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Distribution Models Reveal Important Coastal Habitats for Endangered Leatherback Sea Turtles

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ABSTRACT

Aim: With the development and operation of offshore wind farms along the United States East Coast, it is imperative that we understand the distributions of vulnerable species so we can track and predict potential interactions. We focused on leatherback sea turtles (*Dermochelys coriacea*) as they depend on this region for important stages of their life history. Our research aimed to determine leatherback distributions, the environmental predictors associated with them, and how they currently overlap with active areas dedicated to offshore wind energy.

Location: United States Atlantic Outer Continental Shelf (OCS).

Methods: Satellite transmitters were affixed to 74 leatherbacks off the coasts of North Carolina and Massachusetts between 2017 and 2023. Location data from these transmitters were implemented in boosted regression tree models to predict leatherback distributions in relation to a suite of static and dynamic environmental covariates. We used the model predictions to categorise core habitat and determine its overlaps with active wind energy leases.

Results: The final model predicted a higher probability of leatherbacks in the Mid-Atlantic Bight (MAB) in May and June and Southern New England (SNE) and Nova Scotia in the late summer. We predicted an increased probability of leatherbacks south along the coastline and off the shelf along the Gulf Stream in the winter. We observed notable overlap between core habitat and offshore wind areas in the MAB and SNE peaking in the late summer.

Main Conclusions: Our results highlight the importance of coastal habitat for leatherback sea turtles along the OCS. Conservation efforts that focus on examining direct effects of wind farm construction and operation on leatherbacks in the MAB and SNE are warranted, especially given the proximity between lease areas and key foraging areas.

1 | Introduction

Offshore construction and development can present challenges to implementing effective conservation strategies as they can disrupt habitat and ecological processes (Gill 2005). Anticipating these challenges and their consequences requires consistent

evaluation of potential impacts to vulnerable species and the habitats they occupy. Yet, it can be difficult to ascertain such information when there is limited knowledge on a given species and their suitable habitat. Within the past two decades, there has been a push to develop distribution models to understand the spatiotemporal extent of various species, the environmental

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predictors to their distributions, and the potential interactions with anthropogenic activities (Guisan et al. 2013). Such efforts have been successful in elucidating distributions and identifying overlap with activities such as fisheries (Calich et al. 2018; Eguchi et al. 2017; Breen et al. 2016), shipping activity (Blondin et al. 2020), and development of offshore renewable energy (Bangley et al. 2022).

With the implementation of offshore wind farms (OWFs), the United States Atlantic Outer Continental Shelf (OCS) has become a focus area as it hosts some of the highest resource wind potential in U.S. waters (Musial et al. 2016). Presently, there are operational OWFs off the coast of North Carolina, Virginia, Maryland, Delaware, New York, New Jersey, Rhode Island, and Massachusetts with additional construction taking place off each of those states (BOEM 2021). Despite this offshore development, there is still limited knowledge regarding how OWFs will affect the surrounding habitat and the species that depend on the area for part or all of their life history.

The development of OWFs along the OCS has especially stoked concern for the potential impacts on vulnerable species such as marine mammals and sea turtles (Kraus et al. 2019). The potential impacts range from short-term effects, including induced stress, behaviour disruption, and displacement, to long-term effects, including changes in prey distributions, habitat degradation, and distributional changes (Kraus et al. 2019). While research into these effects has started taking place both along the OCS and in other parts of the world (i.e., Europe), most of this research focuses on marine mammals (RWSC 2024) leaving our knowledge of perceived threats to sea turtles limited.

The OCS plays a pivotal role in the migration cycle for several species of sea turtle including leatherbacks (*Dermochelys coriacea*). In this region, leatherbacks will migrate from nesting beaches across the Caribbean and Florida east coast to foraging areas located along the OCS (Eckert et al. 2006; Dodge et al. 2014; Rider, Avens, Haas, Hatch, et al. 2024). Recent research has shown a high concentration of area-restricted movement along the Mid Atlantic Bight (MAB) and Southern New England (SNE; Rider, Avens, Haas, Hatch, et al. 2024); two regions that consist of multiple operational and under-construction OFWs. At the time of this publication, construction is taking place on an OFW off the coast of Martha's Vineyard, which is directly adjacent to a documented leatherback foraging area on Nantucket Shoals (Rider, Avens, Haas, Harms, et al. 2024).

There is still uncertainty regarding how OWFs may impact leatherbacks. Along Nantucket Shoals, it has been hypothesised that the construction of OWFs has the ability to disrupt zooplankton prey fields (National Academies of Science, Engineering, and Medicine 2024), which may impact leatherback foraging success (Gibbons and Richardson 2009). Additionally, some research suggests that their perceived auditory range overlaps with noises associated with the construction and operation of wind farms (e.g., pile driving, commercial shipping, etc. Piniak et al. 2012). However, our knowledge of direct impacts on their behaviour, health, and distribution is scant (RWSC 2024). Before we can begin to assess these impacts with greater detail, we first need to understand the spatiotemporal distributions of leatherbacks across the OCS and how they currently overlap with OWFs.

In this study, we used satellite telemetry data from leatherbacks tagged along the United States East Coast to develop a species distribution model to (1) predict spatiotemporal distributions of leatherbacks along the OCS, (2) determine the associated environmental correlates, (3) quantify leatherback core habitat, and (4) evaluate how much leatherback core habitat overlaps with both operational and planned OWFs. The product from this study will serve as a baseline for future research to assess potential shifts in leatherback habitat in relation to anthropogenic activity such as the ongoing operation and construction of offshore wind energy.

2 | Methods

2.1 | Leatherback Capture and Tracking

Between 2017 and 2023, leatherbacks were captured off the coast of Cape Lookout, North Carolina, and Cape Cod, Massachusetts during the months of May and August through October, respectively. These times corresponded to the annual migration north to foraging areas in North Carolina and during a foraging period off Massachusetts. Upon capture, we attached a satellite transmitter (MK-10AF, Wildlife Computers, Redmond, WA, USA), capable of communicating both Argos- and Fastloc GPS-derived locations via the Argos satellite system. These transmitters were programmed to relay up to 250 Argos uplinks and four GPS locations per day. For more detailed information on leatherback capture and tagging methods, please refer to Rider, Avens, Haas, Hatch, et al. (2024) and Sasso et al. (2021).

Transmitted location data were prefiltered following methods outlined by Rider, Avens, Haas, Hatch, et al. (2024). Locations from Argos transmissions were processed using the Kalman Filter algorithm provided by the CLS-Argos service which provided location-specific error ellipse information. We retained GPS locations if they were detected by six or more satellites and had a residual error of less than 30m (Witt 2010; Dujon et al. 2014). Prior to track reconstruction, we filtered both datasets to remove erroneous locations, including those on land, classified as 'Z', or implying unrealistic travel speeds (i.e., greater than 5 km h^{-1} ; James et al. 2005). To reduce the influence of capture on turtle movement and equipment error, we excluded the first 24 h of data and any transmissions from prematurely detached tags. Finally, we split tracks at transmission gaps greater than 10 days. Any resulting sub-track with fewer than 15 locations was removed, as it was insufficient for reliable position and behaviour estimation.

The filtered data were used to reconstruct the most likely path for each leatherback by employing a continuous-time correlated random walk (CTCRW) state-space model using the R package 'aniMotum' (Jonsen et al. 2023). The CTCRW state-space model allowed us to account for the uncertainty of locations and irregular time series of the Argos and GPS positions (Jonsen et al. 2020) and has been successfully used to reconstruct paths of leatherbacks and other sea turtle species (Asada et al. 2021; Winton et al. 2018). We predicted positions using an interval of 24h, and checked each model for convergence, fit, and if model assumptions were met (i.e., homoscedasticity of residuals, normality of residuals, and reduced autocorrelation). Since we were

focused on leatherback distributions in the Northwest Atlantic, we filtered all locations within a bounding box from 24° to 48° N and 55° to 83° W.

