Changes in individual habitat during the foraging season. Negative distance to SIE values indicates the whale is within the pack ice. Red bars indicate average values for the period before and after the change-point analysis state shift, with shading indicating ± 1 standard deviation. Whale 3 did not demonstrate a significant change in bathymetry

Table 3 Summary statistics (mean ± standard deviation) of change-point analysis using Mann–Whitney *U* tests before and after the habitat shift illustrated in Fig. 3

	Date	Before		After	
		N	Mean ± SD	*N*	Mean ± SD
Whale 1					
SIE (km)	12 March	110	−0.42 ± 25.21	286	−239.26 ± 75.51
SIC (%)	11 March	106	2.20 ± 4.28	290	73.77 ± 9.09
Bath. (km)	12 March	110	−0.33 ± 0.23	286	−3.66 ± 0.77
SST (C)	6 March	91	1.04 ± 1.26	305	−1.61 ± 0.17
Whale 2					
SIE (km)	9 March	106	30.95 ± 49.15	191	−64.08 ± 43.90
SIC (%)	24 March	169	0.85 ± 2.41	128	24.08 ± 15.80
Bath. (km)	18 March	145	−0.50 ± 0.22	152	−3.77 ± 0.58
SST (C)	25 February	62	2.04 ± 0.76	235	−1.25 ± 0.42
Whale 3					
SIE (km)	8 March	97	14.40 ± 28.18	332	−4.55 ± 7.47
SIC (%)	1 June	403	1.90 ± 3.47	26	30.25 ± 8.46
Bath. (km)	–	–	–	–	–
SST (C)	22 February	46	2.13 ± 0.87	383	−0.21 ± 0.57

All *U* tests listed are significant with $p < 2.2\mathrm{e}{-16}$. SIE specifically refers to the whales' distance to the sea ice extent, with negative values indicating the whale is within the pack ice

Table 4 Differences in foraging and transiting habitat (mean ± standard deviation) using Mann–Whitney *U* tests with statistically significant results in italics

	Foraging	Transiting	*U*	*P* value
Whale 1				
N	203	99		
SIC (%)	51.18 ± 33.84	52.95 ± 33.87	10,131	0.91
SIE (km)	−187.72 ± 136.98	−125.71 ± 96.06	7174	*5.47e−05*
Bath. (km)	−2.76 ± 1.71	−2.23 ± 1.51	7457	*0.00028*
SST (C)	−0.69 ± 1.59	−1.27 ± 0.65	11,641	*0.03*
Whale 2				
N	193	44		
SIC (%)	17.95 ± 18.24	7.68 ± 13.75	6134	*2.65e−07*
SIE (km)	−48.65 ± 52.49	−19.24 ± 67.90	3378	*0.035*
Bath. (km)	−2.14 ± 1.74	−2.06 ± 1.71	4224	0.96
SST (C)	0.65 ± 2.19	−0.75 ± 1.09	5224	*0.02*
Whale 3				
N	20	370		
SIC (%)	2.07 ± 3.57	27.34 ± 11.00	234.5	*< 2.2e−16*
SIE (km)	1.82 ± 16.35	−28.86 ± 12.90	7059	*7.94e−12*
Bath. (km)	−0.17 ± 0.20	−0.40 ± 0.14	5853	*9.27e−06*
SST (C)	0.17 ± 0.90	−1.49 ± 0.15	7382	*< 2.2e−16*

Periods with uncharacterized behavioral states were excluded. SIE specifically refers to the whales' distance to the sea ice extent, with negative values indicating the whale is within the pack ice

between timestamps (ΔSIE, ΔSIC, ΔSST, and Δbath) did not significantly contribute to model performance and were therefore removed from visualization plots.

