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A multi-decadal aerial survey reveals patterns in manatee abundance and response to seagrass die-offs

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Florida manatees (*Trichechus manatus latirostris*) are challenged by human alteration of landscapes and waterways. Coastal eutrophication has increased the frequency and intensity of Indian River Lagoon (IRL) algal blooms, promoting seagrass die-offs in areas that once consistently provided manatee forage. For decades the densest aggregations of manatees in Florida, outside of warm-water sites in winter, occurred in the northern Banana River (NBR) at Kennedy Space Center. Historically, the nearby Mosquito Lagoon (ML) had low numbers. Beginning in 2011, several catastrophic algal blooms caused the die-off of nearly 60% of the areal extent of all IRL seagrasses. Most severe impacts were in the Indian River and Banana River with lesser impacts in ML. This study evaluated several decades of manatee aerial survey data using statistical models to identify the environmental and temporal factors influencing manatee abundance, behavior and habitat use in the NBR (1990–2024) and ML (2016–2024). Using a Bayesian hierarchical model, we evaluated how manatee counts were affected by season, water clarity, and coastwide trends in manatee population size. Manatee abundance was evaluated across four distinct IRL seagrass Die-Off periods: Pre-Die-Off, Initial Die-Off (2011-2015), Secondary Die-Off (2016-2022), and Post-Die-Off (2023-2024). NBR manatee abundance increased well into the Initial Die-Off and then declined sharply until reaching historic lows in 2019. Beginning in 2016, only the ML maintained high seagrass coverage and a notable surge in manatee counts indicated aggregations shifted to ML. The Boosted Regression Tree Analysis top two predictors of abundance were seagrass Die-Offs periods and season. Optimized Hotspot Analysis of NBR manatee spatial distribution was compared to seagrass distribution and revealed that during the Pre-Die-Off, manatee hotspots occurred along deep-water resting areas adjacent to seagrass. Starting in the Initial Die-Off, manatee hotspots shifted toward ever shallower waters presumably to access the receding seagrass beds. The proportion of calves observed also declined dramatically after the Initial Die-Off period. These findings demonstrate that manatees aggregate in traditional areas with extreme fidelity but need to shift to "other pastures" during localized seagrass die-offs. Future shifts from habitat degradation will require best practices and adaptive management to safeguard manatees.

KEYWORDS

Bayesian hierarchical model, boosted regression tree, estuary, habitat use, hotspot, seasonality, warm-water refugia

Introduction

The Florida manatee (*Trichechus manatus latirostris*) is a subspecies of the West Indian manatee and listed as threatened under the US Fish and Wildlife Service (USFWS), Endangered Species Act. Manatees are large, aquatic herbivores that rely on tropical and subtropical conditions and forage on aquatic plants including seagrasses (Thayer et al., 1984; Lefebvre et al., 2001; Valentine and Duffy, 2006; Marsh et al., 2011). They migrate to revisit locations with resources key to survival: forage, places to calve, warm-water refugia, and freshwater (Semeyn et al., 2011). Their distribution, behavior, and survival have been greatly altered by human activities, including disturbance by boat traffic and boat strikes, loss of seagrass from coastal eutrophication and algal blooms (Runge et al., 2017). Winter manatee migrations have been influenced by artificial thermal refuges associated with industrial warm water effluents, such as power plant discharges (Shane, 1984; Deutsch et al., 2003; Laist et al., 2013; Reynolds and Scolardi, 2016).

The USFWS recognizes four regional manatee management units based on fidelity to specific warm-water refuges and fairly discrete distributions (Laist et al., 2013). Manatees within each unit typically return to the same warm-water refuges each winter and exhibit similar non-winter distribution patterns. During winter months, movement between units is generally limited (Laist et al., 2013). Our study focused on individuals in the Atlantic Coast Management Unit found in the northern portion of the Indian River Lagoon system (IRL). The IRL consists of three major water bodies, Indian River, Banana River and Mosquito Lagoon (Figure 1) representing the manatee's northern wintering range along Florida's east coast.

For four decades, the densest aggregation of manatees outside of winter refugia sites occurs in the northern portion of the Banana River (NBR), which is located within the Kennedy Space Center (KSC) and Cape Canaveral Space Force Station security zones and Merritt Island National Wildlife Refuge (MINWR) (Hartman, 1974; Shane, 1983; Provancha and Provancha, 1988). This area was closed to motorized watercraft in 1990 by USFWS and designated a manatee sanctuary in 1992. Elevating its regional importance because elsewhere, watercraft collisions are the leading human-related cause (20–25%) of manatee mortality (Wright et al., 1995; Runge et al., 2017). Manatees are frequently encountered along KSC Banana River seagrass beds from spring through fall (Hartman, 1974; Shane, 1983; Provancha and Provancha, 1988; Provancha and Hall, 1991; Lefebvre et al., 2017; Martin et al., 2015). For decades no other area on the Florida east coast offered as much protected seagrass habitat, nor were there other sites utilized by such large manatee aggregations, with reports indicating that aggregations in spring could account for 50% to 70% of the Atlantic unit (Provancha and Provancha, 1988; Provancha and Hall, 1991; Martin et al., 2015; Edwards and Ackerman, 2016).