One limitation of using telemetry-based data for constructing SDMs is that it primarily yields models based on presence-only data. To combat this, we generated ‘pseudo-absences’ to simulate locations where animals were absent. There are a few methods for generating pseudo-absences for telemetry data (e.g., background sampling, buffer sampling, and correlated random walks) each equipped for dealing with certain questions regarding the spatial and temporal scale of the study (Hazen et al. 2021). For this study, we chose to employ background sampling, which is designed to include the entire range of environmental conditions for which a species could occupy. This method is suitable to use with leatherback telemetry data as they can occupy a wide range of environmental conditions across the Northwest Atlantic (Dodge et al. 2014; Evans et al. 2021), and we are aiming to understand their broadscale distributions across multiple years. To generate pseudo-absences using the background method, we generated a set of pseudo-absences for every presence within the spatial extent of an individual’s locations that fell within the bounding box. Following similar methods to Lopez et al. (2024), we generated four different data sets that corresponded to presence to pseudo-absence ratios of 1:1, 1:2, 1:10, and 1:25.

2.2 | Environmental Variables

Environmental data were gathered and matched to each location using four databases made available by the European Union Copernicus Marine Environment Monitoring Service (CMEMS). Daily physical data including sea surface temperature (SST), northward and eastward surface water currents, sea surface height above the geoid (SSH), mixed layer depth (MLD), and salinity were gathered from the Global Oceans Physics Reanalysis product (2024) at a 0.083° resolution. We used the northward and eastward current measurements to calculate eddy kinetic energy (EKE), and current direction. Bathymetry data were gathered from the ETOPO Global Relief Model at a 15 arc-second resolution (NOAA NCEI 2022). Slope was calculated from the bathymetry data using the R package ‘terra’ (Hijmans 2023). Chlorophyll *a* (Chl-*a*) was collected from the Global Ocean Colour product (2024) at a 4km resolution. Net primary productivity (NPP) was gathered from the Global Low and Mid Trophic Level Biomass Content Hindcast product (2024) at a 0.083° resolution. Dissolved oxygen was gathered from the Global Ocean Biogeochemical Hindcast product (2024) at a 0.25° resolution. All environmental data were selected based on their influence on leatherback movements and distributions in other parts of the world (e.g., Bailey et al. 2012; Dodge et al. 2014; Willis-Norton et al. 2015; Hazen et al. 2018).

At each point, we extracted the value of the environmental parameter. For SST and Chl-*a*, we also calculated the standard deviation within a 0.25° radius buffer region around the point. This was used as an index for frontal systems as used by Dodge et al. (2014) and Willis-Norton et al. (2015). More detailed specifications of each environmental parameter used can be found in Table 1.

Before running the models, we checked for collinearity among the environmental covariates. Collinearity was determined if the correlation coefficient was above 0.8. There was only one instance of collinearity which occurred between Chl-*a* and NPP. While Chl-*a* is typically used as a proxy for prey abundance (i.e., gelatinous zooplankton; Hays et al. 2006, Bailey et al. 2012), it may not be a sufficiently reliable indicator as no significant relationship between gelatinous zooplankton biomass and Chl-*a* has been detected on a global scale (Lucas et al. 2014). Instead, primary productivity proved to be more appropriate, especially when combined with other predictors such as salinity, dissolved oxygen, and SST (Aleksa, Nero, et al. 2018; Lucas et al. 2014). Therefore, we only ran models with NPP and did not include Chl-*a*.

2.3 | Model Fitting

Leatherback presence was modelled as a function of environmental covariates using boosted regression trees (BRTs) as the modelling framework. BRTs are a machine learning model that combines the use of regression trees, which relate a response to their predictors using binary splits, with boosting, a numerical optimization technique that combines many simple models to improve predictive performance (Elith et al. 2008). Compared to other modelling frameworks used for species distribution models like generalised linear and additive models, BRTs can be more advantageous as they can account for correlation and collinearity in predictors, model complex relationships, and are robust to outliers and missing values (Elith et al. 2008).

When fitting BRTs there are two important parameters that together help determine the optimal number of trees that minimizes the residual deviance explained by the model: tree complexity and learning rate. Tree complexity controls the number of splits in each tree while learning rate determines the contribution of each tree to the model as it grows. To find the optimal combination of these parameters, we used the R package ‘caret’ (Kuhn 2008) to test a series of candidate models with different combinations of learning rate (0.1, 0.05, 0.01, and 0.005), tree complexity (1, 2, 3, 4), and number of trees (100–6000 by increments of 100). We specifically fit BRT models using a Bernoulli family appropriate to the binary nature of the response variable (presence/pseudo-absence). This resulted in a set of candidate models which were each tested for accuracy using a k-fold cross-validation method with 10 folds. From these candidate models, we determined the optimal tree complexity and learning rate based on the area under the receiver operating characteristic curve (AUC) and sensitivity (i.e., proportion of correctly predicted presences). Using the optimal tree complexity and learning rates, we fit four more models, each with differing bag fractions (0.25, 0.50, 0.75, and 0.90) using the gbm.step function from the R package ‘dismo’ (Hijmans et al. 2024), which assesses the optimal number of trees using k-fold cross-validation. This additional step was performed as the gbm.step function is capable of fitting a model to a data set with missing values whereas the ‘caret’ package is not. These methods were performed for each set of data with differing ratios of presence to pseudo-absences (i.e., 1:1, 1:2, 1:10, and 1:25). Following Konowalik and Nosol (2021), we selected the preferred model

TABLE 1 | Summary of environmental covariates used in the models.

Parameter	Units	Spatial resolution	Temporal resolution	Source
<i>Dynamic—Physical</i>				
Sea surface temperature (SST)	°C	0.083°	Daily	CMEMS Global Ocean Physics Reanalysis
Sea surface temperature gradient	°C	0.083°	Daily	Calculated as standard deviation of SST
Sea surface height above geoid (SSH)	m	0.083°	Daily	CMEMS Global Ocean Physics Reanalysis
Salinity	ppt	0.083°	Daily	CMEMS Global Ocean Physics Reanalysis
Mixed layer depth (MLD)	m	0.083°	Daily	CMEMS Global Ocean Physics Reanalysis
Northward current (v_0)	m/s	0.083°	Daily	CMEMS Global Ocean Physics Reanalysis
Eastward current (u_0)	m/s	0.083°	Daily	CMEMS Global Ocean Physics Reanalysis
Current Direction	Degrees	0.083°	Daily	Calculated from northward and eastward currents
Eddy Kinetic Energy (EKE)	m^2/s^2	0.083°	Daily	Calculated from northward and eastward currents: $EKE = \frac{1}{2}*(u_0^2 + v_0^2)$
<i>Dynamic—Biogeochemical</i>				
Chlorophyll (Chl-a)	mg/m ³	4 km	Daily	CMEMS Global Ocean Colour
Chlorophyll gradient	mg/m ³	4 km	Daily	Calculated as standard deviation of Chl-a
Net primary productivity (NPP)	mg/m ² /day	0.083°	Daily	CMEMS Global Ocean Low and Mid Trophic Level Biomass Content
Dissolved Oxygen (DO ₂)	mmol/m ³	0.25°	Daily	CMEMS Global Ocean Biogeochemistry Hindcast
<i>Static</i>				
Bathymetry	m	15 arc-second		ETOPO Global Relief Model
Slope	Degrees	15 arc-second		Calculated from Bathymetry

and data set primarily based on the average AUC and mean absolute error (MAE) across 10 folds. If additional performance measures were required for evaluation, we also examined the true skill statistic (TSS), deviance explained, and biological relevancy of predictions to further select models. Biological relevancy was determined by comparing predicted distributions with leatherback tracks from other studies in the same region.

