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Drivers of Habitat Selection by the Endangered Greater Caribbean Manatee in Coastal-Marine Ecosystems

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Received: 1 April 2025 | **Revised:** 5 November 2025 | **Accepted:** 26 November 2025

Keywords: coral reefs | endangered species | estuaries | habitat loss | movement ecology | resource selection functions | seagrass | sirenia | *Trichechus manatus manatus*

ABSTRACT

Habitat selection is a fundamental aspect of animal movement and behaviour, involving strategies that influence population regulation, species interactions, community structure and the generation and preservation of biodiversity. The Greater Caribbean Manatee is a megaherbivorous aquatic mammal with high environmental plasticity, found in a variety of coastal-marine ecosystems from the United States to Brazil. The subspecies is locally threatened because of intense poaching in recent centuries, which has led to the disruption of small populations. In this study, we aimed to understand habitat selection patterns and their variation across study sites, sex, age classes and between captive-released and wild manatees in northeastern Brazil to inform conservation policy. We used high-resolution GPS telemetry data from 20 tagged manatees and applied autocorrelation-informed resource selection functions (RSF) using (i) seagrass meadows, (ii) coral reefs, (iii) estuaries and (iv) freshwater springs as environmental predictors. As a proxy for anthropogenic impact, we also used a predictor combining multiple human activities at sea, which imposes substantial pressures with a subsequent degradation of manatee habitat. All environmental predictors had statistically significant results at the population level. Positive estimates were found for estuaries (1.52), springs (0.85) and seagrass meadows (0.77), indicating that manatees hierarchically select these habitats. The human impact was also positive (1.12), suggesting that the habitats selected by manatees overlap with human-impacted areas. Coral reefs (−0.92) were found to have a negative estimate, indicating that the animals avoid using this habitat. Our results confirm the vital role of seagrass meadows and freshwater in manatee movement behaviour. The selected habitats overlap with human-impacted areas, particularly in areas close to urban centers and ports. This creates obstacles to manatee free movement and the reconnection of subpopulations, highlighting the importance of conserving and restoring these marine coastal habitats.

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1 | Introduction

Habitat loss is a major cause of global biodiversity decline, leading to the gradual decline and eventual extinction of species (Hanski 2011; Tilman et al. 1994). The disruption of species interactions, loss of connectivity and synergistic effects, among others (Hanski 2011; Horváth et al. 2019; Sandor et al. 2022; Tilman et al. 1994), are key factors contributing to this phenomenon. Environmental pressures and human activities restrict how animals use space, increasing their vulnerability to extinction worldwide (Hirt et al. 2021). In response, habitat selection—a fundamental aspect of animal movement and behaviour—becomes essential as it shapes strategies with broad implications for population regulation, species interactions, community structure and the generation and preservation of biodiversity (Morris 2003).

The American manatee (*Trichechus manatus*) (hereafter referred to simply as 'manatee') is an aquatic mammal with high environmental plasticity, occurring in different aquatic ecosystems such as estuaries, bays, lagoons and rivers (Reep and Bonde 2006). Considered a flagship species (Normande et al. 2023), it provides ecosystem services related to provision, ecosystem regulation, education, culture, spirituality and recreation (Izidoro et al. 2022). Classified globally as vulnerable to extinction (Deutsch and Morales-Vela 2024), manatees are severely impacted by habitat loss and anthropogenic threats like coastal development, pollution and watercraft collisions, affecting their genetic diversity and population size (Deutsch et al. 2008; Hunter et al. 2010).

The American manatee subspecies found in Brazil is the Greater Caribbean manatee *(T. m manatus*). Centuries of poaching have driven the decline and fragmentation of the manatee population (De Thoisy et al. 2003; Domning 1982; Jiménez 2002; Montoya-Ospina et al. 2001; Vieira and Brito 2017), to the point that the subspecies is currently classified as endangered in Brazil (MMA 2022). The escalating degradation of estuarine habitats (Medeiros et al. 2021; Meirelles et al. 2024)—critical for birthing and parental care—appears to be forcing females to give birth in high-energy offshore waters, making calf stranding one of the leading threats to manatee conservation in Brazil (Balensiefer et al. 2017; Meirelles 2008; Parente et al. 2004).

The plasticity of manatees' movement behaviour enables them to locate and utilise essential resources, which are crucial for their survival and reproduction (Deutsch, Castelblanco-Martínez, Cleguer and Groom 2022). The availability of resources such as seagrass meadows, aquatic vegetation, algae banks and freshwater sources within habitats is expected to drive manatee movements (Castelblanco-Martínez et al. 2013). Conversely, manatees' habitat use can be constrained by environmental characteristics such as tidal cycles, flood pulses or water temperature, as well as by human interventions such as dams (Deutsch, Castelblanco-Martínez, Cleguer and Groom 2022). Therefore, understanding manatee habitat selection can guide conservation efforts to increase the protection of critical habitats, thereby helping optimise limited resources for biodiversity conservation in tropical regions.

Resource selection functions (RSFs) are a powerful tool for understanding habitat use and informing conservation, but autocorrelation in GPS tracking data can bias the results and provide unrealistically narrow confidence intervals (Boyce et al. 2002; Fieberg et al. 2010). Autocorrelation-informed RSFs offer an alternative approach to mitigate pseudoreplication by weighting each observed location of an animal's movement track, broadening confidence intervals to provide more realistic estimates and reducing bias related to missing data (Alston et al. 2023).

The objective of this study was to test the selection or avoidance of key environmental resources—identified in the literature as important drivers of manatee habitat use in Northeast Brazil—using state-of-the-art analytical methods. We employed the most comprehensive high-resolution GPS telemetry dataset in Brazil to elucidate, for the first time, manatee habitat selection through RSF analysis. Furthermore, we analysed how the selected habitats overlap with human impact and tested for variations in habitat selection across study sites, sex, age classes and between released and wild manatees in the northeast region of Brazil, with the goal of contributing to conservation efforts by guiding the establishment of protected areas and habitat restoration initiatives.

2 | Methods

2.1 | Study Site

This study was conducted in the coastal area (up to 10 m depth) of the Northeast Brazilian Marine Ecoregion (NBME) (Spalding et al. 2007) (see Figure 1), between the municipalities of Piaçabuçu, in the state of Alagoas (AL), and Fortaleza, in the municipality of Ceará (CE).

The study area is divided into three subareas, which correspond to the locations where the manatees were tagged: (i) the Ceará and Rio Grande do Norte subarea (CE/RN), from Icapuí to Areia Branca, which is characterised by the presence of seagrass meadows and freshwater springs; (ii) the Paraíba subarea (PB), from Rio Tinto to Cabedelo, which includes two large estuaries, seagrass meadows and algae banks (Dos Santos et al. 2023); and (iii) the Alagoas subarea (AL), from Japaratinga to Coruripe, which is formed by an extensive coastal coral reef system, seagrass meadows, and several rivers, lagoons and estuaries (Araújo et al. 2006).

