Research Square

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Ecological drivers of movements and habitats of a deep diver: the elusive sperm whale

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Abstract

Background

Understanding the habitat preferences and movement patterns of cetaceans remains challenging due to their wide-ranging movements and prolonged deep-diving behaviors. We aim to characterize the fine-scale movement patterns and space use of sperm whales (*Physeter macrocephalus*) inferred from satellite telemetry and to identify environmental drivers shaping their distribution using species distribution models (SDMs) that integrate surface and subsurface oceanographic variables.

Methods

We deployed the first satellite transmitters (n = 13) on sperm whales in the Azores during 2018, 2023, and 2024. State space models (SSMs) were used to correct positional uncertainty and regularize tracks. We developed SDMs using generalized additive mixed models (GAMMs) on observed and simulated tracks to predict habitat preference relative to static and three-dimensional dynamic variables.

Results

Twelve of the 13 tagged sperm whales remained in the Azores region for their tracking duration (5-156 days), while one moved towards 20°N latitude and returned northwards. These exhibited prolonged residence, strong site fidelity, and foraging behaviour. Integrating three-dimensional predictors enhanced SDM predictive performance. Sperm whale distribution was primarily driven by dynamic variables, with an interaction between surface temperature and salinity, temperature and salinity across depth layers, sea surface height (SSH), and distance to coast. The highest occurrence was consistently predicted around the Azores islands and decreased with distance from the islands. Predicted distribution varied seasonally and interannually, with recurrent offshore hotspots (~ 35°N), reflecting oceanographic variability.

Conclusions

By combining telemetry data with three-dimensional predictors, this study provides a novel approach to enhance predictive performance and advance our understanding of the processes shaping sperm whale distribution in the Azores. Our findings highlight the region as an important foraging hotspot supporting prolonged residence for sperm whales, emphasizing the need to protect their habitats from anthropogenic threats under a changing marine ecosystem.

1 Background

Movement plays a pivotal role in an animal's life history driven by ecological processes that function across space and time [1, 2]. Understanding movement patterns provides insight into the behavioural mechanisms and environmental drivers shaping habitat use and distribution patterns [2–4]. In marine systems, many highly mobile species (HMS; e.g., cetaceans, sea turtles, sharks, seabirds) undertake extensive movements across ocean basins in response to spatial and temporal variability in resource availability [1, 4–6]. Despite their mobility, HMS can exhibit site fidelity to specific areas that provide suitable and predictable habitats [3, 4, 7]. Among HMS, deep-diving cetaceans present particular challenges for movement ecology studies due to their vast distributional ranges, and prolonged periods spent underwater [5, 6, 8, 9]. Their limited surface time further constrains direct observations and reduces the effectiveness of conventional survey methods, making it harder to characterize their spatial ecology [8, 10]. Advances in satellite telemetry have therefore been instrumental in overcoming these challenges, enabling long-term tracking across remote ocean regions [4, 9]. Satellite telemetry has improved our understanding of movement ecology, habitat use, site fidelity, and behavioural responses to environmental variability of deep-diving cetaceans, ultimately informing conservation and management strategies [4–6, 9, 10].

Species distribution models (SDMs) are widely used to describe habitat preferences and distribution patterns of cetaceans across oceanic systems [11, 12]. By quantifying relationships between species occurrences and environmental predictors, SDMs provide a framework to infer the ecological processes shaping habitat use [13, 14]. SDMs play a key role in marine spatial planning and conservation to help identify critical habitats, predict shifts in distribution under changing ocean conditions, evaluate the effectiveness of protected areas and highlight areas of heightened risk from human activities [13, 15, 16]. Traditionally, SDMs have been developed using diverse data streams such as visual observations, ship and aerial surveys, and acoustic detections [17–22]. Although these approaches have advanced our understanding of cetacean distribution, they are often limited by spatial and temporal biases and tend to yield low predictive performance [13, 23]. Integrating satellite telemetry data into SDMs enhances habitat modeling by capturing species-environment relationships at finer spatial and temporal scales, providing broader temporal coverage and improving model predictive performance [11, 12, 15]. Most SDMs for deep-diving cetaceans rely primarily on static and surface environmental variables, overlooking subsurface conditions that more accurately represent the three-dimensional habitats in which these forage [13, 24]. Subsurface oceanographic processes (e.g., vertical temperature and salinity structures, isothermal layer

depth, buoyancy frequency, eddy dynamics) can structure prey fields at depth more directly than surface conditions and influence predator-prey interactions across the water column [13, 24]. Recent studies incorporating subsurface variables into SDMs of top predators (e.g., swordfish, sharks, beaked and sperm whales (*Physeter macrocephalus*)) have reported improved explanatory power and predictive performance [24, 25]. The growing availability and development of such environmental data opens new opportunities to better characterize the habitat of deep-diving cetaceans [22, 24].

Sperm whales (SpW) are a cosmopolitan species found across all deep oceans ranging from tropical lower latitudes to polar hemispheres [26, 27]. They display the most pronounced sexual dimorphism among cetaceans, characterized by differences in size, distribution, behaviour, feeding ecology and social structure, leading to spatial and ecological segregation between sexes [27, 28]. Adult females and their offspring live in long-term stable association called 'social units' and predominantly display nomadic movements ranging hundreds to thousands of kilometers across warm tropical and subtropical waters (0–45°N/S latitudes) [27–29]. Young males (6–16 years) depart their natal social units and progressively move towards higher latitudes, and as adults undertake large-scale migrations between high-latitude foraging areas and lower latitude-breeding grounds [26–28]. Despite distinct distributional patterns between females and males, their movement patterns are influenced by environmental conditions and feeding conditions [30, 31]. As deep-diving cetaceans, sperm whales dedicate most of their time (around 70–75%) to foraging, with the remainder spent resting, socializing, nursing, and other surface activities [27, 30, 32]. Females typically forage on mesopelagic cephalopods during deep dives (700–1200 m for about 30–45 minutes), whereas males may explore wider depths (100–1900 m) and target larger prey such as squid and demersal fish [27, 33, 34].