Low MSSI was predicted for Whale 1 during February and May, south of 63°S, and at least 200 km inside the ice pack (Fig. 4). Whale 2 demonstrated strong relationships with distance to the SIE and SST (Fig. 5). This individual's MSSI was predicted to be closer to 0 when it was at least 50 km inside the ice pack, in warmer waters, and between 2.5 and 4 km water depth. Finally, Whale 3's MSSI was strongly influenced by distance to the SIE and SST (Fig. 6). Low MSSI was predicted when this individual was outside the ice pack and in warmer waters. A slight relationship was also observed with latitude where low MSSI was predicted at 65°S and 66.5°S. Bathymetry showed no influence on Whale 3's behavioral state.

Variable importance was also calculated for each model run (Fig. 7). Distance to the sea ice extent was the only variable that was significantly important for each whale. Sea surface temperature was most influential for Whale 2, and latitude was only important for Whale 1 and Whale 3.

Discussion

The results of this study provide the first satellite tag-based analysis of Antarctic minke whale movement and habitat around the WAP. Although our sample size is small, with only three individuals, we believe the information gained from their tracks combined with ecological data provides support for their pagophilic nature and identifies key environmental factors for predicting presumed foraging spaces.

Transition zones such as the sea ice extent, continental break, and the circumpolar current front exhibit enhanced productivity due to the upwelling and concentration of deep, nutrient rich waters. These zones create ideal habitat for primary production and higher trophic level species. Antarctic minke whales have been observed in sea ice covered areas around Antarctica [11, 34]. The marginal ice zone (MIZ) has been reported to be the best predictor of Antarctic minke whale sightings, with a higher probability of presence farther into the pack ice [11]. Our results show these three individuals remained within the MIZ or in heavily sea ice covered areas during much the foraging season. Satellite telemetry revealed 43% of the whale locations during the foraging season were within 10 km south of the sea ice extent and 89% of the locations were within the pack ice as opposed to open water, quantifying previously indirect observations.

Antarctic minke whales have also been associated with regions south of the Antarctic circumpolar current [11,

Table 5 Description of generalized additive models with covariates, R^2, ΔAIC, and AUC before and after *k*-fold cross-validation

Covariates	R^2	ΔAIC	AUC before	AUC after
Whale 1				
Jday + lat + SIE + ΔSIE + ΔSST + Δbath	0.546	0	0.9672	0.9527
SIE + ΔSIE	0.232	197	0.8526	0.8302
Whale 2				
SIE + ΔSIE + SST + ΔSST + bath + Δbath	0.589	0	0.9690	0.9498
SIE + ΔSIE	0.107	223	0.7647	0.6621
Whale 3				
Lat + SIE + ΔSIE + SST + ΔSST + bath + Δbath	0.762	0	0.9984	0.9974
SIE + ΔSIE	0.535	275	0.9523	0.9520

All models predicted the MSSI and used a Gaussian distribution

Jday Julian day, *lat* latitude, *SIE* distance to the sea ice extent (km), *ΔSIE* change in distance to the SIE, *SST* sea surface temperature (C), *ΔSST* change in SST, *bath* bathymetry (km), *Δbath* change in bathymetry