2.2 | Data Collection

This study used data from 20 GPS-tagged Great Caribbean manatees in northeast Brazil between 2011 and 2022 (see Table 1). The median tracking duration was 3.09 months (SD = 2.93), and the median location GPS location points was 924 (SD = 1978). The animals were separated into two groups: (i) wild: captured in the wild using a net deployed from a customised boat and released at the same site; or (ii) adapted: manatees that stranded, were rehabilitated and released. Once successfully adapted to the wild, they were captured and equipped with tags. In the present study, the decision

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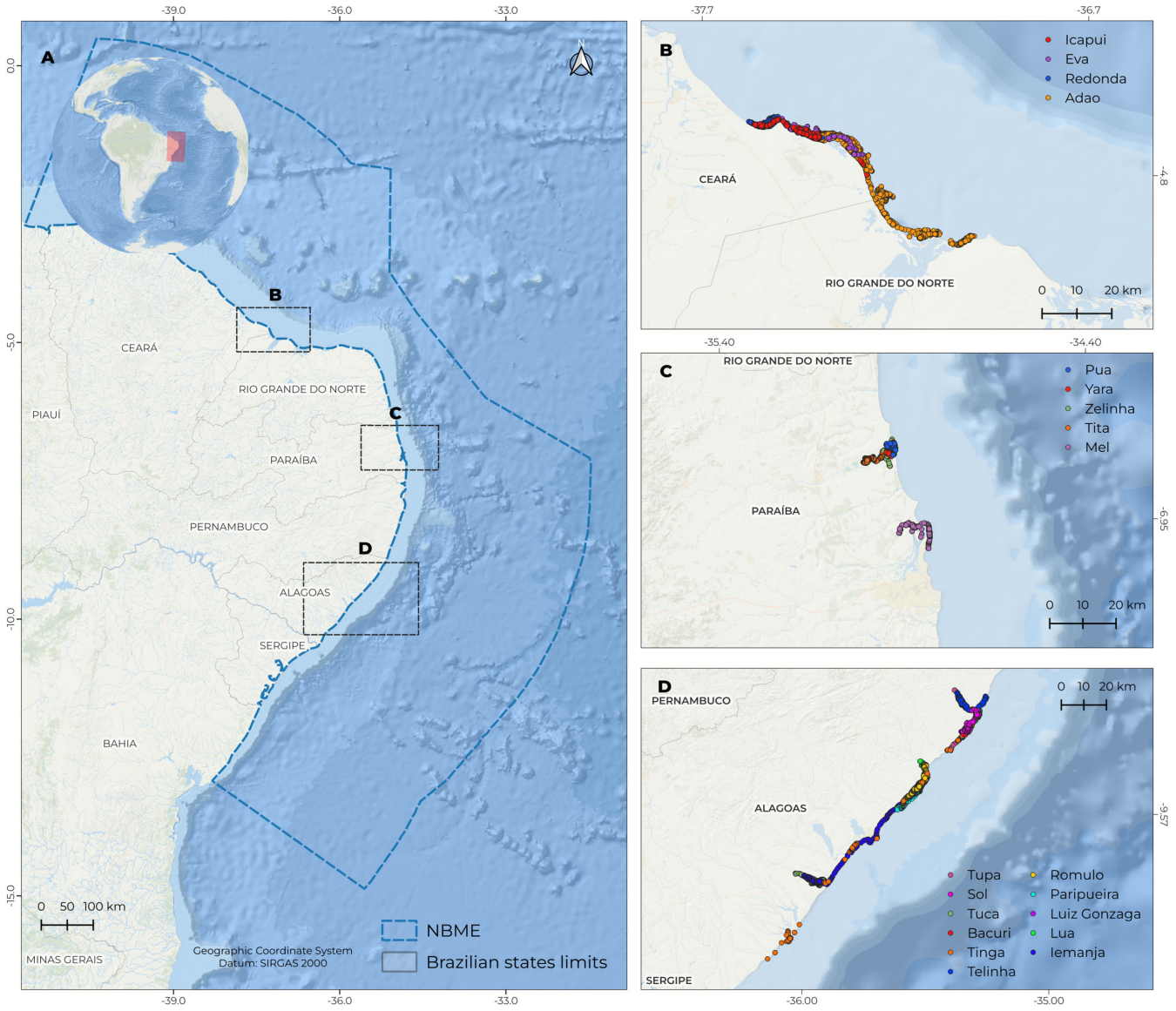


FIGURE 1 | The map illustrates the location of the study site (A), the GPS coordinates of tracked manatees (*Trichechus manatus*), the boundaries of Brazilian states and the three subareas within the NBME: (B) Ceará and Rio Grande do Norte—CE/RN, (C) Paraíba—PB and (D) Alagoas—AL.

was taken to exclude data from recently released manatees (19 from 39) because these individuals typically explore numerous areas prior to establishing home ranges (Normande et al. 2024). The individuals were categorised as subadults (176–225 cm total length) and adults (> 225 cm total length) (Mignucci-Giannoni et al. 2000). The subjects 'Iemanja' and 'Romulo' were classified as subadults, despite their documented measurements exceeding 225 cm. This determination was made based on their behavioural patterns, which exhibited a consistent and prolonged proximity to their mothers throughout the duration of the tracking process.

The tagging system for manatees comprises a belt adapted to the caudal peduncle, a tether and a floating transmitter (Reid et al. 1991). Three models of transmitters were employed: the TMT-462 and TMT-464-2 manufactured by Telonics, which utilise the ARGOS system (Normande et al. 2016); and the other produced by *Fundação Mamíferos Aquáticos*/NORTRONIC, which utilises the GLOBALSTAR network (Dos Santos et al. 2022).

2.3 | Data Analysis

2.3.1 | Environmental Predictors

For the habitat selection analysis, the environmental predictors comprised: (a) seagrass meadows presence and (b) coral reefs presence, both generated by a deep learning algorithm implemented in the Google Earth Engine (GEE) platform (Deeks et al. 2024); (c) estuarine areas (Magris et al. 2021); and (d) locations of freshwater springs, sourced from Aquasis and PPCB/UERN field surveys conducted in the CE/RN subarea and used only in the RSF analysis for this subarea. Please refer to Table S1 for detailed information on each variable and layer generation. As a proxy for habitat degradation, we used a human impact layer generated through a cumulative impact assessment using the additive method (Magris et al. 2021). All predictor datasets were uniformly processed: They were converted to raster format, assigned a consistent spatial resolution of 100 × 100 meters, reprojected to the WGS 1984 World

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TABLE 1 | Summary of tracked manatee data used in this study. Total length is showed in centimetres, sampling period is displayed in months, and location points refer to raw GPS fixes.