Despite long-standing scientific interest, sperm whales remain challenging to study due to their deep-diving behaviour, complex social structures, and wide-ranging movements across ocean basins [27, 29, 30]. The few satellite telemetry studies to date have focused mainly on adult males undertaking latitudinal migrations [26, 34, 35], and for populations outside the North Atlantic [8]. However, knowledge of habitat uses, movements, and behavioural responses to dynamic environmental conditions of social units remains scarce, particularly in the North Atlantic. Previous efforts to model sperm whale distributions have relied on a range of data sources and environmental predictors but identifying the most ecologically relevant combination of variables to accurately characterize their distribution remains challenging [21, 36]. Although recent studies have begun to integrate deep-ocean variables into SDMs for SpW [36], opportunities remain to better integrate telemetry-derived movement data with subsurface predictors to enhance predictive performance and ecological interpretation of sperm whales distribution. This study aims to (a) characterize the fine-scale movement patterns and habitat use of SpW inferred from satellite telemetry, and (b) assess the environmental drivers shaping their habitat preferences by developing ecological SDMs that incorporate both surface and subsurface variables. By combining satellite telemetry with three-dimensional predictors, we seek to refine predictive performance and advance our understanding of the processes shaping sperm whale distribution. The resulting tracking data and SDMs can provide a valuable basis to inform conservation and management efforts of sperm whales in the North Atlantic.

2 Methods

2.1 Tagging procedures

In 2018, 2023 and 2024, we instrumented 15 sperm whales encountered off the central islands of the Azores (36°-39°N; 25°-31°W) (Fig. 1, Fig. S1) with satellite transmitters. All tagged sperm whales were of medium size and were encountered in social groups, and likely were adult females or immatures of either sex. (Table 1). In 2018, we deployed location-only Low Impact Minimally Percutaneous External Electronic (LIMPET, Wildlife Computers mold 240C; [37]) satellite tags in the dorsal fin or at the base of the dorsal fin of whales, using a Dan-Inject rifle at 3–4 meters distance and pressures from 20–25 BAR. In 2023 and 2024, location-only transdermal tags (Wildlife Computers mold 177; [38]) were used, due to reduced transmission periods obtained with the LIMPET tags (Table 1). Transdermal tags were deployed on the dorsum of the whales, immediately anterior or under the dorsal fin using the Aerial Remote Tag System (ARTS) [39, 40], with pressures varying from 10–23 BAR at 2–5 meters distance. All deployments were made from 6–8 m long RHIBS. Prior to deployment, the anchoring elements of all tags were cleaned with 70% ethanol, sterilized under UV light for 30 minutes, and stored in sterilized bags until deployment. Best practice guidelines for cetacean tagging were followed to minimize effects on animals [37].

Table 1

Summary data for each tagged sperm whale: including size class, tag model type, tagging date, location of tag deployment (latitude and longitude), first and last day of detection, total days detected, number of detections, mean daily detections and if it was used for analysis.

Tag Year	Tag ID	Size class	Tag model	Tagging date	First Latitude	First Longitude	First Day	Last Day	Total Days	Total Detections	Mean Daily Detections	Used for Analysis
2018	57933	Medium-small	Limpet	20-Aug-18	38.57543	-28.98217	21-Aug-18	29-Aug-18	5	6	1	No
	57935	Medium	Limpet	27-Aug-18	38.74763	-28.88963	27-Aug-18	15-Sep-18	20	181	9	Yes
	57937	Medium	Limpet	5-Sep-18	38.65007	-28.46596	5-Sep-18	17-Sep-18	13	125	10	Yes
	57938	Medium	Limpet	10-Sep-18	38.88396	-28.46717	10-Sep-18	14-Sep-18	5	26	6	Yes
	57941	Medium	Limpet	11-Sep-18	38.31848	-28.6115	12-Sep-18	18-Sep-18	7	59	8	Yes
2023	244381	Medium	SPOT	2-Aug-23	38.6013	-28.12562	2-Aug-23	14-Oct-23	74	485	7	Yes
	244382	Medium	SPOT	6-Aug-23	38.58894	-29.0402	7-Aug-23	17-Sep-23	32	242	8	Yes
	244383	Medium	SPOT	7-Aug-23	38.81099	-28.42092	9-Aug-23	19-Sep-23	41	214	5	Yes
	244384	Medium	SPOT	15-Aug-23	38.76002	-28.93814	16-Aug-23	18-Aug-23	3	7	2	No
2024	244385	Medium	SPOT	23-Feb-24	38.49965	-28.68265	23-Feb-24	4-Aug-24	156	1279	8	Yes
	244386	Medium	SPOT	28-Feb-24	38.8114	-28.68265	29-Feb-24	6-May-24	56	534	10	No
	244387	Medium	SPOT	3-Jul-24	38.53311	-28.28432	3-Jul-24	18-Jul-24	15	140	9	Yes
	244388	Medium	SPOT	4-Jul-24	38.57904	-29.03137	4-Jul-24	28-Sep-24	85	895	11	Yes
	244389	Medium	SPOT	5-Jul-24	38.64967	-28.58458	5-Jul-24	26-Sep-24	69	583	8	Yes
	244390	Medium	SPOT	19-Jul-24	38.69599	-28.52419	19-Jul-24	26-Aug-24	33	109	3	Yes

*Size classes are grouped: small (< 8 m), medium (between 8- 12m), large (> 12m). Size estimates were made by using boat as scale

2.2 Tracking data processing

We acquired tracking data from the Argos satellite system. The data had been processed and filtered with the Kalman smoothing method to help improve location accuracy and classified into location quality levels with corresponding error ellipses [26, 41]. For each sperm whale, we computed the total number of locations, first, last and total days with locations [3]. We removed Z locations and other erroneous data points (i.e., locations on land, outside of study area). Data from two transmitters were excluded from further analysis because of reduced number of locations (< 5 days with locations or < 10 total locations) (Table 1). Tracking data were processed and analyzed using R version 4.4.0 [42].