The southern portion of Mosquito Lagoon (ML) is within KSC boundaries but managed by MINWR and it is open to the public. Mosquito Lagoon historically, has not experienced large manatee aggregations likely due to a combination of ecological and spatial factors (Deutsch and Barlas, 2016; Edwards and Ackerman, 2016, Martin et al., 2015; Reynolds and Scolardi, 2016). The adjacent Indian River and Banana River lagoons historically supported abundant seagrass beds, providing ample year-round forage, reducing the need for manatees to travel to or aggregate within ML. The ML is more saline and located approximately 34 km from the northernmost known winter warm-water refuge, this distance is considerably greater than typical foraging trips from warm-water refugia documented by telemetry studies (Deutsch and Barlas, 2016). Additionally, elevated boat traffic may have further discouraged manatee use. Seagrass coverage within ML has traditionally been extensive and relatively resilient to algal blooms, likely due to reduced nutrient loading from agricultural, urban, and industrial runoff as a high proportion of this shoreline is conservation-managed (Breininger et al., 2017).

Beginning in 2011, several expansive and persistent catastrophic algal blooms fueled by nutrient loading, occurred throughout nearly the entire IRL. These events resulted in the loss of 58% of the areal extent of seagrass in the IRL (19,000 ha) with the most severe impacts observed in the Indian River and Banana River lagoons over several years (Morris et al., 2022; Phlips et al., 2021). From December 2020 through April 2022, manatee starvation related to this loss resulted in declaration of an Unusual Mortality Event along the Atlantic coast of Florida, with at least 1,255 mortalities (https://myfwc.com/research/manatee/rescue-mortality-response/ume/) (Florida Fish and Wildlife Conservation Commission).

Kennedy Space Center has long been a critical site for aerial surveys that monitor manatee aggregations and habitat use along Florida's east coast. These long-term monitoring efforts provide essential data, which enables KSC and MINWR managers to make informed decisions regarding KSC operations and their potential impacts to manatees and refuge management.

The primary objective of this study was to evaluate aerial survey data using statistical models to identify the environmental and

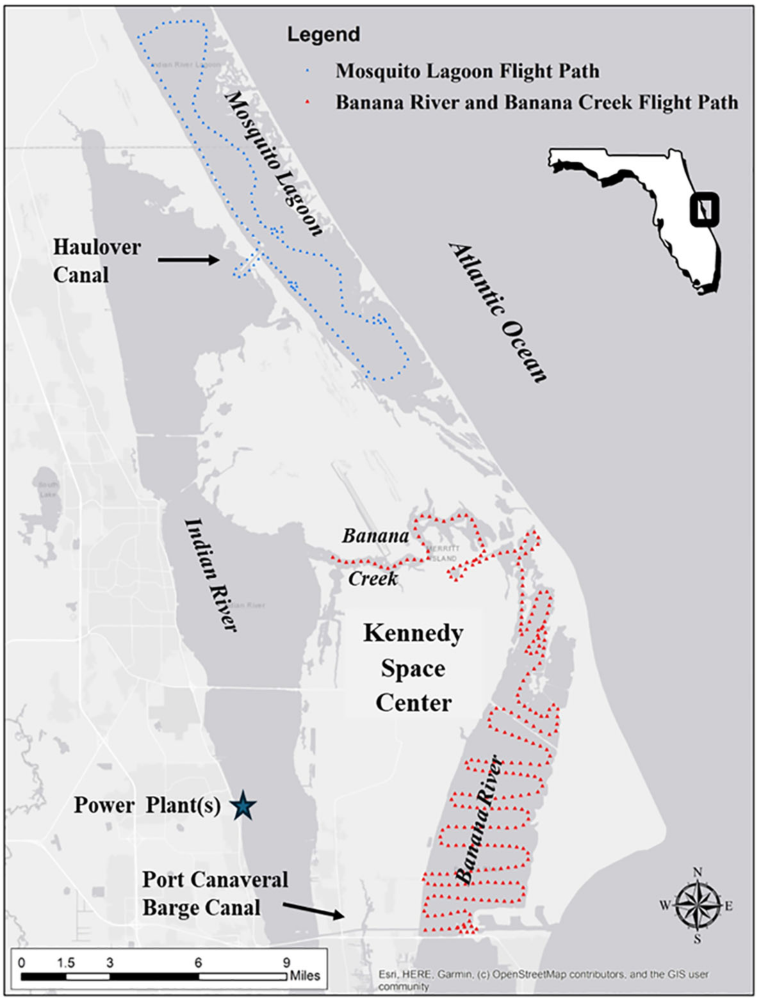

FIGURE 1
Map of the manatee study area at Kennedy Space Center, Florida. Blue star indicates location of power plants warm-water basins. Black arrows indicate the locations of canals connecting the lagoon systems. Dotted lines represent the generalized flight paths used during aerial survey(s). The red flight path covers the Banana River and Banana Creek, while the blue flight path covers Mosquito Lagoon.

factors influencing seasonal and annual variation in manatee abundance, distribution, habitat use and behavior in the North Banana River (NBR; 1990–2024) and Mosquito Lagoon (ML; 2016–2024). We applied Bayesian hierarchical modeling to evaluate how manatee counts were affected by covariates including water clarity (as a proxy for detectability), coastwide trends in manatee population size, seagrass loss, and known seasonal movement patterns of resident manatees that frequently moved in and out of the study area. Additionally, we assessed manatee response to resource limitations, such as during seagrass die-offs, dispersing to alternative foraging areas or increasing use of shallow, typically less accessible seagrass beds. We also assessed whether calf abundance declined in response to reduced regional forage availability. Documenting these patterns of habitat use is essential for guiding and improving conservation strategies, such as protecting seagrass and anticipating shifts in manatee distribution in response to changes in seagrass coverage. These shifts may also influence management actions, including watercraft regulations and the designation of boat speed zones.