Animal ID	Deploy on date	Deploy off date	Age class	Total length	Sex	Life history	Subarea	Sampling period	Location points	Movement model
Adao	21/05/2012 00:00	29/04/2013 04:00	Adult	296	Male	Wild	CE/RN	11.62	3355	OUF anisotropic
Bacuri	28/08/2021 14:00	08/11/2021 02:15	Adult	262	Male	Wild	AL	2.17	737	OUF anisotropic
Eva	21/05/2012 00:00	17/11/2012 03:01	Adult	268	Female	Wild	CE/RN	5.92	842	OUF anisotropic
Icapui	25/05/2012 16:51	14/09/2012 00:30	Adult	281	Female	Wild	CE/RN	3.6	382	OUF anisotropic
Iemanja	30/10/2016 20:03	02/12/2016 23:50	Subadult	239	Female	Wild	AL	1.12	2272	OUF anisotropic
Lua	27/10/2016 00:00	22/06/2017 01:05	Adult	310	Female w/calf	Adapted	AL	8.02	3677	OUF anisotropic
Luiz Gonzaga	17/11/2019 13:36	01/12/2019 23:31	Adult	285	Male	Adapted	AL	0.47	671	OUF anisotropic
Mel	03/11/2019 11:18	14/03/2020 18:29	Adult	254	Female	Adapted	PB	4.48	737	OUF anisotropic
Paripueira	06/11/2016 14:46	29/11/2016 00:00	Adult	276	Female	Wild	AL	0.74	1456	OUF anisotropic
Pua	07/02/2020 11:41	17/03/2020 23:55	Adult	278	Male	Adapted	PB	1.338	117	OU anisotropic
Redonda	25/05/2012 19:01	23/10/2012 03:26	Adult	413	Female w/calf	Wild	CE/RN	5.05	898	OUF anisotropic
Romulo	28/10/2016 00:02	30/01/2017 09:55	Subadult	234	Male	Wild	AL	3.2	4832	OUF anisotropic
Sol	10/11/2015 16:01	06/12/2015 00:00	Adult	249	Male	Wild	AL	0.85	602	OUF anisotropic
Telinha	30/05/2019 13:01	26/08/2019 15:05	Adult	249	Female	Adapted	AL	2.98	2029	OUF anisotropic
Tinga	13/01/2021 12:46	10/02/2021 08:29	Adult	280	Male	Adapted	AL	0.91	365	OUF anisotropic
Tita	18/10/2017 22:03	29/12/2017 16:02	Subadult	217	Female	Adapted	PB	2.43	951	OUF anisotropic
Tuca	30/10/2016 19:02	14/04/2017 00:00	Adult	310	Female w/calf	Adapted	AL	5.09	7924	OU anisotropic
Tupa	23/01/2019 16:05	30/08/2019 07:35	Adult	255	Male	Adapted	AL	7.4	4104	OUF anisotropic
Yara	19/10/2017 17:33	21/11/2017 10:12	Adult	254	Female	Adapted	PB	1.12	438	OUF anisotropic
Zelinha	18/10/2018 14:59	26/01/2019 07:59	Adult	248	Female	Adapted	PB	3.38	1537	OUF anisotropic

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Mercator coordinate system and clipped for the study area using ArcGIS Pro v. 3.3.0 (ESRI 2024). More details on the layers used in the habitat selection analysis are given in the Supporting Information section, where all the spatial layers are also available.

We assessed multicollinearity among environmental covariates using variance inflation factors (VIF) calculated from 10,000 randomly sampled pixels. Covariates with VIF > 5 were considered to exhibit problematic multicollinearity requiring remediation (Dormann et al. 2013). The springs presence covariate showed insufficient variation (present in only 0.2% of sampled pixels) for reliable VIF calculation, although pairwise correlations indicated no concerning relationships with other covariates (all $|r| < 0.7$).

2.3.2 | Habitat Selection

We applied autocorrelation-informed RSFs using the package *ctmm* v. 1.2.0 (Fleming and Calabrese 2023) in the RStudio environment (R Core team 2024) to assess the habitat selection of the tracked manatees. In this method, individual locations are weighted to account for autocorrelation and reduce pseudoreplication and bias in RSFs, therefore improving estimates of confidence intervals and dramatically reducing Type I error (Alston et al. 2023). The framework for this method includes, for each of the 20 animals analysed, the following: (i) data cleaning and outlier removal, handled through visual inspection to exclude locations on land; (ii) plotting empirical variograms and periodograms to reveal features of the movement behaviour, for selecting appropriate movement models[1]; (iii) fitting the most appropriate models, identified using maximum likelihood estimation and subsequently compared using AICc, selecting the best fit model based on the lowest AICc values; (iv) defining availability through autocorrelated kernel density estimation (AKDE) of 95% home ranges to identify areas of relevant use and creating random points—the method iteratively increases sampled 'available' points from each model's stationary utilisation distribution (UD) until the numerical error in the continuous Poisson point process log-likelihood falls below a target threshold (±0.01), giving us confidence in the precision of the likelihood approximation. Model convergence was confirmed by examining the trace output (trace = TRUE), ensuring that the relative parameter updates and the log-likelihood update became negligible, indicating that the optimisation algorithm had reached a stable solution; and (v) modelling resource selection coefficients represented by the log-selection strength ($\log(\lambda)$) for each environmental covariate. A log-selection strength ($\log(\lambda)$) coefficient represents the additive, linear change on a log scale in the relative probability of selection for a one-unit change in the environmental covariate. A positive coefficient value indicates selection for a habitat, while a negative value indicates avoidance. Coefficients are presented with 95% confidence intervals (CI). Results were considered significant when CI do not cross zero (Alston et al. 2023; Calabrese et al. 2016). It is important to note that no temporal stratification was applied in our analysis.

In estimating AKDEs for each individual, we used a hard boundary approach (Normande et al. 2024; Silva et al. 2022) combining shapefile delineations of various aquatic features, including freshwater bodies, mangrove forests and coastal features derived from Magris et al. (2021). A bathymetric boundary representing depths up to 10m offshore was generated using a satellite-derived bathymetry layer (Li et al. 2021) in Google Earth Engine. This 10m depth limit is consistent with previous studies documenting the maximum depth reached by manatees in this region (Alves et al. 2013; Meirelles et al. 2022; Normande et al. 2016). Before applying this mask, we verified that no individual included in this study ventured beyond the 10m contour, ensuring that the boundary excluded only unavailable habitats. This enabled us to predict the spatial utilisation of manatees more accurately, based on realistic ecological principles.

Aiming to understand the population patterns associated with habitat selection, after estimating the parameters and confidence intervals associated with each of the 20 individuals, we applied the *ctmm::mean()* function, which is designed to calculate the population averages of continuous-time movement models and utilisation distributions, as proposed by Calabrese et al. (2016). We also used the *ctmm::mean() function* to compare model coefficients in the different subareas.

We then applied the same function to investigate the effects of sex, age class and group (wild/adapted) on manatee habitat selection. Based on known differences in freshwater use by manatees, we grouped the AL and PB subareas together—where manatees rely on estuarine systems—and excluded animals from the CE/RN subarea, as manatees in this region depend on freshwater springs. This grouping aimed to reflect ecological differences and reduce noise in the analysis.

3 | Results

Collinearity diagnostics showed minimal multicollinearity among covariates, with all VIF values < 2 (seagrass meadows = 1.01; estuaries = 1.99; coral reefs = 1.99; human impact = 1.01; and springs = NaN). The VIF for springs' presence could not be computed because of a lack of variance in sampled pixels, but pairwise correlations revealed no concerning relationships (all $|r| < 0.7$). Therefore, all variables were retained for subsequent analyses.

All the predictor variables investigated in the RSF showed coefficients significantly different from zero for the manatee population analysed in this study. The variables estuaries (1.52, 95% CI [1.17, 1.86]), freshwater springs (0.85, 95% CI [0.06, 1.65]), used only for CE/RB subarea and essentially reflecting its behaviour, and seagrass meadows (0.77, 95% CI [0.56, 0.99]) showed positive estimates, indicating that the manatees selected habitats associated with these features. Additionally, the human impact intensity factor was positive (1.12, 95% CI [0.95, 1.30]), indicating that the habitats selected by the manatees overlap with areas of high human impact. In contrast, coral reefs (−0.92, 95% CI [−1.47, −0.35]) had a negative estimate, suggesting that animals are choosing other habitats at the expense of coral reefs (Figure 2a).