State Space Models (SSM) are commonly used to account for location error from Argos, estimate true locations, regularize positions at a single time interval, and infer movement metrics which can help discriminate between behavioural states (i.e., foraging, resting, transiting, migratory, resident) [34, 41]. We applied SSM using the 'fit_ssm' function from the 'aniMotum' R package to our tracking data (n = 13) [41]. We tested three SSM (Random Walk, Correlated Random Walk and Move Persistence) at different time intervals (2, 4, 6, 8 hours). The best fitting model for all sperm whales (n = 13) was the Correlated Random Walk (CRW) at a 6-hour interval and the fitted tracking data from this model were used for further analysis.

2.3 Movement metrics

We quantified movement metrics and behavioural states from the fitted SSM tracking data. The 'fit_mpm' function from the 'animotum' R package was used to estimate the 'move persistence' (γ_t) [41]. This parameter (scale 0–1) is used to discriminate different behaviours, whereby low move persistence (MP) with relatively slow movements and frequent course switches is indicative of area restricted search (ARS) (foraging), while high MP indicates consistent direct and fast movement (traveling) [43]. We used the 'prep_data' function from the 'bayesmove' R package to calculate the following movement parameters: turning angles, net-squared displacement (square Euclidian distance of each location from the first location) and step lengths (Euclidian distance between consecutive locations) [44]. Displacement was calculated by taking the square root of the net-squared displacement. Displacement can be used as a proxy to infer among different movement strategies (i.e., migration, dispersal, range residency, nomadism) and determine home range size (units of length) [45]. Speed was calculated by dividing the step length between locations by the time difference between those locations (6 hour interval) [3, 26].

2.4 Simulated Pseudo-absences

We generated simulated tracks ('pseudo absences') for each observed track to represent potential absences [12, 16, 46]. Pseudo-absences were built using a correlated random walk (CRW) model, which randomly creates new movement tracks independent of the environment, sampling step lengths and turning angles from each original track at the starting point [12, 16, 46]. We simulated 200 CRW tracks with the same duration and dates of the original tracks within a spatial bounding box surrounding the Azores region (33°N to 44°N, 35°W to 21°W, Fig. S2).

2.5 Environmental variables

We chose environmental variables (dynamic and static) that could be proxies of oceanographic processes and physical structures potentially relevant for sperm whales. We obtained daily physical variables (temperature, salinity, current velocities, sea surface height) from the Global Ocean Physics and Forecast numerical model (GLO4V3R3 product) provided by the Copernicus Marine Service with a spatial resolution of 1/12° (DOI: https://doi.org/10.48670/moi-00016) (Table 2). To better capture the habitat distribution of sperm whales within their foraging depths (700–1200 m) [32, 33], we included dynamic environmental variables at 760 m depth and another mid-range depth of 189 m. Eddie Kinetic Energy (EKE) was calculated using the following formula:

Table 2
Description of environmental (dynamic and static) variables available for habitat modelling. All variables at mid sea water depth are at 189 m and the deep ones at 760 m. **Abbreviations**: logarithmic (log), square root (sqrt), eastward (EW), NW (NW), Eddy Kinetic Energy (EKE)

Type	Environmental variable Available	Units	Spatial Resolution	Source	Distribution	Transformation
Dynamic	Surface temperature	°C	0.083° × 0.083°	Global Ocean Physics Analysis and Forecast - GLO4V3R3	binomial	Log
	Mid temperature (189m)	°C			normal	None
	Deep temperature (760m)	°C			normal	None
	Surface salinity	PSU			normal	None
	Mid salinity	PSU			normal	None
	Deep salinity	PSU			normal	None
	Surface EW current velocity	m s-1			normal	None
	Surface NW current velocity	m s-1			normal	None
	Surface EKE	m s-1			Left	Log
	Mid EW current velocity	m s-1			normal	None
	Mid NW current velocity	m s-1			normal	None
	Mid EKE	m s-1			Left	Log
	Deep EW current velocity	m s-1			normal	None
	Deep NW current velocity	m s-1			normal	None
	Deep EKE	m s-1			Left	Log
	Sea bottom temperature	°C			Left	Log
	Sea bottom salinity	PSU			Left	Log
	Sea surface height	m			normal	None
	Chlorophyll	kg m-3	4 x 4 km	Global Ocean Colour	Left	Log
Static	Distance to coast	km	4 x 4 km	spatial shapefiles	Left	Sqrt
	Distance to 200m isobath	km			Left	Sqrt
	Distance to 500m isobath	km			Left	Sqrt
	Distance to 1000m isobath	km			Left	Sqrt
	Depth	m	15 arc-seconds	Etopo 1. 1 Arc-Minute Global Relief Model	normal	None
	Slope	km			Left	Log
	Distance to seamounts	km	10m	Morato et al., 2008	Left	Sqrt
	Distance to seamounts Large	km			Left	Sqrt
	Distance to seamounts Small	km			Left	Sqrt

$$EKE = 0.5 \times \left(\left(Eastward\ Seawater\ Velocity \right)^2 + \left(Northward\ Seawater\ Velocity \right)^2 \right)$$

Daily chlorophyll values were obtained from the remote sensing Global Ocean Colour (Copernicus-GlobColour) product of Copernicus Marine Service at a 4x4 km spatial scale (DOI: https://doi.org/10.48670/moi-00281) (Table 2). For all dynamic variables we downloaded data for the periods of 1 May- 30 September 2018 and 1 May 2023- 30 September 2024 to match tracking duration.

Depth and slope were extracted from the Etopo Global Relief Model provided by NOAA's National Geophysical Data Center (NCDC, https://www.ngdc.noaa.gov/mgg/global/), which comprises 288 individual degree tiles (latitude/longitude) at a 15-arc-second spatial resolution (Table 2). Spatial shapefiles containing the coastlines and bathymetry were used to calculate distances to the 200 m, 500 m, and 1000 m

bathymetry contours, and the distance to the coast using the "st_distance" function from the 'sf' R package (Table 2). We applied the same function to calculate distances to small and large seamounts derived from a shapefile created by Morato et al. (2008) (Table 2).

All environmental variables were extracted for every original and pseudo-absence track location using the 'terra' [48] and 'ncdf4' [49] R packages.