Methods

Study area

The study area is in the northernmost IRL, located along a temperate and subtropical boundary, and is recognized for its biodiversity of national significance (Swain et al., 1995; Hanisak and De Freese, 2021; Turner, 2021). Within the last 200 years, migration routes available to manatees were altered by human changes in the rapidly urbanizing east-central Florida landscape, especially by the 1950s. The impetus for the greatest changes in the northern IRL was the creation of the Cape Canaveral Missile Test range and later NASA's KSC and subsequent requirements for energy, water transportation, and residential development for employees. The discharge from the Orlando Utilities Commission power plant (1960 -2010) and the Florida Power and Light (FPL) Cape Canaveral Energy Center became the northernmost winter warm-water refugia in the Indian River (Figure 1). Just to the north, Haulover Canal (manmade and stabilized in the late 1800s) allowed movement between Mosquito Lagoon and the Indian River Lagoon; while slightly south, the Canaveral Barge Canal (built in 1965) provided a short connection to the NBR. In the 1960s, the NASA Launch Complex 39 Crawlerway cut off the natural northern connection (albeit very shallow) between NBR and the Indian River Lagoon.

The 75 km² NBR study area includes the northernmost section of the Banana River Lagoon and Banana Creek (33.4 km²), which NASA closed to the public in1962. A middle section (42.6 km²) was closed to motorized watercraft in 1990 by USFWS and the area was designated a manatee sanctuary in 1992. The southernmost section (7.5 km²) is open to all boating activities, providing passage to Port Canaveral, southern BR and the Indian River Lagoon via Canaveral Barge Canal (Figure 1). Water depth over the undisturbed bottom can reach 2.5 m, with a mean depth of 1.2 m, while dredged channels and basins range from 3 to 12 m. The multiple locations of dredged “pockets” that are surrounded by seagrass beds have been previously noted as significant hotspots for manatees (Provancha and Provancha, 1988; Provancha and Scheidt, 1999). Shallow waters (0.5-1.7 m) have provided forage for decades, with various densities of seagrass, primarily *Halodule wrightii* and *Syringodium filiforme*, and macroalgae. Starting with the “Superbloom” in 2011, several large persistent phytoplankton blooms shaded the bottom and caused large-scale die-offs of seagrass (IRL Consortium, 2015; Phlips et al., 2021; Morris et al., 2022). Features in the middle and southernmost sections of the NBR include a broad shallow seagrass bed along the eastern shore and a narrower bed along the western boundary, with a midwater basin (2–3 m depth) and a deeper dredged Intracoastal Waterway (ICW) running north to south. The northernmost section is more complex with a mix of several large dredge holes, created during the development of the KSC in the 1950s and 1960s, along with the ICW, and large shallow seagrass beds.

The ML study area encompasses the southern portion of Mosquito Lagoon which is within the boundaries of KSC managed by the Merritt Island National Wildlife Refuge and is open to the public. This 102.4 km² survey area features large expanses of shallow seagrass beds along the eastern shoreline, narrower beds along the western shore, a generally bare midwater basin (2–3 m depth), and the dredged ICW. Boating occurs in most areas, with heavy boat traffic in the ICW and over the shallow seagrass beds except for a fishing “Pole – Troll” zone along the central eastern shore. In contrast to the NBR, there are very few manmade dredged holes or channels, and they are shallow (2 m).

Aerial manatee survey counts

Systematic aerial surveys of the northern Banana River (NBR) were initiated in 1984 (Provancha and Provancha, 1988), initially encompassing a limited area and was expanded to its current extent prior to 1990. The survey was further extended into the Mosquito Lagoon (ML) in 2016. Surveys were conducted year-round when feasible, with a primary emphasis on twice-monthly aerial flights during the summer months (Miller et al., 1998). Spring and fall received moderate coverage, while winter surveys were conducted least frequently. Most flights were suspended in 2020 due to COVID-19-related restrictions.

Flights were supported by the KSC Flight Operations Group using helicopters (Bell UH-1-H initially and replaced by H135 Airbus starting in 2020). The survey started at the south near Florida State Road 528 causeway (-28.4031, -80.6308) and followed a series of parallel east/west transects spaced at one-half minute latitude increments (approximately 1,000 m; Figure 1). To enable analysis of trends, the ML survey followed flight paths used in special assessments begun in 1977 by other researchers, such as the Florida Fish and Wildlife Conservation Commission (FWC), Florida Power and Light (FPL), and Mote Marine Laboratory (Edwards and Ackerman, 2016; Reynolds and Scolardi, 2016). These surveys started at the southern ML terminus and proceeded north along the eastern seagrass beds to Georges Bar, turned counterclockwise to travel south along the western shore, circled Haulover Canal and continued south to the starting point.