A comparison of the three subareas (Figure 2b–d) revealed that AL ($n = 11$) exhibited significant results for estuaries (1.57, 95%

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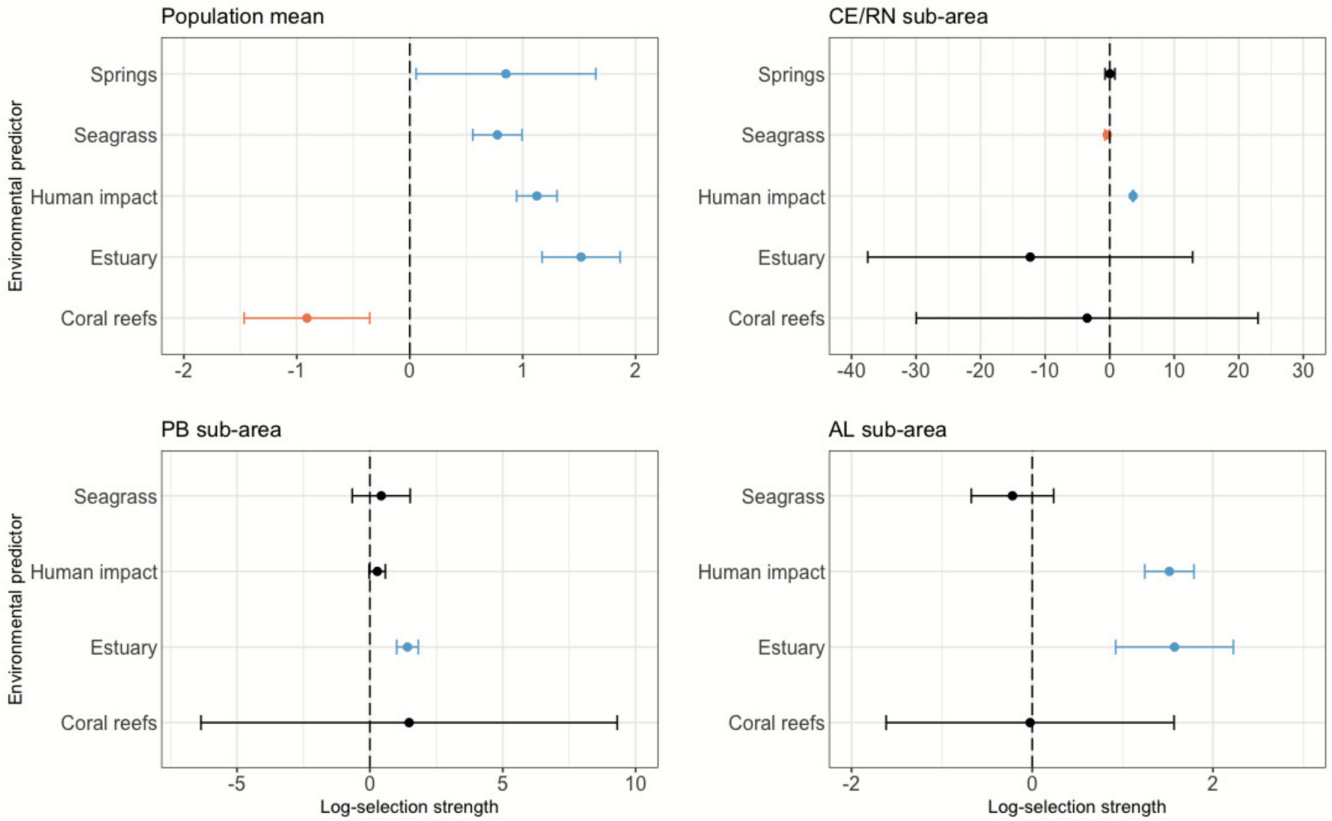


FIGURE 2 | Log-selection strength in log() for all predictor variables (springs, seagrass meadows, human impacts, estuary and coral reefs) related to the (a) population mean and for (b) AL, (c) PB and (d) CE subareas. *Note:* Positive values (light blue) indicate selection for a habitat (preference), while negative values (light red) suggest avoidance. If the interval does not cross zero, the selection or avoidance is statistically significant.

CI [0.92, 2.23]) and human impact (1.52, 95% CI [1.24, 1.79]), while PB ($n = 5$) showed significant results for estuaries (1.41, 95% CI [1.01, 1.82]). In the CE/RN ($n = 4$) subarea, human impact (3.62, 95% CI [3.52, 3.72]) was also significant. In all subareas, the presence of seagrass meadows and coral reefs was not significant. Although the log-selection strength for the mean population was significantly affected by the presence of freshwater springs, this was not considered significant when the CE/NR subarea was analysed separately.

When investigating the effects of sex on habitat selection for AL and PB subareas combined, we found that males ($n = 7$) showed significant selection for seagrass meadows (0.37, 95% CI [0.09, 0.67]), estuaries (1.55, 95% CI [1.09, 2.01]), overlapping with high human impact (1.68, 95% CI [1.46, 1.90]) and an avoidance of coral reefs (−1.53, 95% CI [−2.11, −0.95]) (Figure 3a). While females ($n = 7$) showed significant selection for estuaries (1.68, 95% CI [1.12, 2.25]), seagrass meadows (0.84, 95% CI [0.29, 1.39]) and also overlapped with high human-impacted areas (0.48, 95% CI [0.13, 0.84]) (Figure 3b). Females with calves ($n = 2$) exhibited significant selection for estuaries (3.80, 95% CI [1.63, 5.97]) (Figure 3c).

Regarding age class, adult manatees ($n = 13$) showed significant selection for estuaries (1.62, 95% CI [1.21, 2.02]), and the selected habitats overlap with highly human-impacted areas (1.40, 95% CI [0.63, 2.18]) (Figure 4a). Additionally, estuaries were the only significant variable for subadults ($n = 3$) (2.23, 95% CI [1.12, 3.35]).

Regarding the two groups, wild manatees ($n = 5$) (Figure 4c) showed significant selection only for estuaries (1.75, 95% CI [0.98, 2.51]) and human impact (1.65, 95% CI [1.32, 1.98]). In contrast, adapted individuals ($n = 11$) (Figure 4d) demonstrated significant selection for estuaries (2.21, 95% CI [1.84, 2.59]), human impact (2.15, 95% CI [1.86, 2.44]) and seagrass meadows (0.83, 95% CI [0.51, 1.16]).

As an example, plots of the empirical (red) and theoretical (grey) log-selection strength (Log(λ)) for the wild manatee 'Romulo', with respect to the four environmental predictors used in the AL subarea, are shown in Figure 5.

3.1 | Cumulative Impact Assessment

When analysing the human impact layer overlapping with the study area, the cumulative impact estimates for the study area ranged from 0.46 to 5.97. In general, areas close to urban centres had the highest impact values due to coastal development, land-based pollution (organic pollution, pesticides and fertilisers), port-derived pollution, transport and fishing (Supporting Information). Upstream areas had the lowest levels, and climate change stressors (global warming, UV radiation and ocean acidification) showed similar values in all three subareas.