2.4 | Predicting Leatherback Distributions and Core Habitat

To visualise predicted probability of leatherback presence within the study region, we generated monthly predictions from the preferred BRT model and presence to pseudo-absence ratio data set. Predictions were generated using monthly composites of all dynamic environmental variables in combination with

static variables such as bathymetry and slope. Monthly composites were extracted from the same products used to build the BRT models. All parameters, including depth and slope were resampled to a 0.083° resolution to match that of the majority of environmental parameters used in the analyses.

Predictions were generated using a bootstrapping ($n=100$) method (Braun et al. 2023) in which models were re-fit to 75% of the data at each bootstrap iteration. Each fit model was predicted to monthly composites of all environmental covariates from the study period (i.e., October 2017–December 2023) and then averaged to produce maps displaying probability of presence on a scale of zero to one for each month used in the analyses (i.e., May to January). To assess model uncertainty, we also calculated 95% confidence intervals across all iterations and averaged those for each month. Since we focused on distributions along the OCS, we filtered our predictions within a region defined by the Atlantic Marine Assessment Program for Protected Species

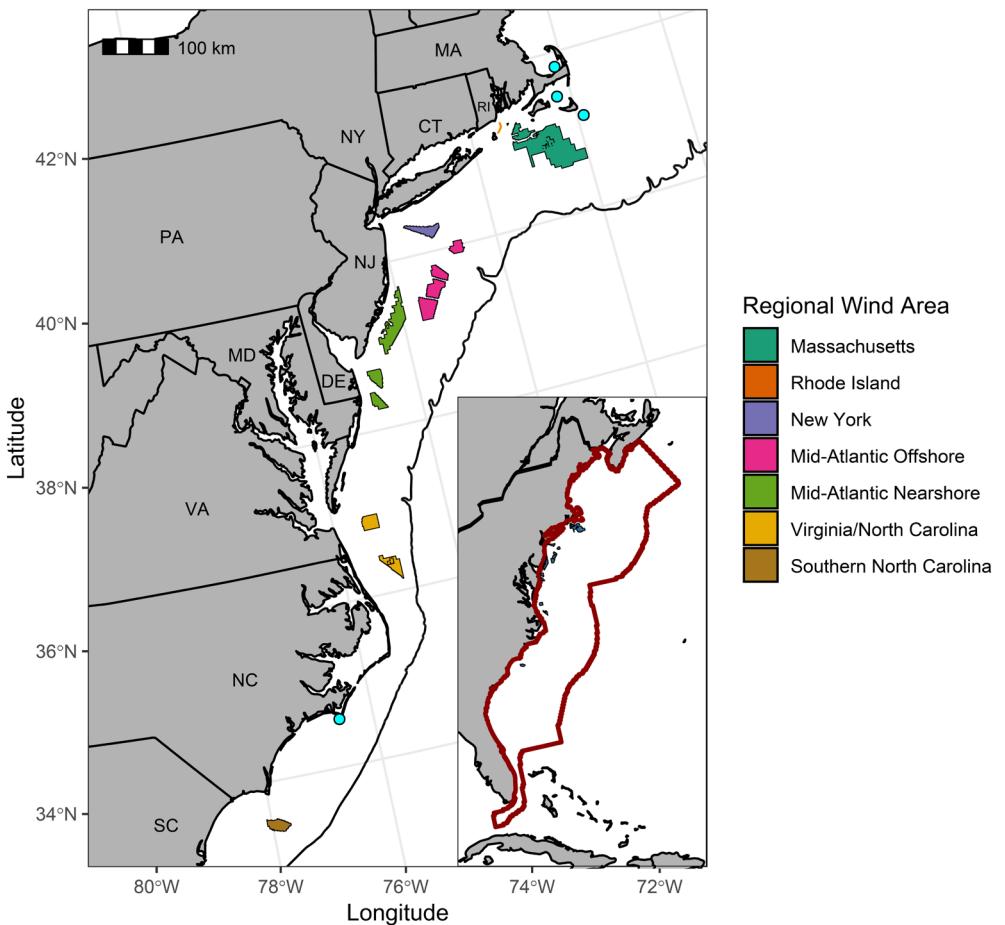


FIGURE 1 | Map of the study area including the active offshore wind energy lease areas (excluding easements) that are colour coded by regions. We filtered leatherback locations within the same study area used for the Atlantic Marine Assessment Program for Protected Species (Palka et al. 2021). The blue points represent the locations that leatherbacks were captured and tagged. The inlaid map includes the entire study area (outlined in red) that we predicted leatherback presence and core habitat. The map is projected using North American Equal Area Albers Conic.

(AMAPPS; Palka et al. 2021). This region encompasses the exclusive economic zone of the United States from South Florida to Maine and further north along the coast of Nova Scotia (Figure 1). This region includes the Atlantic OCS and with that, all proposed and planned OFWs in the region. However, within the broader AMAPPS region, we only predicted leatherback distributions according to the spatial extent of locations recorded during the study.

Based on the predicted probability of presence for each month, we classified core habitat by generating an optimal cut-point to assess whether a cell would be inhabited by a leatherback (e.g., Patel et al. 2021). More specifically, we chose an optimal cut-point that maximises Kappa (i.e., the agreement between predicted and observed species presence while correcting for random chance; Zhang et al. 2019). Using the k-fold cross-validation method, we determined the optimal cut-point for each fold and the final value was averaged across all 10 folds. Based on the optimal cut-point, the probability of leatherback occurrence for each season and year interval was classified as either one (present) or zero (absent). Therefore, predicted probabilities greater than or equal to the cut-point were re-classified as one, and otherwise zero. Core leatherback habitat was then categorised as instances where they were predicted

to be present. We classified core habitat for the mean and 95% confidence interval prediction maps that resulted from the 100 bootstrap iterations.

2.5 | Association With Offshore Wind Energy

To understand the association between predicted leatherback distributions and OFWs, we determined the amount of spatial overlap between the classified core habitat and active lease areas by month. Shapefiles for wind energy lease areas were gathered from the Bureau of Ocean Energy Management (BOEM, beom.gov) and categorised by regional wind development area. Given their proximity, we grouped individual leases by geographic location which resulted in seven total wind development areas (see Figure 1). Both the wind development areas and core habitat were re-projected using the North American Albers Equal Area Conic coordinate reference system. We calculated overlap as the percent of each wind energy area occupied by core habitat per month as well as the proportion of total core habitat within the study region that coincided with the total lease area per month. This was carried out for the mean and 95% confidence interval predictions for core habitat.

3 | Results

3.1 | Leatherback Capture and Tracking

Between 2017 and 2023, a total of 65,691 Argos and 10,192 GPS-derived locations were recorded by 74 leatherbacks that were tagged and tracked for long enough (i.e., >10 days) to be included in the final model (Table 2). After processing these raw locations through the CTCRW model and filtering for those that fell within our study area, we were left with 11,022 estimated locations that were used within the SDMs. Leatherbacks tagged off the coast of North Carolina mostly migrated along the coast into the MAB before either moving north into SNE or off the OCS and into the Gulf Stream (Table S1). A few individuals migrated into the South Atlantic Bight (SAB) where they either moved along the coastline or edge of the OCS (Figure S1). Those tagged off Massachusetts either moved south into the MAB before moving off the OCS and into the Gulf Stream or directly south as they moved towards overwintering or nesting areas in the Caribbean. A few turtles from each tagging location were observed moving farther north past SNE into waters off Maine and Nova Scotia. For more detailed information on movements of these leatherbacks, please see Rider, Avens, Haas, Hatch, et al. (2024).