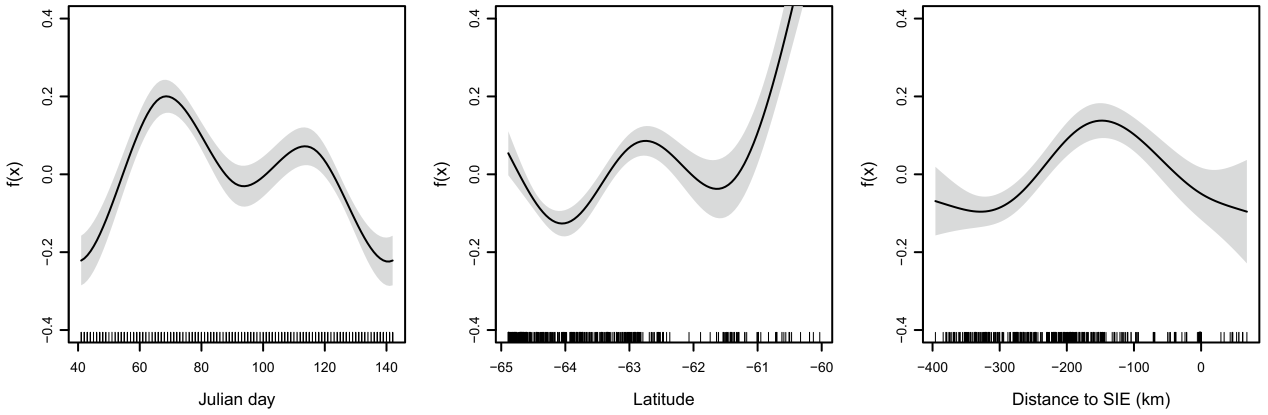

Fig. 4 Smoothed fits of selected environmental covariates modeling the MSSI for Whale 1. The *y*-axis represents the spline function. Tick marks on the *x*-axis are observed points and shading indicates the 95% confidence interval

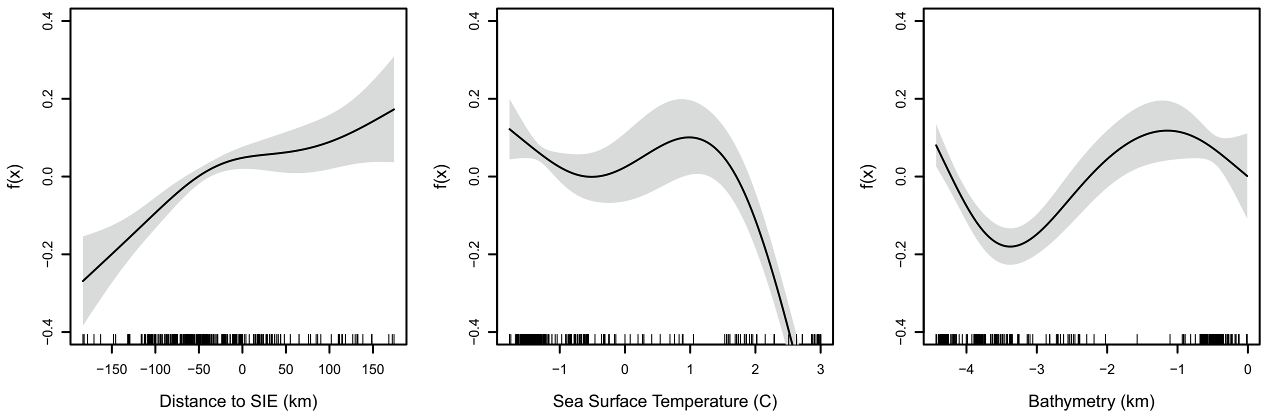

Fig. 5 Smoothed fits of selected environmental covariates modeling the MSSI for Whale 2. The *y*-axis represents the spline function. Tick marks on the *x*-axis are observed points and shading indicates the 95% confidence interval