In the AL subarea, the highest human impact value was 4.71 in the state capital of Maceió, and the values decrease with

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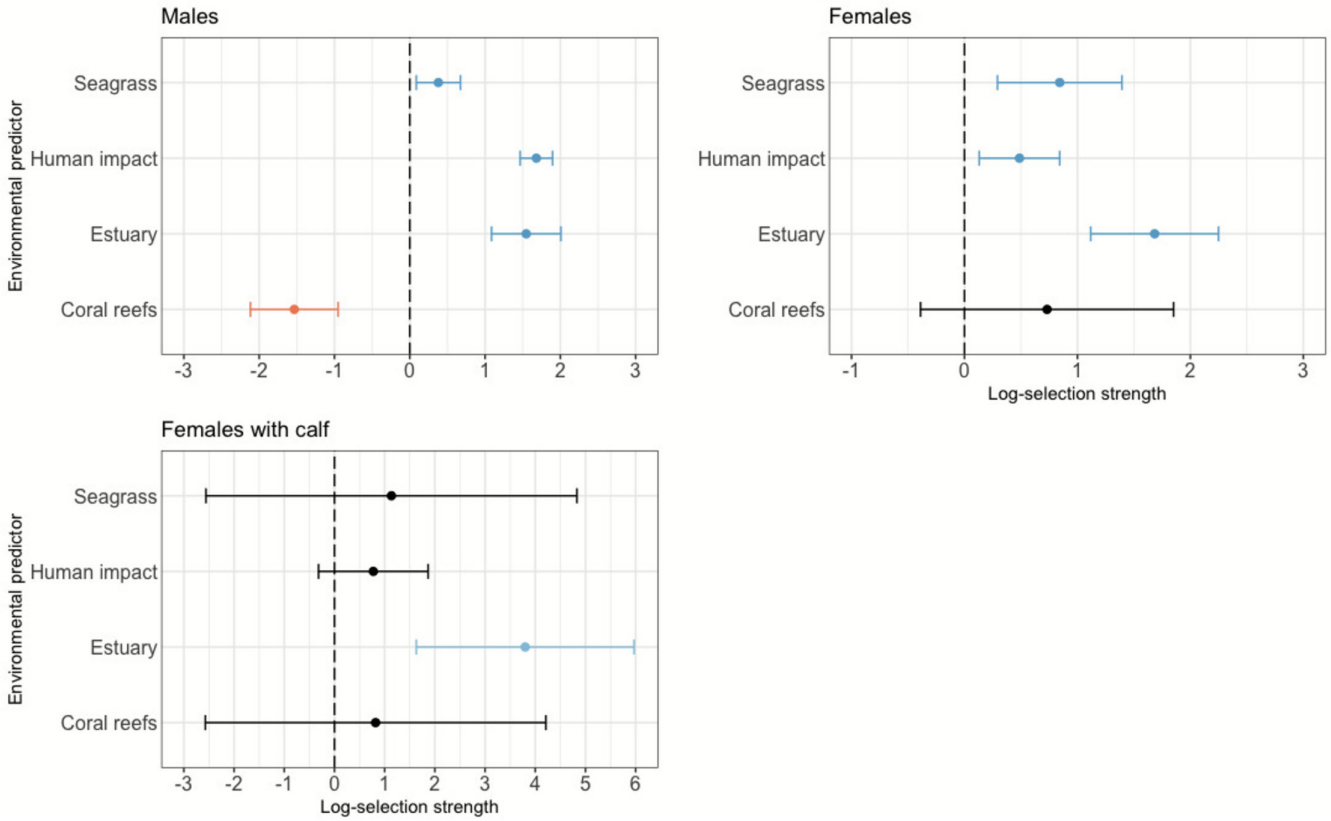


FIGURE 3 | Log-selection strength in log() and confidence intervals for all environmental predictors (seagrass meadows, human impact, estuary and coral reefs) regarding AL and PB subareas and investigating the difference in animal sex ((a) males, (b) females and (c) females with calf). *Note:* Positive values (light blue) indicate selection for a habitat (preference), while negative values (light red) suggest avoidance. If the interval does not cross zero, the selection or avoidance is statistically significant.

distance from the city but increase again (3.09) near Maragogi and the Pernambuco state border. Paripueira and Porto de Pedras, two important areas for manatees in the state, had maximum observed cumulative human impact values of 2.85 and 2.63, respectively.

The PB subarea showed a maximum CHI of 4.03 in the Cabedelo area. The Barra do Rio Mamanguape MPA showed low values of human impact, ranging from 1.87 in the mouth of the river to 0.64 upstream. Additionally, in the CE subarea, the maximum CHI value observed was 3.82 off the coast of Areia Branca (RN State), where oil infrastructure is present. In the Icapuí municipality, the CHI value was relatively constant around 2.35.

4 | Discussion

Our study represents a novel application of a RSF workflow incorporating autocorrelation-informed techniques to investigate habitat selection by sirenians. By combining a high-resolution GPS dataset with the most up-to-date regional-scale habitat mapping, we identified estuaries, freshwater springs and seagrass meadows as critical environmental variables influencing manatee presence in northeastern Brazil, with estuaries being the most strongly selected. However, these habitats significantly overlap with areas of high human impact, underscoring a major conservation challenge and the need for continuous monitoring of habitat degradation.

4.1 | Freshwater Sources

The findings of this study indicate that freshwater habitats, represented by estuaries in the AL and PB subareas and springs in the CE/RN subarea, play an important role in shaping the habitat selection of manatees along the northeastern Brazilian coast and likely for the coastal ecotype of the subspecies. Estuarine habitats were identified as a significant factor across all groups analysed in this study, with the exception of the CE/RN subarea, where manatees are known not to enter estuaries (Choi-Lima 2017) and instead rely on natural springs within coastal-marine environments to access freshwater sources (AQUASIS 2006). Freshwater springs also were found to be significant for the population, even though the layer was only used for the CE/RN individuals.

The CE/RN subarea is within the semiarid coast, characterised by a climate influenced by the Brazilian dry forest, known as the *caatinga*, and limited freshwater input from river sources, resulting in elevated salinity levels (Favero et al. 2020). Conversely, in the other subareas (AL and PB), influenced by the Brazilian Atlantic Rainforest, manatees typically depend on rivers for their freshwater needs. These variations in climate between sites significantly influence the movement

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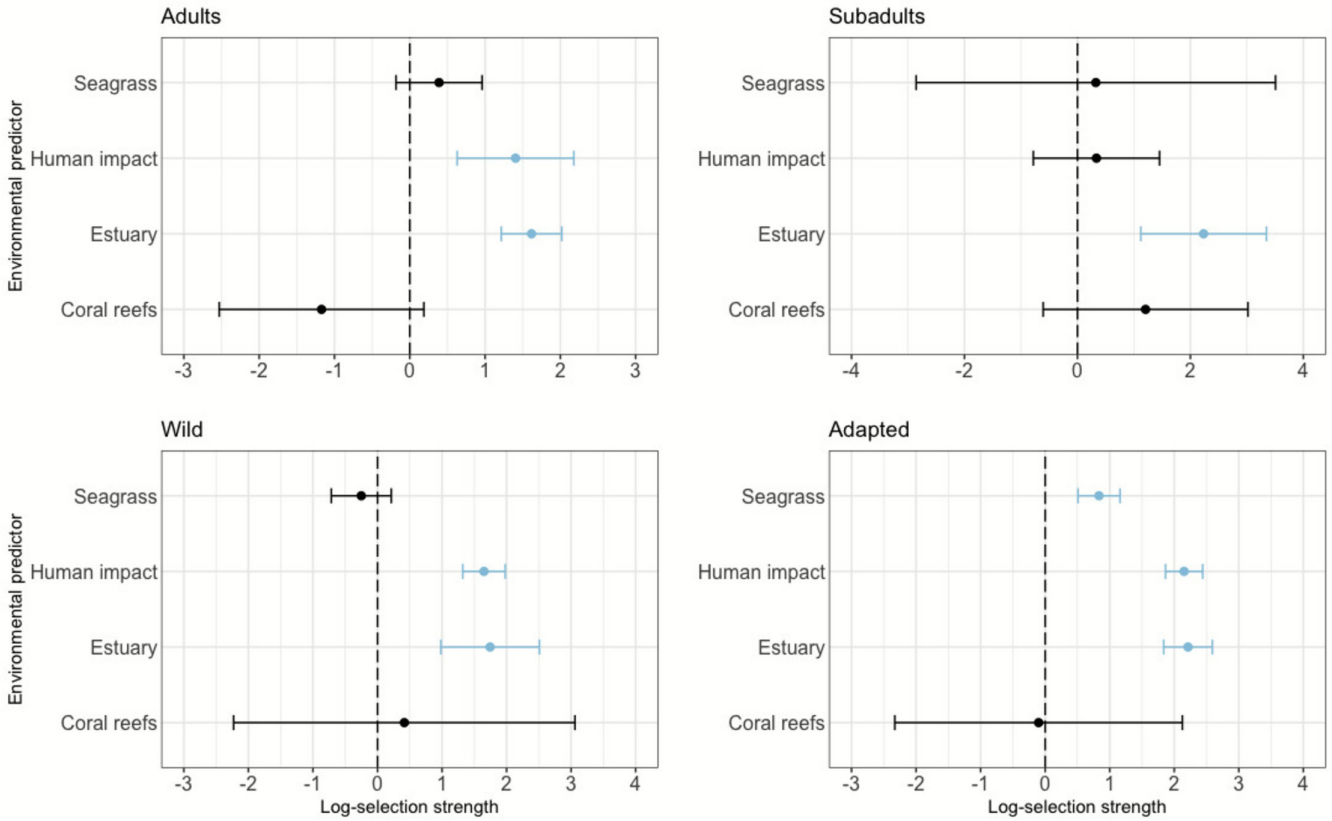