2.6 Habitat modeling

We followed the Species Distribution Modeling (SDM) framework by Hazen et al., [12] and Pérez-Jorge et al., [46] to predict habitat preferences of sperm whales. Preceding model implementation, we compared patterns of environmental preference of sperm whales between original and pseudo-absence tracks by applying density plots (Fig. S3). We further evaluated collinearity among pairs of candidate environmental covariates using the Pearson's correlation coefficient, selecting only variables with correlations < 0.7 and of ecological relevance (Table S1). In the case of sea bottom salinity and sea bottom temperature which were highly correlated (r = 0.916), sea bottom temperature was selected due to its greater importance in driving the model (Table S1). As a result, 18 of the 28 candidate environmental variables were retained for model fitting (Table S1).

We applied generalized additive mixed models (GAMMs) to the original and simulated tracks of sperm whales and the environmental covariates. We fitted binomial distribution GAMMs with a logit link function, using restricted maximum likelihood (REML) for model optimization and including individual IDs as a random effect, via the 'gam' function from the 'mgcv' R package [50]. For a binary response in the model, we assigned a value of 1 to the original data points (presence) and a value of 0 to the pseudo-absence data points. Due to missing values in deep-water variables, we excluded approximately 7% of data points from the pseudo-absence replicates, as GAMMs are sensitive to missing data [12].

We built GAMMs using backward selection of relevant environmental covariates beginning with a full model including smooth terms of all candidate environmental covariates. Furthermore, we included two biologically interpretable interactions between temperature and salinity across depth gradients implemented as bivariate smooth terms to capture their joint, non-linear effects on habitat preferences [50]. We chose these interactions based on current understanding of oceanographic processes that may influence sperm whale distribution within the study region [46]. The final model was selected based on the lowest Akaike Information Criterion (AIC) value (Table S2). After model selection, we restricted the smoothing splines to a maximum of 5 degrees of freedom via the k-parameter to prevent model overfitting, and maintaining ecological interpretability of the functional relationships between the response variable and covariates [46].

We evaluated model performance based on predictive performance, explanatory power and biological/ecological realism by using the following metrics: Area Under the Receiver Operating Characteristic Curve (AUC) and percent of deviance explained (R^2) [12, 16]. Deviance explained (i.e., explanatory power) reflects the model's ability to account for variability in the dataset [16]. In presence-only SDMs with simulated pseudo-absences, AUC reflects discrimination between observed presences and sampled environmental conditions and provides an index of model performance in identifying suitable habitats [51]. AUC was inferred through an identical parameter termed the 'concordance index' (c-index), which was computed using the 'rcorr.cens' function from the 'Hmisc' R package [52]. The AUC ranges from 0–1, whereby values < 0.5 indicate low performance, 0.5–0.7, moderate performance, 0.7–0.8, good performance, 0.8–0.9, very good, and > 0.9 excellent performance in model prediction [53]. Following Farchadi et al. (2025), we took into account *ecological realism* –a model's ability to predict realistic patterns of species distributions based on biological plausible relationships with environmental variables, that are consistent with observed ecological processes and knowledge of the focal species – to qualitatively evaluate model outputs.

We further conducted a sensitivity analysis to examine the robustness of whale-environment relationships to the selection of simulated tracks. Two of the 200 CRW tracks per whale were randomly selected and models were rerun 40 times [12, 46]. For each simulation, we computed the AUC and variance explained (R^2) and took the mean and standard deviation of AUC and R^2 across all simulations. Moreover, we measured if key predictors from best fitted model remained significant across iterations (measured as count). Lastly, we assessed the relative importance of each covariate in driving model preference by applying the 'bm_VariablesImportance' function of the 'biomod2' R package [54]; however this function is not applicable to GAMMs that include interactions.

2.7 Habitat prediction maps

We produced habitat preference maps for sperm whales based on the best GAMM selected. Environmental covariates were extracted following the same procedures as described above, at a monthly resolution (using first day of each month) for 2018, 2023, 2024. For prediction purposes, these variables were projected from their original resolution onto a regular grid matching the spatial resolution of the fitted models (0.083°x0.083°) within the study extent (32 − 24°W, 35–41°N) and generating a prediction dataset used to build habitat maps.

3 Results

3.1 Tracking data

Two sperm whale tracks (ID 57935 and 244384) had insufficient locations and were excluded from analysis (Table 1). The remaining 13 transmitted an average of 47 days (range 5-156 days), with a mean of 8 locations per day (Table 1, Fig. S4). Duration of tracks from Limpet tags was substantially shorter (mean 11 ± 7 SE days) than that of SPOT tags (62 ± 42 SD days) (Table 1).

3.2 Movement and behavioural patterns

Only one sperm whale (ID 244386) left the Azores shortly after being tagged, travelling 2651 km southwest of the Azores and reaching approximately 20 °N (Fig. 1a, Table S3). It stayed in this area for about 26 days before transiting back up north. This whale traveled a total of 6522 km at a daily average speed of 4 km/h (± 1.71), moving, on average, 95 km (± 38.13) per day, with a maximum of 311 km (Fig. 1a, Table S3). Since this individual showed transitory movements, with high move persistence (0.89 ± 0.09, Table S3) and barely utilized the marine habitats of the Azores, it was excluded from the SDMs.

The remaining 12 sperm whales stayed within the Azores region for the duration of their tracking period and primarily used habitats off the central group of islands (Fig. 1b). Whale ID 244385 showed the longest residence time (156 days) and primarily stayed west of Faial Island, around Graciosa and east of S. Jorge (Fig. 1b, Table 1). This individual traveled a total of 7341 km but remained within 221 km from the tagging position (Table S3). Three whales (ID 244383, 244389, 243390) exhibited wider ranging movements (> 400 km), extending to the Mid-Atlantic Ridge and offshore banks, while one individual also moved towards the eastern islands (Fig. 1b, Table S3).

The movements of all whales that stayed within the Azores were characterized by short step lengths (average 12 ± 8 km), slow speeds (average 2 ± 1 km/h) and high turning angle density at 0 radians, remaining within a 100 km radius from their first position (max displacement of 475 km) (Fig. 2, Table S3). They displayed move persistence of 0.25–0.75, consistent with area restricted search (foraging) and potentially other behaviours (e.g., resting, socializing) (Fig. 2, Table S3).