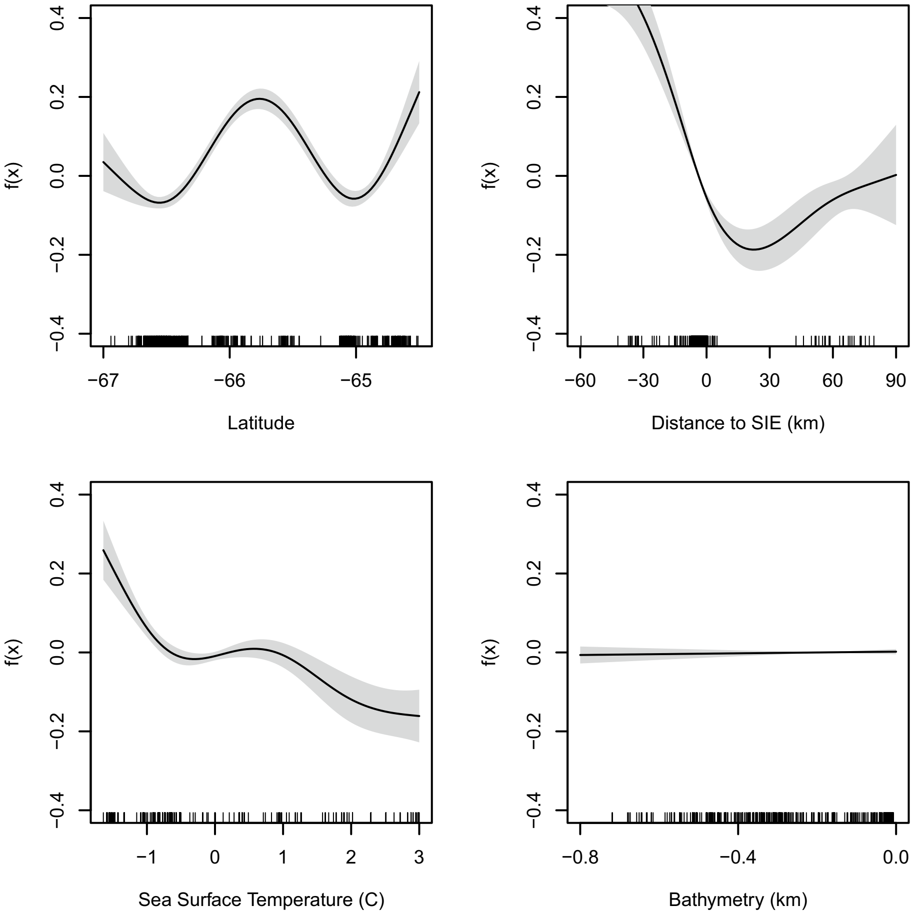

Fig. 6 Smoothed fits of selected environmental covariates modeling the MSSI for Whale 3. The *y*-axis represents the spline function. Tick marks on the *x*-axis are observed points and shading indicates the 95% confidence interval

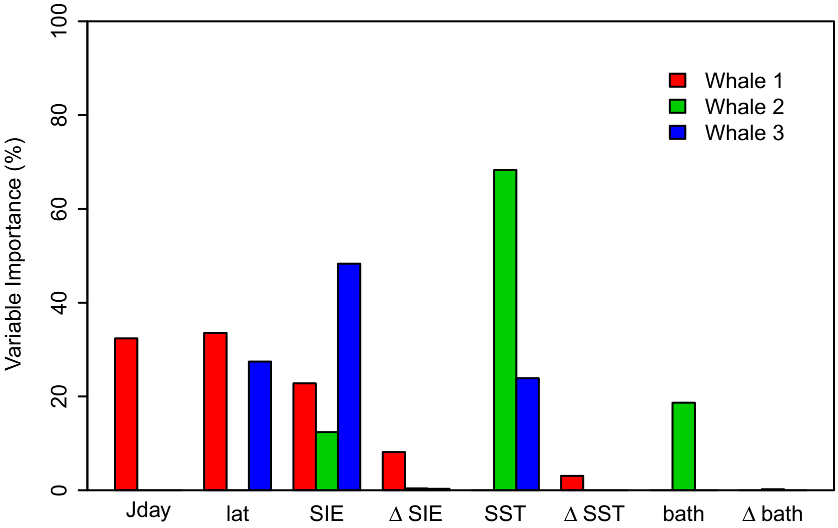

Fig. 7 Relative variable importance for each whale's prediction model, excluding ice-only models

35, 36] as well as on the continental shelf and shelf break [35, 37, 38]. Geographical observations from the present study confirm minke whale association with these transition zones. During the foraging season, these three whales remained south of the southern boundary of the Antarctic Circumpolar Current. In addition, Whale 2 followed the continental shelf break as it traveled along the sea ice extent, while the other two individuals remained in the shallower waters of the continental shelf.