FIGURE 4 | Log-selection strength log() and confidence intervals for all environmental predictors (seagrass meadows, human impact, estuary and coral reefs) regarding AL and PB subareas and investigating the difference in animal age ((a) adults and (b) subadults) and group ((c) wild and (d) adapted). *Note:* Positive values (light blue) indicate selection for a habitat (preference). If the interval does not cross zero, the selection or avoidance is statistically significant.

behaviour of the manatees, determining whether subpopulations make use of rivers and estuaries (Lima 1997) and can influence the amount of space used (Normande et al. 2024).

In our study, there were significant positive estimates for the population mean of freshwater springs, although this was not considered significant when the CE/NR subarea was analysed separately. This may occur if the presence of freshwater is correlated with another variable in the population but not in the subpopulation. However, as we tested for pairwise correlation and found none, we believe that we can refute this explanation. Therefore, this result should be treated with caution because of the potential influence of confounding variables.

Consistent with our study, manatees are known to make regular visits to freshwater sites after grazing in seagrass meadows, suggesting a preference for regular freshwater intake (Castelblanco-Martínez et al. 2013). Capable of adapting to both freshwater and saltwater environments, manatees live in coastal-marine waters and freshwater riverine systems. However, they can regulate the balance of electrolytes in their blood, allowing them to survive during periods of limited access to freshwater (Ortiz et al. 1998, 1999). While the plants they consume are composed of 60%–95% water, providing a substantial water source, marine seagrasses have higher salt content than freshwater grasses (Reep and Bonde 2006).

The kidney structure of manatees suggests an ability to concentrate urine, conserving water when necessary, especially in the saltwater environment (Hill and Reynolds 1989; Ortiz et al. 1998). However, it is well documented that manatees living in saltwater environments travel great lengths to find and drink freshwater (Castelblanco-Martínez et al. 2013; Dos Santos et al. 2022, 2023; Flamm et al. 2005; Normande et al. 2016; Reid et al. 1991; Slone et al. 2013).

Freshwater sources are often hotspots of manatee activity during dry seasons when freshwater is scarce (Deutsch, Castelblanco-Martínez, Groom, and Cleguer 2022). Satellite-linked telemetry revealed that manatees in various regions regularly travel to discrete freshwater sources, emphasising the vital role of freshwater in their lives. These journeys can cover considerable distances, ranging from offshore seagrass beds, where they graze, to inland creeks or canals, where freshwater is available for drinking (Slone et al. 2013).

In the context of a climate change scenario, freshwater sites have been shown to play a fundamental role. These sites, in conjunction with seagrass meadows, have been found to mediate the impact of climate change on the distribution of the manatee (Deeks et al. 2024). In this sense, the protection of freshwater sites is critical to the conservation of manatee populations.

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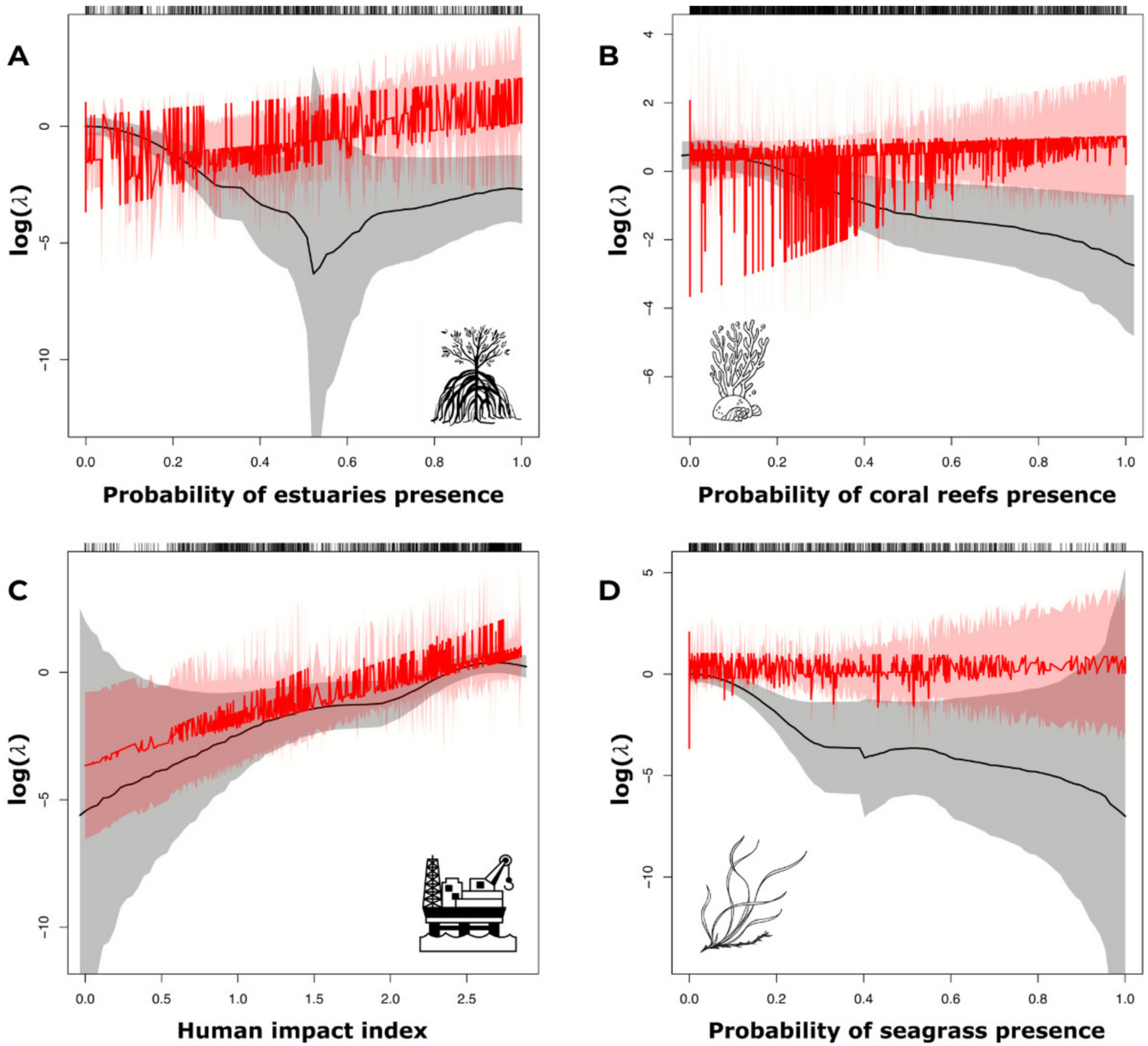


FIGURE 5 | Plots of the empirical (red) and theoretical (grey) log-selection strength in log (λ) with respect to a covariate of interest ((a) estuaries, (b) coral reefs, (c) human impact and (d) seagrass meadows) for the wild male manatee 'Romulo' tracked in the AL subarea.