3.3 Species Distribution Models

3.3.1 Model performance and habitat preferences

The best fitting GAMM included distance to coast, an interaction of temperature and salinity at surface, mid and deep temperatures and salinities, sea surface height and (Table 3, Table S2). This model had an average of 40% of deviance explained (SD = 0.04) and an average AUC of 0.88 (SD = 0.018), which is indicative of a good performing model (Table 3). All environmental covariates and interactions were significant amongst most of the pseudo-absence simulations (32–35 out of 40 replicates, Table 3), however, consistency in significance was lower than in models without interaction terms (Table S4)

Table 3
Summary results of best selected GAMM (Model 4_IntS wK5 in Table S2), including mean deviance explained (SD), mean AIC (SD), mean AUC (SD) across 40 simulations. N-significant is based on significance of the variables with p values less than 0.1 across 40 simulations.

Variable	edf	Ref.df	Chi.sq	n-significant (n/40)
Interaction: Log Surface temperature and surface salinity	3.719	3.95	154.94	34/40
Mid temperature	3.84	3.986	191.71	34/40
Deep temperature	3.712	3.954	47.66	32/40
Mid salinity	3.997	4	515.8	35/40
Deep salinity	3.913	3.995	437.98	34/40
Log Sea bottom temperature	3.964	3.999	45.84	35/40
Sea surface height	3.981	4	105.66	33/40
Sqrt Distance to coast	4	4	1044.17	33/40
Tag ID	10.806	11	583.44	35/40
R^2: 0.40 (0.04); **AIC**: 5152.989 (312.269), **AUC**: 0.88 (0.018)				

Sperm whales primarily occupied habitats within ~ 75 km from the islands (Fig. 3b), with distance to coast contributing 24% to overall habitat preference (Fig. S5a). Their habitat preference was further associated with warmer and more saline surface waters (6% and 12% respectively; Figs., 3b, S5a). At mid depths, SpW preferred increasing water temperatures (8%) and decreasing salinity (13%), while in deeper waters they favored colder and less saline waters (11%, 10%, respectively; Figs., 3b, S5a). In addition, preferable habitats were characterized by sea surface heights > 0.1m (9%) and sea bottom temperatures ranging between 3.5°C and 10°C (1%; Figs., 3b, S5a).

3.3.2 Predicted distributions

Sperm whale predicted distribution varied across years and months (Fig. 4). Despite this, there were consistent patterns of higher probability of occurrence around all islands of the Azores, followed by areas between the central and western groups of islands, and south of the central group (Fig. 4). The probability of occurrence decreased with distance from the islands, reaching the lowest values in the open ocean farthest from the archipelago (Fig. 4). Standard error values of estimates of occurrence were generally low across the study region (< 0.2) and exhibited low variation in predicted areas of occurrence (Fig. S6).

Interannual variability in sperm whale predicted occurrence primarily reflected differences in the timing and extent of the offshore distribution (Fig. 4). In 2023, predicted offshore occurrence was higher in February and March compared to the rest of the year, reaching approximately 35°N and 26°W (Fig. 4). In contrast, in 2018, predicted offshore occurrence was highest in September and October (Fig. 4), while in 2024, it increased across the region from May to September. In May 2024, sperm whales were predicted to occur mainly around the central and eastern islands, extending south to 35°N latitude, shifting towards southwest of the central islands (~ 35–38°N, 28–31°W) between June and August. By September and October, predicted occurrence expanded across much of the region, encompassing waters surrounding all islands and extending south to 35°N and 27–32°W (Fig. 4).

4 Discussion

To the best of our knowledge, this is the first satellite telemetry-based study to quantify movements, habitat preferences and spatial distribution of sperm whale from social units in the central North Atlantic waters. Our tracking data provides novel insights into the movement patterns, behaviours and spatial use of sperm whales around the Azores, a well-known habitat for the species in the North Atlantic. By integrating satellite telemetry with environmental variables across the water column, this study further enhanced the development of species distribution models for a deep-diving species.

4.1 Movement and behavioural patterns

Twelve out of 13 of sperm whales (SpW) tracked in this study remained within the Azores region for the duration of their tracking period (5-156 days). These SpW were primarily tracked during the summer (June-September), yet one whale remained in the Azores from February to August indicating that individuals can extend their presence beyond the summer months. Sperm whales predominantly used the waters around the central islands, where they have been tagged, with some individuals expanding their movements into offshore waters (n = 3), or other island groups, consistent with previous observations [51, 55]. Their movements were characterized by short step lengths (45 km daily average), slow speeds (< 2.5 km/h), relatively straight trajectories with low tortuosity, low displacement and intermediate move persistence. This combination of metrics is consistent with prolonged habitat use and predominantly foraging-related behaviours, with slow movements and semi-straight courses between foraging dives with slow movements [29, 56]. These findings further highlight the importance of the Azores as a foraging ground for sperm whales [55]. Nevertheless, tracking periods certainly include other behaviours, such as socializing, resting or nursing, which are also consistent with this type of movements.

Our results indicate that sperm whales exhibit significantly longer residence in the Azores (up to 5 months) than previously reported, although these values represent only the minimum time spent in the area, as tags stopped transmitting before animals left the region. Using photo-identification data, Boys et al., [57] and Ferreira et al., [7] reported residence periods of approximately 3 weeks and 12.9 days, respectively. These differences result from restrictions in observation effort and spatial coverage of photo-identification studies, and illustrate well the limitations of this technique to study the movements and distribution of highly-mobile, deep-divers.

Beyond extended residency, SpW showed low displacement, remaining within 100 km of their tagging location and moving a maximum of 475 km within the Azores region. Low displacement, combined with habitat preference towards the central islands suggests a type of site or island fidelity [3, 31] rather than nomadic movements at a regional scale, as previously observed [27]. Similar site fidelity patterns among social units have been documented in the Eastern Caribbean [31] and the Mascarene archipelago [8]. These spatially constrained movement patterns may indicate limited connectivity with social units in other Atlantic regions, contrasting with expectations of wide-range migrations [7, 58], although this hypothesis requires confirmation.