Surveys were only initiated when winds were less than 18–20 knots, sea state was based on the Beaufort scale ranging from smooth water to small waves with few whitecaps (Edwards and Ackerman, 2016) and cloud cover was less than 60%. These criteria helped standardize environmental conditions and maximize visibility into the water column. If during a survey, water clarity was deemed poor over large areas, or if sea state, wind speed, or cloud cover exceeded acceptable levels, the survey data were excluded from analyses. Surveys began at 0900 h local time and typically were completed by 1100 h. Surveys were performed from an altitude of 152 m at a speed of 75 knots, with two dedicated observers (left and right side of the platform), and they followed the survey methods described by Provancha and Provancha (1988). An integrated geographic coordinate system (Loran) was used to collect location of the helicopter simultaneous with observer callouts on environmental conditions and manatee observations to a data recorder using headsets. Since 2006, the data were integrated with a GPS and a touchscreen input program. Attribute data for each sighting included the number of manatees in a group (number of adults and calves, with calves defined as animals 30 to 50% of adult size and typically in close proximity to larger manatees) (Provancha and Provancha, 1988), behavior (resting, feeding, traveling, or cavorting) (Edwards and Ackerman, 2016), water clarity (good, fair, or poor), sea state, wind, cloud cover, glare, and light penetration.

Habitat data – seagrass and bathymetry

Annual trends of seagrass abundance were characterized by percent cover values from fixed transects located within the study site and IRL wide. Data sources included long-term transects surveyed for KSC, which are located within the study site and used the Daubenmire Method to determine percent cover (Daubenmire, 1968; Provancha and Scheidt, 1999), and long-term transects in the study area and the remainder of the IRL that are part of the Saint John’s River Water Management District (SJRWMD) IRL Seagrass Monitoring Network, which sampled 1m² quadrats along transects to determine percent cover per 1m².

To compare percent cover in different regions within the IRL, SJRWMD transects were grouped into nine geographic regions (Morris et al., 2001, Morris et al., 2022). Seagrass areal extent was obtained from SJRWMD seagrass maps interpreted from aerial imagery (SJRWMD, 2024). Since mapping did not occur every year, the spatial extent for a mapping year was carried over to the following year(s) until a new map year was available (e.g., 1992 map was also used for 1993). For each flight, the spatial location of each manatee was intersected with the map from the corresponding year, and the sighting was classified as either occurring over "open water" (bare or no seagrass) or "seagrass" (presence of seagrass). The percentage of manatees occurring over the two habitat types (open water or seagrass) was calculated and then related to manatee distribution over habitat type and behavior type.

To calculate the relative depth, not actual depth of each sighting, bathymetry (m) from the NOAA map (NOAA NCEI CUDEM 2020) was extracted for each manatee sighting location using ArcMap (v.10.2, Esri, Redlands, CA). To adjust for the relative depth of the water column, for each sighting, the Mean Water Level, -0.2 m (NAVD 88) was subtracted from the extracted depths (Hall et al., 2014). Since water temperatures were not available for the entire span of the study, daily minimum air temperature (°C) for Titusville, Florida, was downloaded from the Global Historical Climatology Network (Vose et al., 2012) and used as a proxy to water temperature (Hardy et al., 2019).

Data analysis

Boosted Regression Tree Analysis (BRT; Elith et al., 2008) was used to investigate the effects of environmental, temporal, and other observational covariates on the observed manatee counts during surveys of the NBR. Briefly, BRT is a machine learning approach that iteratively fits regression tree models to the data, using optimization methods to gradually increase emphasis on observations modeled poorly by the existing collection of trees. Key elements of BRT analysis are the use of random subsets of data in multiple replicates, which improves the final predictive performance, and sequential fitting within replicates to build on trees fitted previously, which focuses estimation on the hardest observations to predict. BRT models with the total adult manatee count during each survey as the response variable were fit using the dismo package (Hijmans et al., 2023) in R version 4.4.1 (R Core Team, 2024), following the methods described in Elith et al. (2008).

Predictors tested were Season, Year, Mean Water Clarity, Minimum Air Temperature (Tmin). Seasons were defined as, winter (December - February), spring (March-May), summer (June-August) and fall (September-November). Manatee abundance was evaluated across four distinct time periods, each defined by the relative combined status of the stressors, seagrass die-off and algal bloom(s). Pre-Die-Off (1990–2010): Seagrass was abundant and stable, providing extensive foraging habitat for manatees. Initial Die-Off (2011–2015): A massive loss of seagrass that was triggered by the onset of a "Superbloom", as documented by the IRL Consortium (2015); Phlips et al. (2021). Secondary Die-Off (2016–2022): Continued die-off with scarce seagrass and recurring and widespread algal blooms. Post-Die-Off (2023–2024): Seagrass remained scarce, though limited signs of recovery have begun to emerge. We used different geographic levels of seagrass cover to investigate if manatees were most affected by seagrass abundance at local or regional scales.

Seagrass percent cover data was represented by KSC Long-term seagrass transects and from SJRWMD transects (Morris et al., 2022) which are grouped into geographic regions. For NBR, percent cover data included KSC Long-term transects and the portion of the Banana River-SJRWMD transects that occur within KSC (BRKSC). Mosquito Lagoon transects-SJRWMD (ML) and KSC Long-term transects represent the ML study area. The North IRL transects – SJRWMD (NIRL) represents the warm-water refuge area. The remaining regions are at increasing distances to the south of the study area, the portion of Banana River -SJRWMD transects that occur south of KSC (BRS), North Central IRL transects-SJRWMD (NCIRL), South Central IRL transects – SJRWMD (SCIRL), and South IRL transects – SJRWMD (SIRL).