3.2 | Model Fitting

Based on the AUC and MAE, the optimal preference ratios were 1:10 and 1:25. Even though the ratio of 1:25 had the lowest MAE, the models using the ratio of 1:10 had higher TSS and explained more of the deviance. Thus, the preferred model required a tree complexity of 4, a learning rate of 0.05, 3900 trees, and a bag fraction of 0.50 (Table 3). While models with bag fractions of 0.75 and 0.90 had slightly higher performance metrics, we ultimately chose the model with 0.50 as it produced biologically

realistic predictions of leatherback distributions consistent with the current literature.

For the preferred model, bathymetry (15.69%), dissolved oxygen (12.46%), and NPP (12.01%) had the highest relative influence on leatherback presence, while current direction (4.56%), slope (3.95%), and MLD (3.16%) had the lowest (Table 4). The partial dependence plots from the preferred model showed non-linear relationships with most of the environmental covariates (Figure S2).

The partial dependence plot for bathymetry indicated that leatherbacks preferred both oceanic waters greater than 5000 m deep as well as neritic areas closer to shore. We also observed an association for bathymetric slopes above 25° suggesting a preference for the continental shelf edge. In terms of physical features, leatherbacks appeared to prefer MLDs between 100 m and just below the surface. There were also higher associations with negative SSHs, higher SST and Chl-a gradients, and slightly higher EKE. For temperature, leatherbacks preferred SSTs above 15°C with higher preference for temperatures of 20°C and warmer. The range for salinity preference ranged between 27 and 35 ppt peaking at 31 ppt. Leatherbacks were associated with dissolved oxygen levels around 225 mmol/m³ which decreased at 250 mmol/m³ and then sharply increased around 300 mmol/m³. Finally, leatherback presence had a positive relationship with NPP, showing preference for increasing productivity; however, this association decreased at very high levels.

3.3 | Predicting Monthly Leatherback Distributions and Core Habitat

Leatherback presence and core habitat were predicted in the study area during all months, with seasonal patterns

TABLE 2 | Summary of leatherbacks captured and tagged off the coasts of Massachusetts (MA) and North Carolina (NC) between 2017 and 2023.

Tagging location	Year	N	Curved carapace length (cm)	Curved carapace width (cm)	Tracking duration (days)
MA	2017	1	149.7	113.0	68.0
MA	2018	1	153.5	112.0	161.0
NC	2018	7	151.3 ± 10.8	104.4 ± 9.0	167.7 ± 41.0
MA	2019	9	144.9 ± 7.2	109.6 ± 9.5	115.2 ± 39.5
NC	2019	12	151.2 ± 12.9	112.4 ± 10.8	120.5 ± 56.8
NC	2021	2	143.0 ± 23.4	105.1 ± 18.4	190.0 ± 24.0
MA	2022	11	155.9 ± 6.1	112.4 ± 2.7	81.0 ± 50.2
NC	2022	10	148.3 ± 8.2	96.4 ± 30.6	178.1 ± 62.1
MA	2023	17	155.4 ± 7.9	114.4 ± 5.9	98.1 ± 42.1
NC	2023	4	149.4 ± 9.2	106.4 ± 6.8	79.0 ± 26.4
MA	Total	39	152.9 ± 8.2	112.6 ± 6.3	98.1 ± 44.9
NC	Total	35	149.7 ± 11.0	105.1 ± 18.9	145.6 ± 60.9
	Total	74	151.4 ± 9.7	109.0 ± 14.2	120.6 ± 57.9

TABLE 3 | Model performance metrics for the 16 different models run using different combinations of presence to absence ratio and bag fraction. All models were performed using a tree complexity of 4 and a learning rate of 0.01 for the 1:1 ratio and 0.05 for all others. Models were cross-validated using the k-fold method where each metric was calculated for each fold and then averaged across all 10 folds and presented below. The preferred model (bold) was selected based on the area under the receiver operating characteristic curve (AUC), mean absolute error (MAE), true skill statistic (TSS), deviance explained, and biological relevancy of predictions. Values in parentheses represent the standard deviation across 10 folds.

Presence to absence ratio	Bag fraction	Number of trees	AUC	MAE	TSS	Deviance	Max Kappa
1:1	0.25	5300	0.820 (0.010)	0.347	0.503	34.041	0.484
	0.50	5500	0.822 (0.007)	0.346	0.510	35.286	0.499
	0.75	6200	0.824 (0.011)	0.344	0.511	36.762	0.495
	0.90	6350	0.823 (0.011)	0.344	0.509	36.776	0.518
1:2	0.25	2500	0.823 (0.009)	0.312	0.508	37.810	0.393
	0.50	2650	0.826 (0.008)	0.311	0.507	40.399	0.409
	0.75	3250	0.828 (0.006)	0.308	0.512	43.842	0.419
	0.90	2850	0.828 (0.007)	0.310	0.510	41.829	0.395
1:10	0.25	3400	0.826 (0.006)	0.135	0.502	32.712	0.224
	0.50	3900	0.831 (0.005)	0.134	0.510	35.742	0.230
	0.75	3800	0.832 (0.007)	0.134	0.512	36.016	0.220
	0.90	3550	0.833 (0.008)	0.134	0.513	35.114	0.231
1:25	0.25	3700	0.822 (0.006)	0.065	0.497	29.031	0.155
	0.50	4550	0.828 (0.006)	0.065	0.507	32.615	0.141
	0.75	3850	0.830 (0.009)	0.065	0.508	31.266	0.151
	0.90	4550	0.831 (0.008)	0.065	0.510	33.024	0.156

TABLE 4 | Relative influence of environmental covariates on leatherback presence according to the preferred model.

Environmental variable	Relative influence (%)
Bathymetry	15.69
Dissolved oxygen	12.46
Net primary productivity	12.01
Chlorophyll-a gradient	10.14
Sea surface salinity	9.77
Sea surface temperature	9.15
Sea surface height	7.73
Sea surface temperature gradient	6.85
Eddy kinetic energy	4.63
Current direction	4.56
Slope	3.95
Mixed layer depth	3.16

north-south and inshore-offshore (Figures 2 and 3). The optimal cut-point value calculated from the preferred model was 0.23 meaning that any grid cell that had an estimated value for the probability of leatherback presence greater than 23% was

classified as core habitat. Between May and June, we predicted leatherback distributions and core habitat nearshore as they shifted from the SAB around Cape Hatteras and into the MAB, with a higher probability of leatherback presence off the coast of Maryland and Virginia (Figures S3 and S4). The predicted distributions started to shift into SNE in July with a higher likelihood of leatherbacks off the coast of Massachusetts as well as farther north off the coast of Maine and Nova Scotia. This high likelihood continued into August and September especially off Nantucket and along the shelf edge from George's Bank to the Scotian Shelf. In October, the likelihood of leatherbacks off Nova Scotia and Massachusetts begins to decrease as their distributions and core habitat shift southward towards North Carolina. While core habitat in November extends from Nova Scotia to the SAB, we predicted higher probabilities of leatherbacks near Cape Hatteras. Finally, we predicted higher probabilities of leatherbacks in December and January south of Cape Hatteras into the SAB as well as off the continental shelf and along the Gulf Stream.