The association of minke whales with sea ice, the southern boundary of the Antarctic Circumpolar Current, and the shelf break is likely due to high prey abundances, particularly Antarctic krill (*Euphausia superba*) and ice krill (*Euphausia crystallorophias*) [14, 39]. Antarctic minke whale foraging behavior is characterized by high feeding rates, defined by the number of feeding lunges per dive, compared to larger baleen whales [24]. This behavior, representing a high proportion of minke whale foraging effort, occurs when the whales target krill under the sea ice [24]. Minke whales have also been associated with deeper krill aggregations, relative to humpback whales [6]. These previous observations demonstrate the variability in minke whale foraging behavior and habitat conditions as they target krill aggregations and avoid interspecies competition by exploiting sea ice habitat and the varied bathymetric complex of the WAP.

The combination of sea ice, sea surface temperature, and bathymetry in the present study's models appears to successfully predict presumed foraging habitat for these three individuals, yet should be viewed with some caution. The GAMs used in this study identified relationships between environmental covariates and the whales' behavioral states. The major limitation of GAMs is the flexibility of the model, which has the potential to overfit the data. To account for this flexibility, highly correlated variables were removed. We also assessed model residuals against the observed locations and found no patterns, indicating that little to no spatial autocorrelation was present in the models.

The MSSI [16] was used to evaluate the whales' movement patterns and detect changes in behavioral states throughout the length of the tracks. The temporal resolution of the whales' location data restricts the ability of the MSSI to capture all foraging bouts. However, it can provide an understanding of the predominant behavior over a period of a few days. Antarctic minke whales have been directly observed predominantly foraging over a period of 18 h [24], which suggests our MSSI behavioral states are likely indicative of the whales' primary behavior on a multi-day to weekly scale. We acknowledge the limited temporal resolution of the telemetry data and spatial resolution of the environmental data in these models. However, we believe the reliability of our model performance is satisfactory for our purposes of gaining a better understanding of intra-seasonal Antarctic minke whale movement patterns and presumed foraging spaces.

We conclude that foraging spaces around the WAP are highly individualized between these three minke whales, but can generally be associated with pack ice habitat over the continental shelf. As the season progressed and the sea ice advanced, these whales traveled farther from the coastline and demonstrated foraging behavior in greater ice concentrations and in cooler, deeper waters.

Abbreviations

AIC: Akaike information criteria; ARS: area-restricted search; AUC: area under the curve; DCRW: first-difference correlated random walk; DMSP: defense meteorological satellite program; GAM: generalized additive model; GEBCO: general bathymetric chart of the oceans; IBCSO: International Bathymetric Chart of the Southern Ocean; MSSI: Multi-Scale Straightness Index; NASA: National Aeronautics and Space Administration; NOAA: National Oceanic and Atmospheric Administration; NSIDC: National Snow and Ice Data Center; OISST: Optimally Interpolated Sea Surface Temperature; SIC: sea ice concentration; SIE: sea ice extent; SSM: state-space model; SSMIS: special sensor microwave imager/sounder; SST: sea surface temperature; WAP: western Antarctic Peninsula.

Authors' contributions

JFL conducted the main analysis and led the writing of the manuscript. ASF collected whale location data as well as provided expertise on whale behavior and animal movement analysis. MJO and TLD provided expertise on the study region, statistical methods, animal behavior, and sea ice dynamics. All authors read and approved the final manuscript.

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Not applicable.

Competing interests

The authors declare that they have no competing interests.

Availability of data

The dataset used and analyzed during this study is available from the corresponding author upon reasonable request.

Consent for publication

Not applicable.

Ethics approval

This research was conducted under National Marine Fisheries Service permit 14097, ACA permit 2009-013, and Duke University Institutional Animal Care and Use Committee protocol A49-12-02.

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