4.2 | Foraging

Our results indicate that seagrass meadows play a significant role in shaping the habitat selection of manatees. The use of this habitat is well documented in the literature (see, e.g., (Castelblanco-Martínez et al. 2013; Deutsch, Castelblanco-Martínez, Groom, and Cleguer 2022; LaCommare et al. 2008; Lefebvre et al. 1999; Normande et al. 2016; Slone et al. 2013). However, to the best of our knowledge, this is the first time it has been demonstrated using RSF techniques.

Because of its substantial body size and herbivorous diet, manatees can spend up to 8 h a day feeding and ingesting 5%–10% of their body weight daily, from a diverse range of plant species (Reep and Bonde 2006). Nevertheless, in many areas, seagrass represents the primary food source and the best source of nutrients for coastal manatees (Allen et al. 2018; Alves-Stanley et al. 2010; Arévalo-González et al. 2024; Castelblanco-Martínez et al. 2009; Garcés-Cuartas et al. 2025), and its rapid decline places it as one of the most endangered ecosystems on earth (Waycott et al. 2009), demanding urgent conservation action.

Despite the importance of seagrass to the manatee's diet and habitat use, there is evidence that their diet can vary between sites (Allen et al. 2018; Alves-Stanley et al. 2010; Borges et al. 2008) and seasons (Merson et al. 2014), according to the availability of the feeding resources in different geographical areas. Manatees are also known to exhibit opportunistic feeding behaviour (Castelblanco-Martínez et al. 2009). In some areas, for example, the presence of reefs covered with algae is a determining factor in its occurrence (Paludo and Langguth 2002).

The present study has yielded negative and statistically significant results regarding the influence of coral reefs on manatees'

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presence at the population level. This finding suggests that manatees generally avoid these habitats or that their use of suitable sub-environments within reefs might only be detectable at finer spatial resolutions. Therefore, the role of coral reefs in manatees' habitat selection remains to be fully understood. For example, while some empirical studies indicate the importance of these areas for providing shelter, food and travel routes (Borobia and Lodi 1992; LaCommare et al. 2008; Paludo and Langguth 2002), others using aerial surveys and more rigorous analytical approaches have found no correlation between this habitat and the species distribution, as shown by studies in Brazil (Alves et al. 2013) and Mexico (Olivera-Gómez and Mellink 2005). Furthermore, the results indicate that seagrass may be a preferred food source for manatees in northeast Brazil. However, no significant results were found for the log-selection strength of coral reefs when the subareas were analysed individually, suggesting that further studies are necessary to gain a deeper understanding of dietary variation across different geographical areas.

4.3 | Sex, Age Class and Group

While the male manatees demonstrated selection for all seagrass meadows and estuaries and avoidance of coral reefs, the evidence is insufficient to confirm that the females avoid coral reefs. Furthermore, females with calves ($n = 3$) selected only estuaries. Despite its small sample size, this latter result suggests an important role of estuaries in the context of parental care, potentially reflecting the reduced home range size and movement rate of mother-calf pairs (Flamm et al. 2005; Reid et al. 1995).

Another limitation of our study relates to the considerable variation in tracking duration between individuals. Nevertheless, we believe that this did not greatly influence the mean results. By calculating the selection strength for each animal and driver individually, we were able to determine which environmental predictors were selected for or avoided within that specific time frame. In this sense, each animal contributed equally to the final mean results.

Regarding the distinct selection according to age class, our findings revealed that adult manatees exhibited a preference for estuarine habitats, with their selected locations overlapping with those that had high human impact. In comparison, subadult manatees only demonstrated a preference for estuaries. Despite being classified as subadults based on total body length and behaviour, two of the three subadult individuals remained with their mothers and exhibited very similar movement patterns, as indicated by satellite tracking, possibly resulting in some noise in our results. Prior studies in Florida have shown that newly independent subadults adopt the same migratory patterns as their mothers and demonstrate strong philopatry to their natal summer and winter ranges (Deutsch et al. 2003; Reid et al. 1995).

A comparative analysis of wild and captive-raised manatees revealed that only the captive-raised individuals exhibited a discernible preference for seagrass meadows. These meadows provide a nutrient-rich food source for manatees (Rodrigues 2018; Arévalo-González et al. 2024) and offer a safe, predictable foraging environment. This reliability likely makes seagrass meadows particularly attractive to released animals, underscoring their importance for rehabilitation and highlighting key characteristics for selecting release sites. Conversely, our RSF results indicated similar patterns for other habitat predictors between wild and released manatees. This suggests successful adaptation to natural conditions, supporting the efficacy of the Brazilian manatee release program (Normande et al. 2015). Consequently, future release sites should be selected based on such resource selection patterns to align with manatee habitat preferences. Nevertheless, sustained capture and tagging of wild manatees remain essential to fully elucidate movement behaviours across different parts of their range.

4.4 | Human Impact and Conservation

The Northeast Brazil manatee population is estimated to consist of approximately 1100 individuals, as determined by aerial surveys (Alves et al. 2016). This population, being the southernmost, exhibits lower genetic diversity compared to many other manatee populations (Luna et al. 2021). This reduced genetic diversity may be attributed to the population's small size and persistent pressure from anthropogenic threats, including habitat loss and instances of newborn strandings (Balensiefer et al. 2017; Meirelles 2008; Parente et al. 2004).

Despite the common assumption that manatees predominantly occupy pristine, high-quality habitats, our findings suggest a more complex relationship between manatees and their environment. In our study, human impact emerged as a 'selected' variable for all groups analysed except when PB was analysed separately. This positive association between log-selection strength and elevated levels of human activity suggests that critical manatee habitats often overlap with heavily impacted coastal zones. Rather than avoiding these impacted environments, manatees might be compelled to use them because of the presence of critical resources, such as freshwater discharge points, or abundant aquatic vegetation that may thrive in nutrient-enriched waters. These results highlight the vulnerability of key manatee habitats and underscore the need to manage human activity in these areas to ensure the species' long-term survival.

In the AL subarea, important areas for manatees such as Paripueira and Porto de Pedras had medium to low levels of human impact, while Maceió had higher levels because of urbanisation, boat traffic and port-derived pollution. In previous studies (Normande et al. 2016, 2024), manatees established their home ranges in the north of the state, in the Costa dos Corais Marine Protected Area (MPA), and in the south, where there are several coastal lagoons with abundant freshwater and food resources. However, they move from one area to the other and must cross disturbed areas, where they are exposed to several threats.

The high levels of human impact in Pernambuco state, especially close to the state capital Recife and the port of Suape, may represent an obstacle to the species conservation because of the difficulties in linking the isolated population in Alagoas to the population ranging from the north of Pernambuco to the east coast of Ceará state (Alves et al. 2016; Lima et al. 2011). Notwithstanding the implementation of a conservation

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translocation program in the region since 1994 and its favourable outcomes in terms of reconnection of isolated populations, manatee adaptation to the wild (Normande et al. 2015) and reproductive success of released females (Attademo et al. 2022).