3.4 | Association With Regional Offshore Wind Development

Regional wind development areas contained core leatherback habitat, but due to the highly migratory behaviour exhibited by leatherbacks, the overall proportion of core habitat that overlapped with wind areas was relatively low across all months

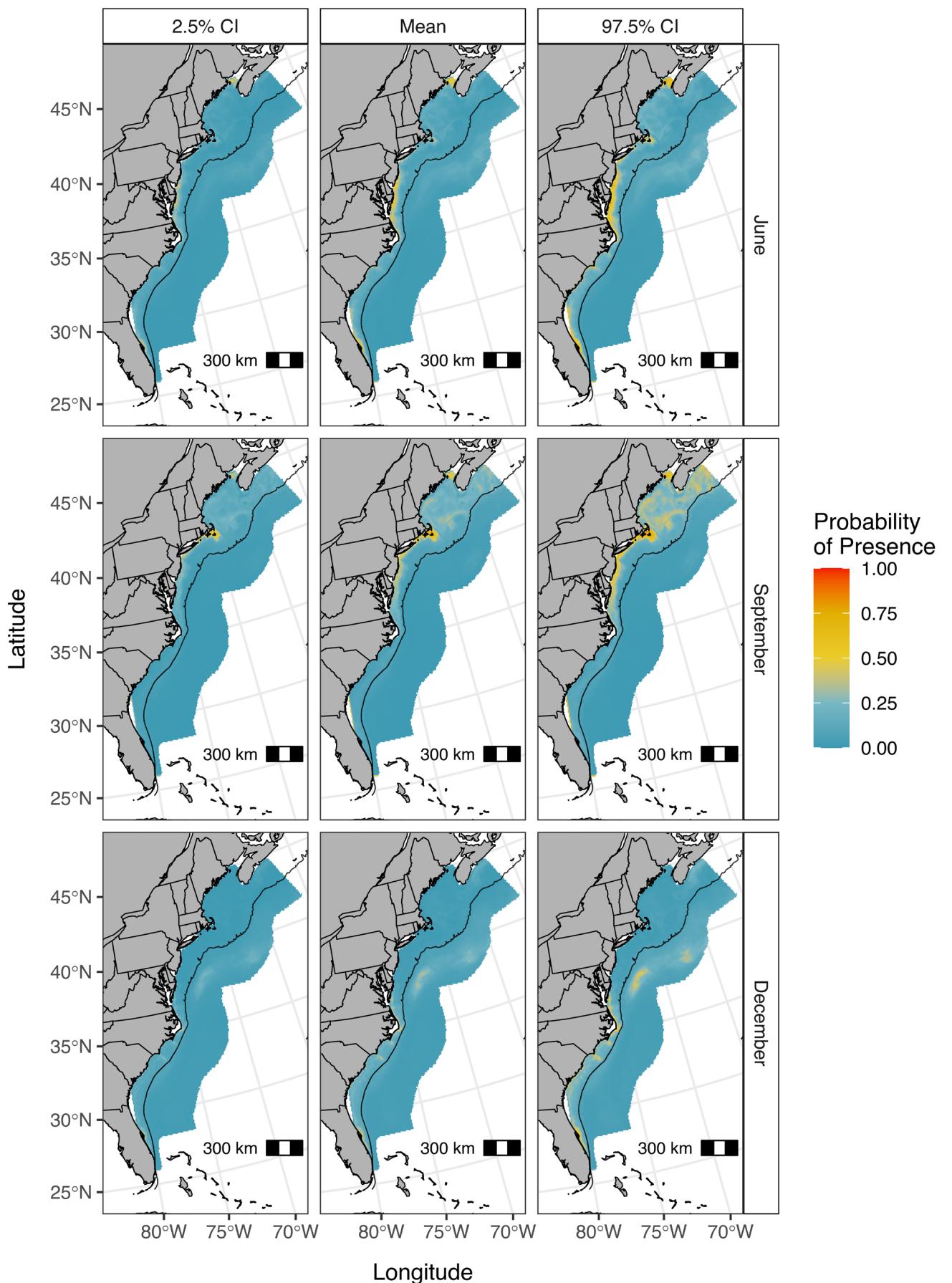


FIGURE 2 | Legend on next page.

FIGURE 2 | Mean (and 95% confidence interval) predicted leatherback distributions for June, September, and December. Predictions were averaged across 100 bootstrap iterations for each year/month combination of the study period (i.e., October 2017 through December 2023) and further averaged for each month (i.e., May through January). Predictions from the remaining months can be found in Appendix S3. The black line represents the continental shelf edge. The map is projected using North American Equal Area Albers Conic.

never exceeding 3.88% (Table 5). Across all wind areas, leatherback core habitat mainly overlapped with those closer to shore, especially in the Mid-Atlantic Nearshore and Rhode Island areas (Figure 4). We observed almost complete overlap with the Mid-Atlantic Nearshore areas between June and November and Rhode Island between June and October. A similar pattern occurred in the New York and Massachusetts areas with an increase in overlap from July to November in New York and September in Massachusetts. However, the percent of overlap was relatively low, only rising above 50% in New York in July and never exceeding 25% in Massachusetts throughout the year. The Mid-Atlantic Offshore areas were predicted to experience the least amount of overlap throughout the entire year with a slight increase in November that did not exceed 10%. In the Virginia and North Carolina areas, we predicted overlap to increase in June, decrease throughout the summer months, increase in October, and decline again in the winter. We predicted the Southern North Carolina area to experience very little overlap between June and November, but with relatively higher overlap in May, December, and January. The overall proportion of core habitat that overlapped with all wind areas peaked in July at 3.88%. However, this decreased down to ~2% between August and November and dropped further below 0.5% in December and January.

4 | Discussion

In this study, we used telemetry data from 74 leatherback sea turtles to estimate suitable habitat and derive monthly distributions across the Atlantic OCS. While the current literature has examined leatherback distributions in other parts of the world (Lopez et al. 2024; Willis-Norton et al. 2015), studies focused on the Atlantic OCS are relatively recent (DiMatteo et al. 2024), and no distribution models using telemetry data have yet been synthesised. Our model revealed distinct relationships with environmental covariates, highlighting specific habitats along the OCS with increased probability of leatherback occurrence near shore. Based on these results, we categorised core habitat areas and assessed their potential overlap with active OWF areas. We offer recommendations for refining distribution models for leatherbacks in this region and emphasise the importance of this information for guiding conservation and management strategies, particularly as OWF construction and operation continues.

4.1 | Environmental Relationships With Leatherback Distributions

One of the most significant findings from this study was the strong association between leatherback core habitat and coastal areas along the OCS. Among the environmental variables, bathymetry had the greatest relative influence, indicating not only a higher

likelihood of leatherback presence in oceanic waters—as supported by existing literature (Dodge et al. 2014; James et al. 2005)—but also a preference for shallower depths. This aligns with several studies that emphasise the importance of coastal habitats for leatherbacks in other parts of the world (Houghton et al. 2006; Robinson et al. 2016). For instance, Robinson et al. (2016) documented year-round leatherback occurrences in shallow waters (<50 m) off southern Africa, linking this pattern to elevated levels of NPP.

A likely driver of this coastal affinity is the aggregation of gelatinous zooplankton, the leatherback's primary prey. Leatherbacks have been observed foraging on various jellyfish species in several coastal regions, including Nova Scotia (Heaslip et al. 2012), southern New England (Patel and Siemann 2020), North Carolina (Grant and Ferrell 1993), and the United Kingdom and Ireland (Houghton et al. 2006). Alongside Robinson et al. (2016), our study also found a positive relationship between NPP and leatherback presence, which may reflect prey availability—especially when considered alongside other environmental variables. When combined, SST, dissolved oxygen, salinity, and NPP proved more effective at explaining gelatinous zooplankton abundance than primary productivity alone (Aleksa, Nero, et al. 2018; Lucas et al. 2014). By parameterizing our model with a tree complexity of four, we may have captured the intricate interactions among NPP and other predictors, offering a more informed proxy for gelatinous zooplankton distribution.

Following the same logic, it is also possible that leatherbacks are targeting prey species aggregating along the continental shelf edge. Topographic features and regional hydrography have been linked to aggregations of gelatinous prey species (Graham et al. 2001; Witt et al. 2007), which would explain our observed preference for higher bathymetric slopes. It is likely that the frontal dynamics at the shelf edge, including tidal mixing and upwelling, promote high productivity leading to increased prey abundance near or at the surface (Negroni 2023). Indeed, leatherbacks were observed displaying foraging-like movement behaviour along the Atlantic OCS edge (Rider, Avens, Haas, Hatch, et al. 2024).