One sperm whale (ID 244386) left the Azores a few days after being tagged and moved southward to 20°N. Based on its distinct movement patterns (i.e., fast speed, large displacements, and high move persistence), we hypothesize this individual was either dispersing to locate new foraging areas or a young whale searching for mating opportunities [27, 29]. Interestingly, similar displacements were recently documented in adult males migrating from foraging grounds in Norway, passing the Azores to areas south of 30°N, which have been suggested as breeding grounds for the species [26].

4.2 Species distribution and Habitat preference

4.2.1 Model selection and performance

During the selection process, we chose a model that retained variables contributing more than 5% to habitat preference, with contributions derived from more complex candidate models and used as a complimentary guide within the selection process (Fig. S5b; Models 1–4 in Table S2). The only exception was sea bottom temperature, that despite contributing < 5% to habitat preference was retained in the final model, since it is a proxy of subsurface thermal conditions that have been associated with higher prey densities and the deep foraging behaviour of sperm whales [8, 22]. Although some alternative models yielded slightly higher AUC and R^2 values than our final model (Table S2), predictions consistently identified similar SpW distribution hotspots across models (Figs. S7, S8). Thus, we prioritized a simpler model that remains easy to interpret and readily applicable as a management tool [12], while emphasizing ecologically meaningful drivers of sperm whale distribution [15, 16, 23].

Our final model showed excellent performance, with an average AUC of 0.88 and 40% deviance explained, exceeding typical performance of SDMs developed for sperm whales (Table S5) [17–19, 22, 24, 51, 59]. Moreover, all tested models showed strong performance, with AUC > 0.86 and deviance explained > 33% (Table S2). Compared to other data sources, satellite tracking data can capture habitat use across time over extended periods and are largely independent from accessibility and environmental factors, thus improving SDM performance (Table S5) [11, 12, 23]. This, combined with the inclusion of static, dynamic and subsurface variables further enhanced the descriptive power and predictive performance of our models [13], corroborating previous studies that employed similar modeling approaches for deep diving cetaceans [11, 17, 24].

4.2.2 Habitat preferences

Our model shows that the distribution of sperm whales was primarily influenced by distance to coast, along with dynamic variables such as temperature, salinity and sea surface height (SSH) (Fig. S5a). This is consistent with other studies that reported that sperm whale habitat preferences are often associated with dynamic variables, particularly sea surface temperature (SST), temperature gradients and SSH [18–20, 59]. Yet, most studies have only considered dynamic variables at the surface [13]. By integrating dynamic variables in deeper water layers (i.e., 189 m and 760 m), our models captured the oceanic structures and processes that deep-diving foraging sperm whales explore.

Our results indicate that sperm whales show distinct temperature and salinity preferences across depths, in agreement with findings from other areas [24]. These temperature and salinity ranges are consistent with the properties of major water masses present in the Azores region, including the Eastern North Atlantic Central Waters (ENACW), North Atlantic Central Waters (NACW), surface water masses that dominate the surface and intermediate depths (up to ~ 1500 m), and the North Atlantic Deep Water below 2000 m depth [60, 61]. This suggests that sperm whale habitat use may be structured along vertical and horizontal gradients associated with these water masses. In addition, the interaction of temperature and salinity at the surface suggests that SpW may respond to oceanographic gradients associated with frontal zones [62], defined by horizontal and vertical contrasts in temperature, salinity and density that commonly occur at boundaries between water masses [63]. Ocean fronts along with sea surface height, eddies and meanders are characteristic of mesoscale systems in the Azores [64] that play a pivotal role in shaping upwelling and downwelling process, known to enhance primary productivity, attract prey aggregations and serve as foraging hotspots for marine top predators [63, 65]. Sperm whales likely exploit these mesoscale areas to reach prey aggregations in deep, cold, and less saline waters [8, 20, 24]. The strong affinity of sperm whales towards negative SSH further suggests they target enriched pelagic waters associated with upwelling processes within mesoscale systems [8, 12, 18, 63].

Beyond dynamic variables, distance to coast was the most important variable shaping the habitat preferences of sperm whales (24% of importance, Fig. S5a). The complex topography near the islands (steep island slopes and nearby seamounts), combined with oceanographic conditions and regional circulation, facilitates the upwelling of nutrients and aggregation of prey close to the islands [60, 64, 66, 67]. More productive coastal waters offer better foraging opportunities for SpW [30, 31], shaping their preference for habitats near the islands. Furthermore, preferences for coastal habitats may also be shaped by social processes, including culturally transmitted site fidelity and social cohesion within stable units, as well as the potential role of coastal habitats for supporting communal calf care and enhancing protection of individuals [31, 68]. While previous studies often highlighted the influence of other static features, including depth, slope, and distance to seamounts [17, 19, 51, 59], these covariates were not significant in our analysis, supporting the idea that sperm whales foraging around the Azores may respond more strongly to dynamic processes in the water column.

4.2.3 Predicted distribution

In general, predicted distribution hotspots around the islands of the Azores agree with predictions from previous modelling studies [51]. However, our models predicted high density around the western group of islands (Corvo and Flores), where no track locations were recorded, and that usually have lower sighting records of the species [51, 55]. We suspect these predictions reflect the influence of distance to coast, combined with favorable oceanographic conditions that persist throughout the year in the western islands. Interestingly, our model also identified a previously undocumented distribution hotspot in the offshore waters south of the Azores (~ 35°N). This region is strongly influenced by the Azores Current (AzC) and the associated Azores front (AzF) that forms a convergence zone with large mesoscale anticyclonic structures in the north, cyclonic eddies in the south, filaments and meanders, that enhance local productivity [67, 69, 70]. During the summer the AzC/AzF at the surface is masked by a well-developed thermocline, while in the winter this stratification weakens and the mixed layer deepens [70]. Higher predicted sperm whale occurrence during most summers and early spring 2023 in this offshore area may reflect the shifts in vertical productivity associated with

these dynamic frontal processes. Although the AzC is not detectable at the surface during the summer, it persists at depth, possibly providing increased foraging opportunities for sperm whales south of the Azores [70].