To guard against overfitting, we included as a potential predictor a covariate generated as a random normal vector with mean = 0 and standard deviation = 1 (Eguchi et al., 2017) to serve as a benchmark for assessing which predictors were useful in the model. To judge which variables were useful, we plotted the relative variable influence, which is a measure of how often a predictor was selected for tree splitting weighted by the resulting model improvement averaged over all trees, scaled so that values of all variables sum to one (Elith et al., 2008). For variables with high influence (those greater than the random variable), we plotted partial dependence (the effect of a variable on the count with all other variables at their average value).

We focused on estimating the abundance of manatees that used the study area in summer because during this period manatee regional movements were minimal (Miller et al., 1998) and thus it made sense to define a sub-population within the area during this time. A hierarchical Bayesian model was used to estimate manatee abundance in the NBR and ML in summer, implemented using Markov Chain Monte Carlo sampling (MCMC). We chose this approach because it allowed more flexibility in handling differences in sampling among the years. It also allowed incorporation of random effects to account for unexplained spatial and temporal effects, and to adjust for overdispersion which is common in state space models. This model can be described as a hierarchical model with a Markovian process sub-model for abundance in each year, and an observation sub-model for the observed count during each survey within each year. The data for this model consisted of replicate counts during aerial surveys of the NBR and ML each summer, C_{byj}, where b indicated lagoon (NBR or ML), y year, and j the replicate survey. Based on previous information, it was assumed that in each summer season a group of manatees of size N_{by} used the NBR or ML, and that during each replicate count j, only a portion of this total was present within the study area at the time of the survey and available to be counted. We hypothesize that manatees became more local to KSC later in summer. The simplest way to model this was as a positive linear effect of time on availability (a manatee resident to the system was more likely to be present at KSC during a survey as time went by over the summer). Of those present, only a portion were observed (others were missed due to detection error). Because there was not enough information in the replicate counts to separately estimate both presence and detection, a confounded detection parameter D_{yj} was included which was modeled with covariates related to both presence within the study area (the time since the beginning of the summer season, t_{yj}) and detection if present (water clarity based on the mean observed water clarity during the survey $pClarity_{yj}$). This model can be described as a hierarchical model with a process sub-model for abundance in each year:

$$N_{by} \sim Poisson\,(\lambda_{by})$$

$$Log(\lambda_b y) = abundance - intercept_b + \beta_{sea\_grass,b} * sea\_grass_{by} + \gamma_y$$

and an observation sub-model for the observed count during each survey within each year:

$$C_{byj} \sim Binomial(D_{yj},\ N_{by})$$

$$Logit(D_{yj}) = observation - intercept + \beta_{Clarity} * pClarity_{yj}$$
$$+ \beta_{present,b} * t_{yj} + \psi_{yj}$$

Both γ_y and ψ_{yj} are the abundance and observation level random effects, and the terms with β are the covariate effects. For all unmodeled parameters, except for the standard deviations of the random effects, normal priors with mean = 0 and standard deviation = 100 were used, which were uninformative on the logit scale contained mostly between ± 6. The prior for the effect of time on presence ($\beta_{present}$) was constrained to be positive to reflect the assumption that presence increased over the summer. For the priors for standard deviations of the random effects, weakly informative prior distributions were used by taking the right half of a normal distribution with mean 0 and variance = 5. This produced a distribution similar in shape to the Half–Cauchy distribution recommended by Gelman (2006), but with a much shorter tail. We implemented the hierarchical Bayesian models using JAGS 4.3.0 (Plummer, 2003) and R with the package jagsUI (Kellner, 2024). For each analysis, we ran an adaptation phase of up to 10,000 iterations decided automatically by JAGS, and then discarded samples as burn-in until Gelman-Rubin convergence diagnostic (R-hat) were less than 1.01 and the number of effective samples was estimated to be greater than 4,000 for all parameters, except for individual levels of the random effects. We did not thin the MCMC posteriors (Link and Eaton, 2012). We tested model goodness of fit using a Bayesian p-value approach that compared the fit of the observed data to the equivalent fit of data simulated under the model with estimated parameters (Kéry and Royle, 2020).

Other effects were addressed in several ways. The effect of water clarity on detection was modeled as a constant parameter across surveys because consistency in methodology isolated it as a simple function. The trend in availability over time was modeled as the same linear trend for all years, reasoning that this effect was a constant linear increase over the summer. During any survey, there were also other factors that could affect either the presence or detection of a manatee in the study area, such as temperature, sources of fresh water, or smaller scale and undocumented patterns in habitat. A random effect on detection-availability ψ_{yj} was included to allow for unmodeled heterogeneity in detection (e.g., unmeasured effects such as observer experience).