The influence of physical oceanographic features on leatherback presence may reflect their foraging behaviour as well. We observed a higher occurrence of leatherbacks in regions characterised by negative SSHs, which are generally associated with cold, nutrient-rich waters (Bakun 2006). This pattern is consistent with findings from the Gulf of America (formerly Gulf of Mexico) where leatherbacks were also found in areas of low SSH, coinciding with zones of elevated productivity conducive to aggregations of gelatinous zooplankton (Aleksa, Sasso, et al. 2018). Similarly, along the Gulf Stream, extended residency times by leatherbacks have been documented in regions exhibiting negative SSH anomalies, further suggesting foraging activity (Chambault et al. 2017). In these regions, leatherbacks were often observed in proximity to physical

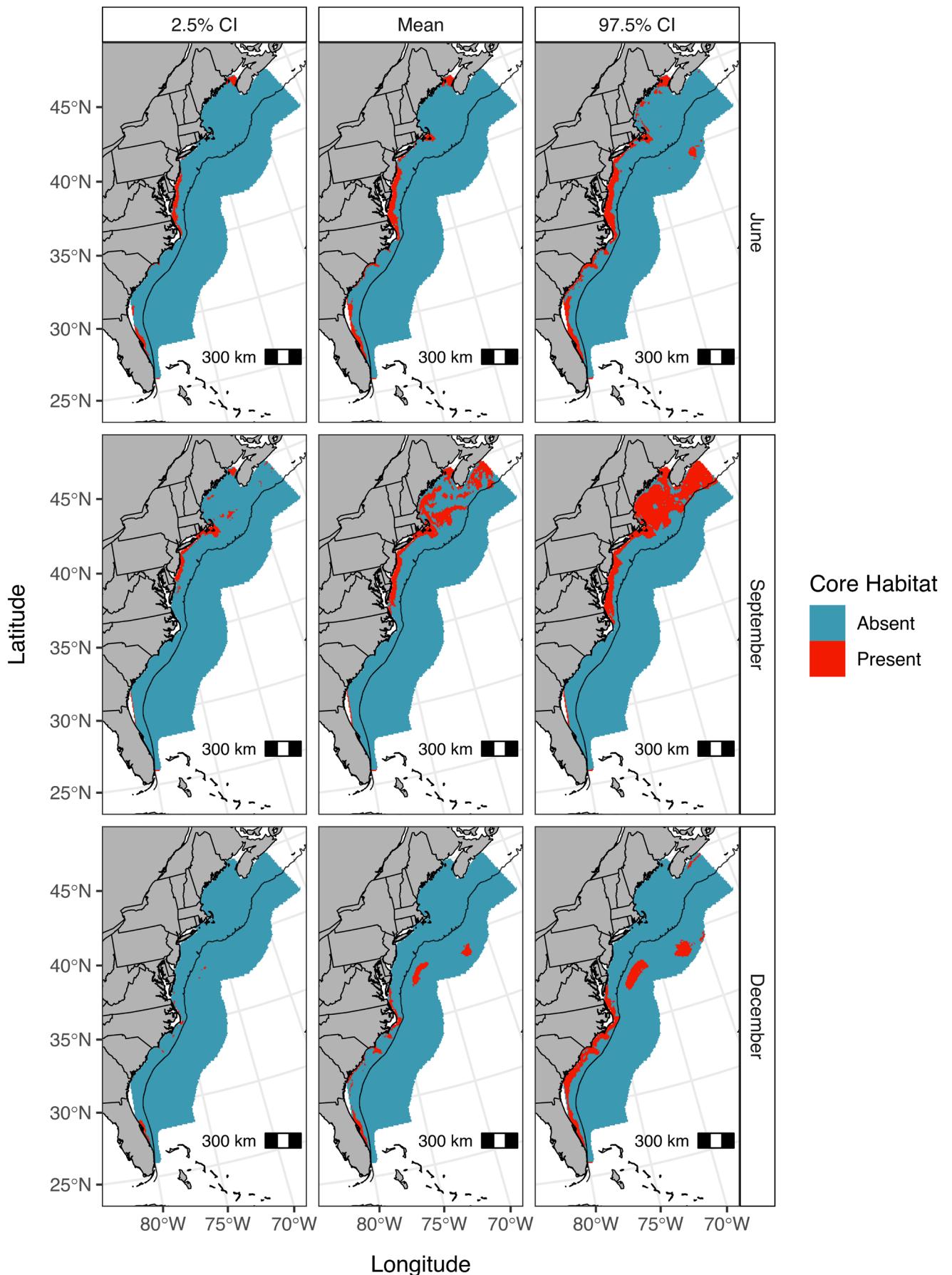


FIGURE 3 | Legend on next page.

FIGURE 3 | Leatherback core habitat for June, September, and December based on the predicted leatherback distributions in Figure 2. Core habitat was defined using an optimal cut-point defined as the threshold value that maximised kappa. Any predicted probability above the cut-point was defined as core habitat (i.e., red). In this case, any grid cell with a probability greater than 23% was included. Predicted core habitat from the remaining months can be found in Appendix S4. The black line represents the continental shelf edge. The map is projected using North American Equal Area Albers Conic.

TABLE 5 | Monthly predicted leatherback core habitat area and the overlap with all wind areas across the study area. Values are expressed as the mean and 95% confidence interval (CI) calculated over 100 bootstrap iterations of the final model.

Month	Total core habitat (km ²)		Total overlap with wind areas (km ²)		Proportion of core habitat overlapping with wind areas (%)	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
May	76,223	38,079–128,297	884	58–2005	1.16	0.15–1.56
June	70,755	33,067–113,326	2746	1466–3450	3.88	4.43–3.04
July	91,845	40,422–180,370	2708	879–4617	2.95	2.18–2.56
August	117,491	35,671–225,219	2335	160–3961	1.99	0.45–1.76
September	133,179	41,464–226,716	3110	1729–4652	2.34	4.17–2.05
October	158,304	62,684–226,391	3062	1475–3671	1.93	2.35–1.62
November	90,478	18,486–187,010	1985	68–4038	2.19	0.37–2.16
December	44,328	8918–102,325	162	1–560	0.37	0.01–0.55
January	54,743	13,539–113,326	83	15–429	0.15	0.11–0.38

features characterised by strong SST and SSH gradients which can also be linked to heightened zooplankton biomass (Powell and Ohman 2015). Indeed, our results indicated that SST and chl- α gradients, along with EKE, were positively associated with leatherback presence, reinforcing the connection between dynamic ocean features and foraging behaviour. These connections have been suggested in other parts of the world (Northern Atlantic: Hays et al. 2006; Southwest Indian Ocean: Lombardi et al. 2008; Western Pacific: Benson et al. 2011).

Leatherbacks can occupy a wide breadth of temperatures due to their thermoregulatory abilities (Bostrom et al. 2010) as demonstrated by our results which indicated a preference for SSTs between 10°C and 32°C. Within this range, predicted leatherback presence was highly influenced by temperatures above 20°C. The 15°C isotherm has been suggested to drive their northern limits (McMahon and Hays 2006) which would explain the concentration of leatherbacks in Nova Scotia in the summer and the southward shift during the late fall when temperatures drop below 15°C. The estimated temperature preferences also align with their core body temperature, which is typically between 25°C and 27°C (Casey et al. 2014). However, their occurrence in waters cooler than their core body temperature may be driven by prey availability and the associated increased body heat production from constant swimming and foraging (Bostrom et al. 2010) rather than ambient thermal preferences. For example, lion's mane jellyfish (*Cyanea capillata*) were observed to begin deteriorating at 19°C off Connecticut (Brewer 1989) and 18°C off Nova Scotia (Nordstrom et al. 2020). Similarly, sea nettles (*Chrysaora quinquecirrha*), though they show greater tolerance for warmer

conditions, begin to senesce at temperatures between 20°C and 30°C (Gatz et al. 1973). Through their large size and thermal inertia, leatherbacks are likely able to exploit their prey in cooler waters as they have been tracked in known foraging areas diving from 17°C to 18°C surface waters into sub-thermocline layers as cold as 1°C (James, Davenport, and Hays 2006; James, Sherrill-Mix, et al. 2006). While it may not be beneficial to occupy waters slightly cooler than their core body temperature, it could be a necessary trade-off given the phenology and distributions of their prey.