4.3 Limitations of the study

All sperm whales were tagged in the central islands of the Azores. Given the restricted movements observed in most tracks, our tracking data is unlikely to represent the full extent of movements of SpW in the region. This limitation is further exacerbated by the low sample size of this study. Our results suggest that SpW associate with static and dynamic features that enhance biological productivity and foraging opportunities. However, we could not corroborate this by explicitly accounting for productivity in the models (e.g., prey biomass, chlorophyll concentration). Chlorophyll *a* was highly correlated with other significant predictors driving the habitat models and was removed from the models. To overcome this issue, future studies could use other models, such as Boosted Regression Trees (BRT), which are more robust to collinearity amongst environmental variables [15]. Prey biomass estimates from SEAPODYM, which have proven useful in modeling habitat preferences of cetaceans [20, 46], were not yet available for 2023–2024.

4.4 Conservation and management implications

This study provides the first detailed description of the movements, behaviour and habitat preferences of sperm whales belonging to social units in the Azores. Our findings highlight the critical importance of the region as a foraging habitat for the species. Sperm whales are one of the main targets of the whale-watching industry in the Azores. Oliveira et al., [32] found that disturbance from whale-watching vessels induced behavioural responses in sperm whales likely to impact their energetic balance. This is of conservation concern, especially because our study indicates prolonged residence of the species in the region, which implies a higher risk of exposure to whale-watching disturbance and of chronic disturbance effects. The Azores lies within important commercial cross-Atlantic shipping routes. Given the prolonged residence of sperm whales in the region, they may be at higher risk of ship collisions and underwater noise pollution [71, 72]. Ocean warming has led to shifts in the distribution, timing, and duration of seasonal migrations, and reduction of suitable habitats in several cetacean species [5, 67, 73]. A similar shift in sperm whale distribution and residence may occur, as water temperatures in the Azores are projected to increase by approximately 0.027°C/year [67]. Moreover, their main prey (e.g., cephalopods) are highly sensitive to thermal changes, and projected ocean warming can alter their distribution and abundance [8, 74], ultimately influencing SpW habitat use, foraging dynamics and energetic intake.

By improving our understanding of sperm whale habitat use and movements, as well as the underlying drivers, this study can contribute to conservation and management efforts to mitigate risks to the species. Dynamic ocean management (DOM) offers a novel and adaptive framework that integrates near real-time data to inform management decisions in response to changing oceans and human uses [5, 12, 75]. For species like sperm whales, whose distributions are strongly influenced by dynamic features, DOM can help identify areas and periods of heightened risk. Our model can be easily implemented in such frameworks to inform the conservation of sperm whales under shifting ocean uses and threats.

5 Conclusions

This study presents the first quantification of fine scale movement patterns and habitat preferences of social unit sperm whales in the Mid-North Atlantic inferred from satellite telemetry. By integrating telemetry data with three-dimensional environmental predictors, our study presents a novel modelling framework that substantially improves predictive performance compared with previous habitat models for sperm whales and advances our understanding of the processes shaping their distribution in the region. Our findings indicate prolonged residence and strong site fidelity in the Azores, further highlighting the region as an important foraging habitat for the species. Our results further suggest strong associations with dynamic ocean conditions driving their habitat preferences and we also identified a previously undocumented habitat hotspot in a productive area of the Azores. Ultimately, the baseline knowledge gained from this study will help inform the conservation of the species and their meso-and bathypelagic habitats from anthropogenic threats under a changing marine ecosystem.

Declarations

Ethics approval and consent to participate

Tagging was authorized by the relevant authorities (Regional Directorate for Sea Affairs, Autonomous Region of the Azores) and undertaken under permits 80/2017/DRA, LMAS-DRAM/2018/06, LMAS-DRPM/2023/02, and LMAS-DRPM/2024/01.

Consent for publication

Not applicable

Competing interest

The authors declare no conflicts of interest.

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Author Contribution

MAS conceived the study, with input from SPJ and MDR. RP, MAS, SPJ and CO collected the data. MDR led the analysis of the data and interpretation of results, with contributions from SPJ, MAS, EH, and MJ. MDR wrote the manuscript. All authors critically reviewed and edited the manuscript and approved the final version.

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Data Availability

Location data used for modelling are accessible in the GitHub data repository (see below): these are only the state-space-modelled tracks (the Correlated Random Walk (CRW) at a 6-hour interval). All R codes used in the workflow for the development of SDMs are accessible in the GitHub data repository. https://github.com/AzWhaleLab/Sperm-whale-habitats.git

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Figures

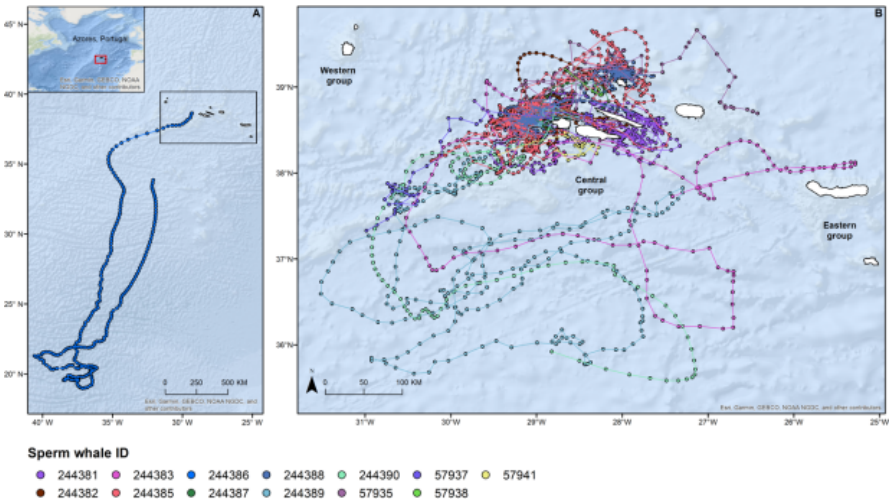


Figure 1

Estimated satellite track positions from State Space Models (Correlated Random Walk at 6-hour interval) of A) a whale transiting outside the Azores region (ID 244386) and B) twelve sperm whales staying within the region. The figure shows the Azores Archipelago, which is comprised of three island groups: western (islands of Corvo and Flores), central (Faial, Pico, São Jorge, Terceira, Graciosa) and eastern (São Miguel and Santa Maria).