Low levels of human impact were observed in Barra do Mamanguape MPA, a very important site for manatees (Dos Santos et al. 2022, 2023; Normande et al. 2016, 2024). However, Cabedelo is also an important area used by several manatees and at a much higher pressure because of urbanisation, pollution, boat traffic and port-derived pollution (Dos Santos et al. 2023).

The CE/RN subarea had the lowest maximum CHI levels among the three subareas, despite being located far from the major urban centres of Fortaleza and Natal. Despite lower overall urbanisation, manatees exhibited an exceptionally strong and precise selection for areas of higher human impact within CE/RN (3.62, CI [3.52, 3.72]). This seemingly counterintuitive result is likely driven by the specific anthropogenic features present. The region contains extensive oil infrastructure and is a hotspot for shrimp and salt farms, activities that have caused substantial estuarine habitat loss and are the primary drivers of the area's exceptionally high rate of newborn manatee calf strandings (Meirelles et al. 2024). We hypothesise that this overlap between industrial activities and the limited resources available in degraded habitats compels manatees to use impacted areas, explaining why CE/RN was the only subarea where natural estuaries were not selected.

The absence of small boat traffic and small-scale fishing on the CHI layer (Magris et al. 2021) may underestimate the actual level of disturbances, particularly in areas where these activities are concentrated, once boat collision and bycatch are traditionally considered very significant threats to manatees range-wide (Balensiefer et al. 2017; De Thoisy et al. 2003; Montoya-Ospina et al. 2001; O'Shea and Lex Salisbury 1991; Rathbun et al. 1983). Nevertheless, the CHI layer used here still served as a reasonable proxy for overall habitat degradation and human impacts along the coastal zone. These impacts are not currently available in GIS databases for Northeast Brazil, but new advances in remote sensing and machine learning may make it possible to obtain this information at a regional scale, and this possibility should be explored in further assessments. Furthermore, subsequent studies could include other proxies, such as the distance to the closest marina as an indicator of tourism impacts.

Targeting specific management actions to reduce the overall anthropogenic impacts in areas where manatees' populations overlap could significantly enhance conservation outcomes (Wilson et al. 2007). This includes establishing or expanding seagrass restoration zones within manatees' home ranges or in critical foraging areas to ensure long-term food availability. Improving sewage treatment in coastal areas and implementing strict protection and water quality standards around freshwater springs that serve as essential refuges can be very beneficial in reducing exposure to stressors, once these habitats are generally subjected to high human impacts. Similarly, evaluating and rerouting or regulating shipping lanes and recreational boating corridors to minimise the risk of collisions and chronic disturbance is important. By prioritising these spatially informed interventions, including the protection of areas within currently protected areas by restricted zones and proposing new ones, management strategies can more effectively safeguard the habitats most vital to manatee survival and recovery.

The persistence of the manatee population in Northeast Brazil, despite recent research gains and rescue initiatives, remains uncertain because of the confluence of direct anthropogenic pressures, climate change, small population size and restricted genetic diversity—posing a severe threat to this southernmost population. In this context, our research provides critical insights: It identifies seagrass meadows and freshwater sites as vital habitats requiring conservation priority and exposes the significant degradation that these key habitats endure. This evidence highlights the need for immediate action to reduce anthropogenic impacts and initiate restoration programs.

Author Contributions

Iran C. Normande: conceptualization, investigation, funding acquisition, writing – original draft, methodology, visualization, validation, writing – review and editing, formal analysis, project administration, data curation. **Ana Carolina O. Meirelles:** formal analysis, methodology, writing – original draft, writing – review and editing. **João C. G. Borges:** data curation, funding acquisition, resources, writing – review and editing. **Emma Deeks:** formal analysis, methodology, writing – original draft, writing – review and editing. **Fernanda L. N. Attademo:** data curation, resources, writing – review and editing. **Carolina N. Souza:** writing – review and editing, visualization. **Fábia O. Luna:** data curation, funding acquisition, resources, writing – review and editing. **Rafael A. Magris:** formal analysis, methodology, writing – original draft, writing – review and editing. **Robson G. Santos:** conceptualization, funding acquisition, resources, supervision, writing – original draft, writing – review and editing.

Acknowledgements

The authors express their gratitude to the dedicated professionals who played pivotal roles in various phases of this study, including caregivers, veterinarians, biologists, and administrative personnel involved in the rescue, rehabilitation, capture, release, and tracking of manatees in Brazil from ICMBio/CMA, FMA, ICMBio/Costa dos Corais, and ICMBio/Barra do Mamanguape EPAs, all the institutions within the REMANE, the Costa dos Corais Long-term Ecological Research (PELD-CCAL). We also would like to thank AQUASIS and PCCB/UERN for providing freshwater springs data for this study and the Long Live the Manatee Project conducted by the Aquatic Mammal Foundation and sponsored by Petrobras through the Petrobras Socioenvironmental Program. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Funding

IN's work was supported by an International Mobility Scholarship from CNPq (200559/2022-2) and a CAPES Doctoral Scholarship (88887.921467/2023-00). ED received funding from Natural Ecological Research Council (NERC) (grant # NE/S007229/1). RGS was funded by National Council for Scientific and Technological Development (CNPq) (research productivity grant # 312099/2023-1). Data collection was part of the Sirenia Monitoring Project, funded by PETROBRAS for IBAMA's environmental licensing in the Potiguar Basin. ACOM work was support by Yaqu Pacha e.V, Nuremberg Zoo, and Pairi Daiza Foundation. CNS is grateful for the support provided to CAPES by the postdoctoral fellowship (#88887.006274/2024-00).

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Ethics Statement

Research permits and authorisations were obtained for the research (SISBIO 43406; 45568; 25597; 25473; 24767; 41337; 74626; 81090), and the research protocols were approved by the CEUA UFAL Animal Ethics Committee under number 18/2023.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this study are publicly available in the Movebank data repository (www.movebank.org) under the study '*Trichechus manatus* Sirenia NE Brazil' movebank ID 1936932457. Spatial layers and RSF script are available in the Supporting Information section.

Endnotes

In this study, the Ornstein-Uhlenbeck Foraging (OUF) anisotropic model best fit 18 individuals, while the Ornstein-Uhlenbeck (OU) anisotropic movement model best fit two individuals. The OU anisotropic movement model describes an animal's motion as a mean-reverting process directed towards a central attraction point, while permitting directional bias in movement speed or permeability through its diffusion and relaxation parameters. This results in an elliptical home range that reflects persistent directional constraints in movement. The OUF anisotropic model extends this by incorporating directed movement towards resource gradients, in addition to central attraction, thereby shifting and reshaping the distribution of space use towards areas of higher resource availability. Within the ctmm framework, these models provide the mechanistic basis for generating autocorrelated kernel density estimates (AKDE) that accurately represent range residency and anisotropic space use, which in turn allows resource selection functions to distinguish habitat preference from movement constraints and foraging behaviour.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Detailed information on each layer used as predictor in this study with description, method used, resolutions and source of the data. **Figure S1:**. Maps illustrating the habitat categories used to access manatee resource selection in the three subareas (A) CE/RN, (B) PB and (C) AL. Although mangrove was not used in the analysis, it is shown here to facilitate visualisation of the rivers in the region. Freshwater springs are shown as dark pink rectangles and occur only in the CE/RN subarea. **Figure S2:** Cumulative human impact in the study area, focusing on the areas that overlap with GPS positions obtained from tracked manatees. **Data S1:** Supporting Information. **Data S2:** Supporting Information.

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