We observed a high relative influence of dissolved oxygen on predicted leatherback presence. While leatherbacks displayed a close association with lower levels of dissolved oxygen in some areas, there was a drastic increase at higher levels. This may correspond with the timing of leatherback presence at northern foraging areas and the annual strength of the Labrador Current. The Labrador Current travels south along the coasts of Labrador and Newfoundland transporting cool, oxygen-rich waters towards Nova Scotia and as far south as the MAB. Since the current is strongest in the fall and winter (Lazier and Wright 1993), the heightened oxygen-rich waters may correspond with leatherback presence in their foraging areas off Massachusetts and Nova Scotia. Indeed, the interaction between the Labrador Current and Gulf Stream promotes a high biomass of zooplankton in the region (Vinogradov et al. 1998) which may contribute to blooms of gelatinous zooplankton. Additionally, the waters transported by the Labrador Current are less saline (Lazier and Wright 1993), which may explain why we observed leatherbacks show a preference for lower salinity levels ~31 ppt. However, this

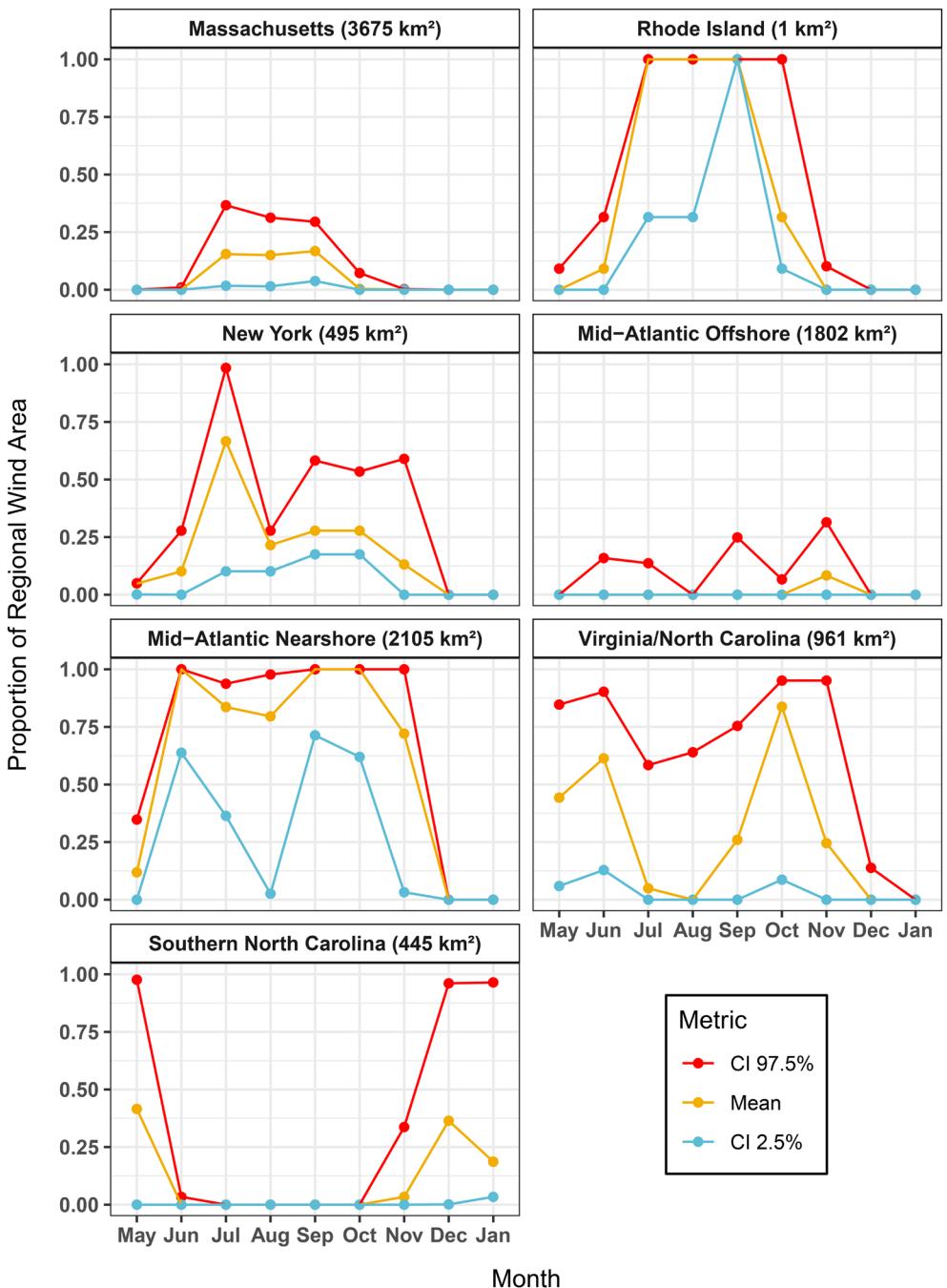


FIGURE 4 | The proportion of each wind area ($n=7$) occupied by the predicted mean and 95% confidence interval core habitat of leatherbacks along the United States East Coast per month. The total area of each wind area can be found next to the label for each plot.

could also be attributed to their affinity for coastal waters which are inherently less saline.

4.2 | Predicted Leatherback Distributions

Consistent with regional tracking studies, our model predicted high leatherback presence in the MAB and SNE from June to November. These areas are increasingly recognised as important feeding grounds supported by direct observations in SNE (Dodge et al. 2018; Patel and Siemann 2020) and by behaviours indicative of foraging—co-occurring with known prey blooms (Brown et al. 2002; Bologna et al. 2017) – in the MAB (Rider,

Avens, Haas, Hatch, et al. 2024). Thus, our model's predictions add further evidence for the ecological significance of these regions for leatherbacks.

Our predictions showed several discrepancies with regional tagging and survey observations, notably by predicting core habitat extending into the Bay of Fundy (July to October) and identifying an overall low amount of core habitat in the SAB. There is little evidence that the Bay of Fundy serves as important habitat for leatherbacks—while leatherbacks have been observed there, their abundance and prey availability are lower compared to other regions (James, Davenport, and Hays 2006; James, Sherrill-Mix, et al. 2006; Nordstrom et al. 2019). In comparison,

our predictions along the Scotian Shelf are consistent with tagging studies documenting these areas as foraging sites from late summer into late fall (James, Davenport, and Hays 2006; James, Sherrill-Mix, et al. 2006). We also predicted leatherback core habitat to decrease across the area in November which corresponds with departure times of those tagged off Nova Scotia (Sherrill-Mix et al. 2007).

Model predictions of core habitat in the SAB were opposite to those developed by DiMatteo et al. (2024) who predicted a higher abundance of leatherbacks in the SAB throughout the year (Figure S5). Our low estimates of leatherback presence in the SAB during the summer may be due to sampling bias as the leatherbacks we tagged in North Carolina in May were undertaking their migration to northern foraging areas, while those tagged off Massachusetts were mostly foraging and migrating south towards Caribbean nesting beaches via oceanic waters. Further, the aerial survey data from DiMatteo et al. (2024) may have detected post-nesting movements of turtles from Florida beaches that remained within the SAB to forage. Prey species such as cannonball jellyfish (*Stomolophus meleagris*) were observed to be the most abundant offshore of Georgia and South Carolina in the spring as well as the late summer and fall (Faulk et al. 2023), which would align with both sets of predictions.