The spatial distribution of manatee counts for each georeferenced sighting, the number of manatees in a group (number of adults and calves) were compared using the Optimized Hotspot Analysis Tool in Arc Pro v.3.3.3 (Esri Inc, Redlands, CA) to determine if manatee distribution was random or non-random/clustered during Die-Off periods: Pre-Die-Off (1990–2010), Initial Die-Off (2011–2015), Secondary Die-Off (2016–2022), Post-Die-Off (2023–2024).The analysis identifies areas of hotspots (clustered), coldspots (avoided or not observed), and non-significant sighting areas (random) by creating a fishnet of manatee counts and applying spatial autocorrelation across increasing fixed distances and nearest neighbors, continuing until a calculation of the optimal scale of distance is determined. The optimal distance is then used to calculate a Getis-Ord Gi* statistic, z-score, and p-value (Getis and Ord, 1992). The significant positive z-scores indicate the intensity of clustering, significant negative z-scores indicate areas of absence, extremely low presence, or avoidance. The non-significant z-scores reflect the random presence and distribution of the remaining manatees. The results of hotspot analyses for each period were then overlaid and visualized on maps of seagrass representative of each period.

To assess habitat selection, we calculated the proportion of manatees observed over seagrass for each year and constructed the 95% binomial confidence intervals for these proportions (Agresti, 2013). We then compared these to the proportion of seagrass for the study area derived from maps for that year. If in a given year the proportion of seagrass fell outside the 95% confidence interval for manatee occurrence, we considered this as evidence for habitat selection (Neu et al., 1974).

For several metrics of manatee life-history traits measured during surveys, we fit a loess locally weighted regression of degree 2 and plotted the raw data with the smoothed estimate and 95% confidence intervals, as an aid to detecting patterns (Venables and Ripley, 2013). To evaluate patterns in the proportion of calves observed over time, we calculated and plotted the annual proportion pooled across all surveys within each year. To evaluate patterns in manatee behavior (Hartman, 1979), we plotted the annual proportion of manatees observed during surveys in each of the three behavior classes (resting, feeding and traveling). To evaluate patterns in the water depth at the locations in which manatees were recorded during surveys, we plotted the annual mean depth.

Results

Patterns in manatee counts

From 1990–2024, 385 surveys were conducted in the NBR and from 2016–2024, 89 surveys were conducted in the ML (Table 1). Manatees were observed year-round in the NBR, with seasonal manatee counts highest in spring (maximum of 1,072 in 2012), followed by summer (maximum of 757 in 2012). Counts were

TABLE 1 **Summaries for KSC manatee aerial surveys over the Northern Banana River and Mosquito Lagoon by seagrass Die-Off period.**

Lagoon and die-off period	Number of surveys	Min – max manatees	Mean total per survey ± SD	Mean adults	%Calves
BR 1990-2024	385	0-1072	194 ± 187.2	177.1	8.8
BR Pre-Die-Off (1990-2010)	254	0- 934	177.7 ± 150.0	161.9	8.7
BR Initial Die-Off (2011-2015)	41	1- 1072	489.8 ± 241.8	438.2	9.7
BR Secondary Die-Off (2016-2022)	55	1- 447	101.0 ± 115.2	93.3	4.1
BR Post-Die-Off (2023-2024)	35	1-420	119.2 ± 105.0	116.2	2.1
ML 2016-2024	89	1 - 1084	462.2 (282.6)	442.7	4.2
ML Pre-Die-Off (1990-2010)	NA				
ML Initial Die-Off (2011-2015)	NA				
ML Secondary Die-Off (2016-2022)	53	1 – 1032	442.8 ± 284.8	415.0	5.7
ML Post-Die-Off (2023-2024)	36	1 – 1084	490.7 ± 280.8	483.2	2.6

typically very low during cold periods (air temperature below 10 ° C). Annually, manatee counts in NBR progressively increased from 1990, peaked in 2012, declined sharply to historically lowest numbers in 2019, and remained low until 2023 when numbers increased slightly. In ML, manatees were observed year-round, with seasonal counts highest in summer (maximum of 1,084 in 2022) and spring (maximum of 1,032 in 2017). When compared with NBR from 2016–2024, counts were substantially greater during all seasons and years (Figures 2, 3; Supplementary Figure 1; Table 1).

Comparing seagrass and summer manatee counts in NBR

Seagrass areal extent in NBR ranged from a high of 5,012 ha prior to die-off events and widespread seagrass die-offs, to a low in 2019 when seagrasses had decreased to 242 ha, a 95% loss; this trend was also reflected in transects percent cover. Seagrass loss in NBR crashed following the 2011 "Superbloom" (Figure 3). When comparing summer manatee counts to seagrass percent cover,

FIGURE 2
Box plot showing the annual mean number of adult manatees observed per flight by season (**(A)** – Winter, **(B)** – Spring, **(C)** – Summer, **(D)** – Fall) during aerial surveys over the KSC portions of the Northern Banana River (NBR - red) (1990-2024) and Mosquito Lagoon (ML - blue) from (2016 -2024). Boxes show region containing the central 50% of the data, the whiskers show the 1.5 times the inter-quartile range, and the dots the most extreme outliers.

manatee counts increased after the NBR decline, more than doubled in 2012 but then declined precipitously in 2016, slightly increased in 2017 and then declined and remained low until 2023 when limited signs of recovery have begun to emerge. In ML summer surveys starting in 2016 (Secondary Die-Off), manatee numbers were higher than NBR and remained high, and seagrass percent cover was also higher than NBR (Figure 3).