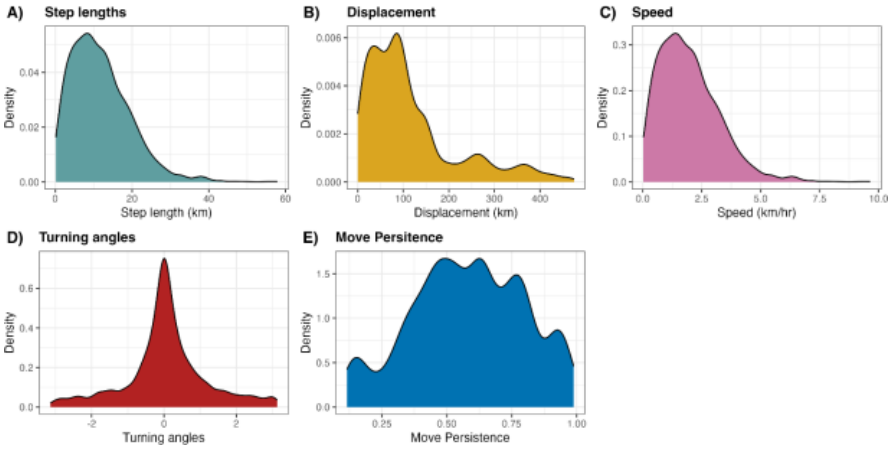


Figure 2

Density of movement metrics for 12 sperm whales using 6-hour interval estimated state space tracks: A) Step lengths between consecutive positions (km); b) displacement (distance of each position from first position, km); c) speed (km/h); turning angle (radians); and e) move persistence (γ_t, scale 0-1).

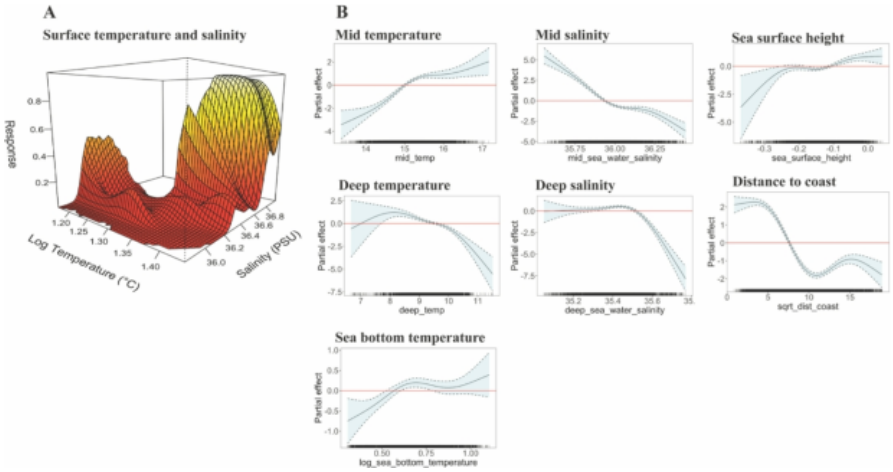


Figure 3

Generalized additive mixed model outputs for sperm whale preference. A) interaction of temperature and salinity, b) other environmental covariates (dynamic and static). Dashed lines with blue shade represent the 95% confidence intervals for the fitted relationships. Red line at 0 represents the zero-effect baseline, where the predictor has no influence on the response variable. Transformations for the scales are as follows: Log scale transformation to normal value is 0.5 (3.2°C), 0.75 (5.6°C), 1 (10°C), 1.2 (15.8°C), 1.25 (17.8°C), 1.3 (19.9°C), 1.35 (22.4°C),1.4 (25.1°C).

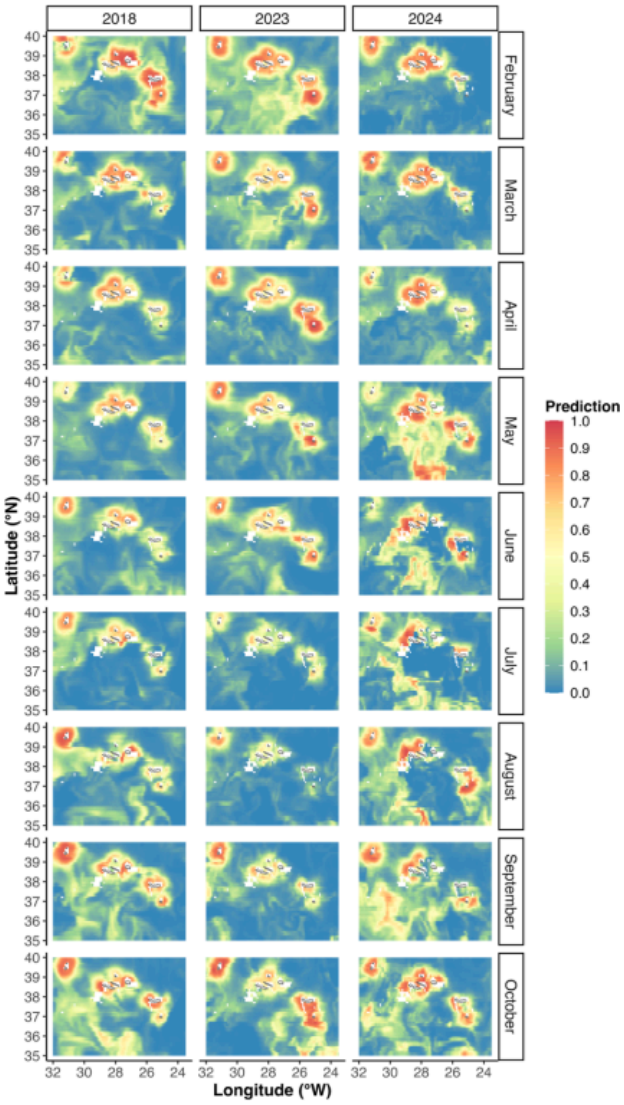


Figure 4

Predicted monthly habitat preference of sperm whales for 2018, 2023 and 2024. Scale is 0-1 with 1 being the highest probability of sperm whales occurring. See Fig. S5 for standard error values.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SpermwhalehabitatdriversSupplementalMaterialsMovEcol.docx