Our predictions of leatherback occurrence in the oceanic waters to the east of the OCS differed from those by DiMatteo et al. (2024) as well. Our model identified (mean) core habitat in this offshore region only during the colder months (December, January, May), whereas DiMatteo et al. (2024) predicted higher abundances between June and November (Figure S5). The observed affinity for this area in our model likely reflects seasonal movements associated with the Gulf Stream, as leatherbacks are known to migrate from the MAB into adjacent oceanic waters, potentially in pursuit of ephemeral patches of prey that form along eddy boundaries (Eckert et al. 2006; Hays et al. 2006). This movement has been observed to take place both at the beginning and end of the foraging season in the MAB and SNE (Rider, Avens, Haas, Hatch, et al. 2024). Estimates by DiMatteo et al. (2024) may be a result of leatherback observations along the shelf edge south of Massachusetts and Georges Bank as well as the use of the distance to the 500 m isobath in their model. Given that there were few (if any) leatherbacks observed by aerial observers in the offshore swaths of predicted high densities June through November (DiMatteo et al. 2024), using distance to the 500 m isobath as a predictor variable may cause a mirroring effect where higher densities inshore of the 500 m isobath result in higher abundance estimates offshore of the 500 m isobath.

The discrepancies between these two models highlight the vast amount of uncertainty that remains even after the completion of large-scale studies. Indeed, each type of data used to construct the models offers distinct advantages and limitations. Aerial survey studies can provide systematic observation data across the entire study region but can have influential biases (Buckland et al. 2001, 2004; Hatch et al. 2022; Thomson et al. 2013), and often only collect data on a few select days within the timeframe of interest. Comparatively, tagging studies can provide detailed movement data throughout the timeframe of interest but may introduce bias due to the small sample sizes and the initial

tagging location (Hays et al. 2020). In this study, we tagged in two relatively inshore locations, which may have biased our results towards the U.S. Atlantic shelf, an area with documented leatherback aggregations but which has been historically under sampled. Sightings sources suggest that the wider Atlantic shelf hosts a large number of foraging turtles. DiMatteo et al. (2024) estimate monthly populations between 10,000 and 55,000 leatherbacks on the U.S. Atlantic shelf from April to November. Based on tracking data from other studies, this area of the OCS likely provides foraging opportunities post nesting (Evans et al. 2021; Hays et al. 2006; Fossette et al. 2010) and between nesting seasons (James et al. 2005; Dodge et al. 2014; Rider, Avens, Haas, Hatch, et al. 2024).

We believe our predicted distributions present fundamentally new information on the importance of nearshore habitat for some proportion of the leatherback population we tagged. Combining data sets from multiple sources (i.e., tracking, by-catch, and survey) can help address this issue from an analytic perspective, and indeed integrating telemetry and point observation data has already been proven useful in strengthening SDMs of leatherbacks in the Southeastern Pacific (Liang et al. 2023). Regardless of the improvements in analytic capacity, additional data are needed to parameterize and test the validity of future models, especially given the high levels of plasticity observed in leatherback migratory behaviour and annual variability in environmental conditions.

4.3 | Association With Offshore Wind and Conservation Implications

Across each month of the study period, we demonstrate that leatherbacks may be exposed to OWFs along the Atlantic OCS throughout their migration, especially during their foraging seasons in the MAB and SNE. Given the predictions of coastal affinity, we recommend monitoring for leatherbacks in nearshore lease areas during times of predicted overlap. Monitoring effort should focus on the MAB as this region may support foraging opportunities for several nesting populations including those in Florida (Eckert et al. 2006; Rider, Avens, Haas, Hatch, et al. 2024; Stewart et al. 2016).

Interestingly, we did not observe a large amount of overlap between leatherback core habitat and the Massachusetts wind areas despite the area being regarded as important foraging area for leatherbacks (Rider, Avens, Haas, Harms, et al. 2024). Foraging in this area has mostly been observed along Nantucket Shoals as well as in Nantucket Sound (Rider, Avens, Haas, Harms, et al. 2024; Patel and Siemann 2020) while the active lease areas are established to the southwest of Martha's Vineyard. Nonetheless, leatherbacks do travel through these OWF areas as they arrive and depart for the foraging season. Even with this low direct overlap, there is concern that construction off Martha's Vineyard could disrupt prey fields along the nearby Nantucket Shoals (National Academies of Sciences, Engineering, and Medicine 2024). Thus, leatherback behaviour, especially foraging, must be monitored as these wind areas develop.

It is unclear how OWFs might impact leatherbacks. The presence of wind turbines in great numbers was estimated to disrupt the

stratification of the water column (Carpenter et al. 2016) which could impact the vertical distribution and availability of prey. Conversely, OWFs may propagate jellyfish populations. There is evidence that jellyfish larvae showed preference for settling on artificial structures and developing into dense concentrations of polyps promoting jellyfish blooms (Duarte et al. 2012). Further, Vodopivec et al. (2017) suggested that offshore structures can promote the propagation of jellyfish by enhancing connectivity with shore-based populations and establishing connectivity at a regional scale. Yet while an increase in prey availability around these structures may be beneficial, it could also pose a risk of exposing leatherbacks to vessel strikes and cable entanglements which already top the list as hazards for this species (Archibald and James 2018; Dodge et al. 2022). Lastly, noise pollution from construction and operation could significantly alter behaviour (Piniak et al. 2012) as noises related to construction such as pile driving and vessel activity were observed to alter diving behaviour in loggerheads (DeRuiter and Doukara 2012) and time spent performing different behaviours in greens (Díaz et al. 2024).

5 | Conclusions

The distribution model presented here provides critical information that not only furthers our understanding of leatherback ecology in the region, but can also be used to inform potential interactions with OWFs, shore-based fisheries, pelagic longline fisheries and commercial shipping activity. From an ecological perspective, our results suggest that leatherbacks migrating along the OCS prefer coastal environments. Other than Robinson et al. (2016), this is the only study to demonstrate the importance of nearshore areas outside of the nesting season and the only study to do so in the Northwest Atlantic. It is critical that leatherbacks continue to be monitored in these nearshore habitats as their affinity is likely linked to prey distributions. Further, without detailed knowledge regarding these distributions, which can have multi-decadal oscillations in abundance (Smith et al. 2016), it will be difficult to predict how leatherback distributions might change over time. With respect to understanding interactions with anthropogenic threats, we recommend that the output of this model be used in conjunction with those presented by DiMatteo et al. (2024) as each highlights important areas that should encourage continued monitoring going forward (MAB/SNE and SAB, respectively).

Author Contributions

Mitchell Rider analysed data, designed the study, and wrote the original draft; Chris Sasso, Larisa Avens, and Heather Haas secured funding; and all authors contributed to field work as well as contributed to writing, editing, and reviewing the manuscript.

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Ethics Statement

All procedures and methods were reviewed and approved by the National Marine Fisheries Service's Atlantic Institutional Animal Care and Use Committee (IACUC). NOAA Fisheries reviewed and approved the animal study. All work was conducted under ESA permit 21,233 issued to the National Marine Fisheries Service Southeast Fisheries Science Center.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw location data for all tagged leatherbacks used in this study is currently being made available on NOAA's National Centers for Environmental Information (NCEI) website. While this dataset is undergoing review, we have made the data available on Dryad at the following link: <https://doi.org/10.5061/dryad.dncjsxmb6>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70131>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70131-sup-0001-AppendixS1.docx.