Factors affecting summer manatee counts in the NBR

The BRT model results provided general patterns that explain how factors influence manatee counts in NBR. A tree complexity of 3, a bag fraction of 0.5, and learning rate of 0.01 were selected for the final model configuration. For variables identified as influential we used partial dependence plots of the average predictions over each variable's range, with all the other variables at their observed values. The most influential variable on manatee counts by survey was Die-Off period (24.4% relative influence), followed closely by season (14.9% relative influence), and water clarity (14.6% relative influence; Figure 4). Other influential variables were Tmin, year, and BRS. All other variables were less influential than the random check variable, indicating that they were less useful as predictors of manatee counts by survey (Figure 4). Results from BRT showed that seagrass cover in the NBR had little relative importance on manatee counts until the beds were nearly gone. The partial dependence plots indicate that among the Die-Off periods, the Initial Die-Off had the strongest influence on manatee counts. Counts increased markedly above the mean during this event, while remaining lower before and after (Figure 5; Table 1). The effect of air temperature was a sharp rise in counts between 7–10 degrees (Figure 5). The effect of temperature varied by season (Figure 6) with a stronger effect in spring than the other seasons. Manatee counts decreased as water clarity declined. Manatee counts showed a gradual increase over the years with a slight bump in the early 2000s, and counts showed a sharp increase as seagrass percent cover increased in BRS above the lowest values (Figure 5).

Summer manatee abundance model in NBR

Few covariates had support in the summer abundance model, which corrected for detection and temporary emigration (Table 2; Figure 7). Water clarity did influence detection. The temporal trend

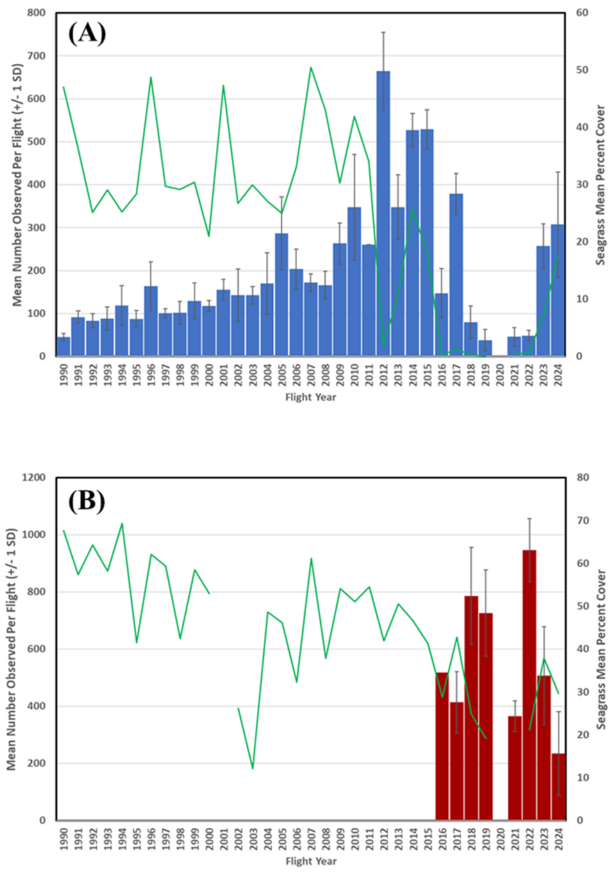

FIGURE 3
Mean number of manatees observed per fight during summer surveys. **(A)** Northern Banana River (NBR -blue bars) from 1990-2024. **(B)** Mosquito Lagoon (ML - red bars) from 2016-2024. Black bars are 1 Standard Deviation. The green line depicts mean seagrass percent cover from annual Kennedy Space Center long-term seagrass transects for each respective area. No flights flown in 2020 due to Covid restrictions.

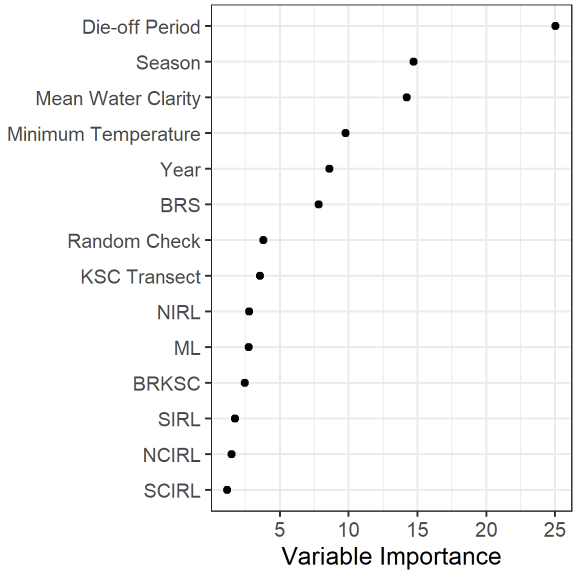

FIGURE 4
The relative contributions (variable importance) of predictor variables for the boosted regression tree model for manatee counts. Die-Off periods: Pre-Die-Off (1990–2010),Initial Die-Off (2011–2015), Secondary Die-Off (2016–2022), Post-Die-Off (2023–2024).; Season – winter, fall, spring, summer, Mean Clarity – mean water clarity; Tmin – Minimum Air Temperature; year; Banana River Kennedy Space Center transects (BRKSC), Banana River South transects (BRS), Mosquito Lagoon transects (ML), North Central IRL transects (NCIRL), North IRL transects (NIRL), South Central IRL transects (SCIRL), South IRL transects (SIRL). Data on seagrass cover provided by transects outside study area were collected by the St. Johns River Water Management District.

for summer availability in the NBR was positive, but the trend did not differ from zero in ML. Seagrass cover unexpectedly had little effect on summer abundance, having coefficients that overlapped zero. The Bayesian model did not show evidence of a lack of fit based on the goodness of fit check (Bayesian p-value for the abundance portion of the model was 0.50 for NBR and 0.50 for ML and for the observation portion of the model 0.45 for NBR and 0.50 for ML).

Spatial patterns of seagrass and manatees within NBR

Optimized Hotspot Analysis showed that the spatial distribution and clustering of manatee sightings differed greatly between periods in relation to seagrass beds (Supplementary Table 1; Figure 8). For the Pre-Die-Off period, several large hotspots were identified with some adjacent to or over deep holes

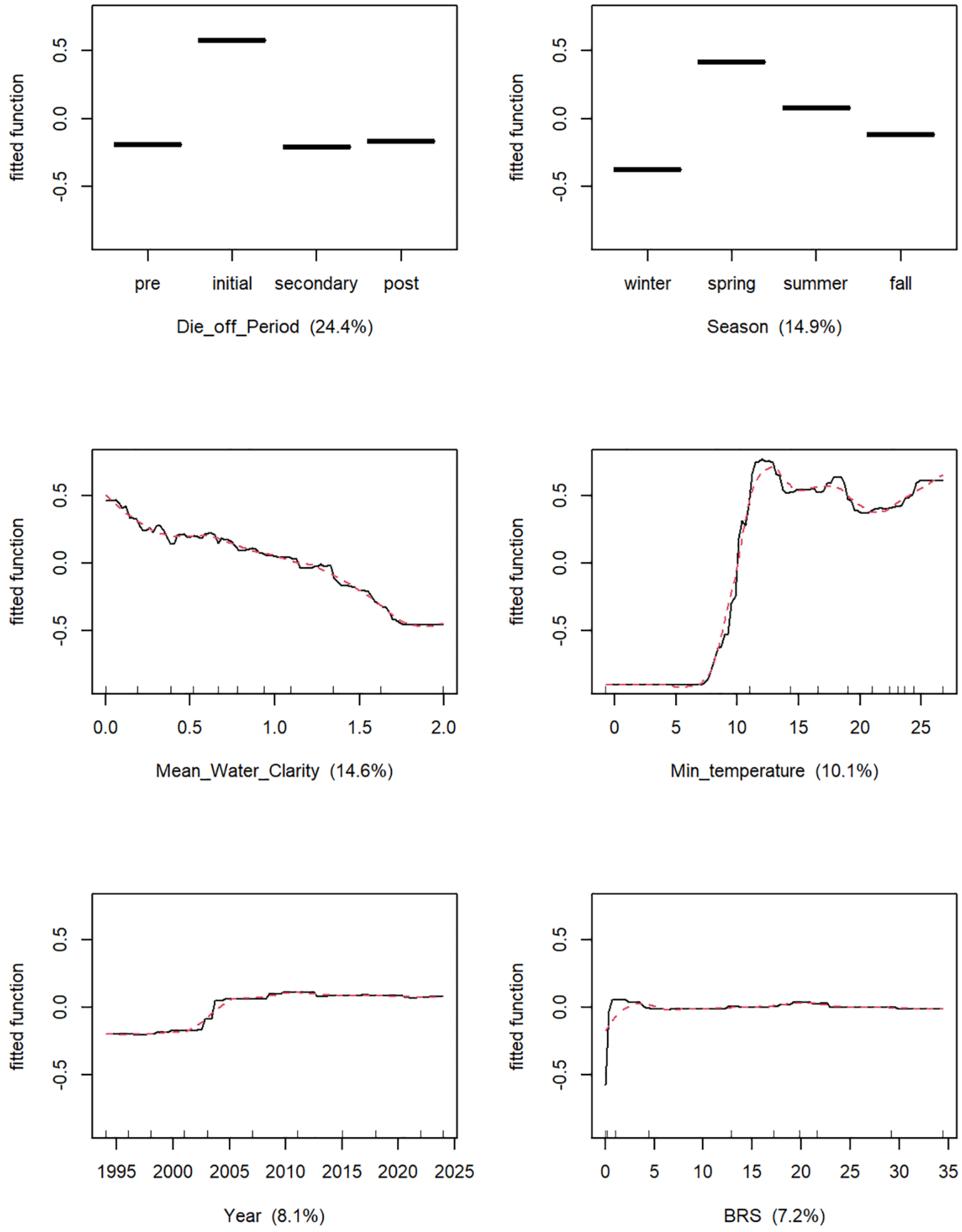

FIGURE 5
Partial dependence plots for the six most influential variables in the boosted regression tree analysis for manatee counts. Y axes are model predicted counts on the log scale centered to have zero mean over the data distribution. Rug plots on bottom of plots show the distribution of data across that variable, in deciles. The red line is a smoothed version of the fitted function provided by the model fitting routine. Tmin is minimum air temperature (C), Mean Clarity is 0 (good), 1 (fair), and 2 (poor), BRS percent seagrass cover in Banana River South.

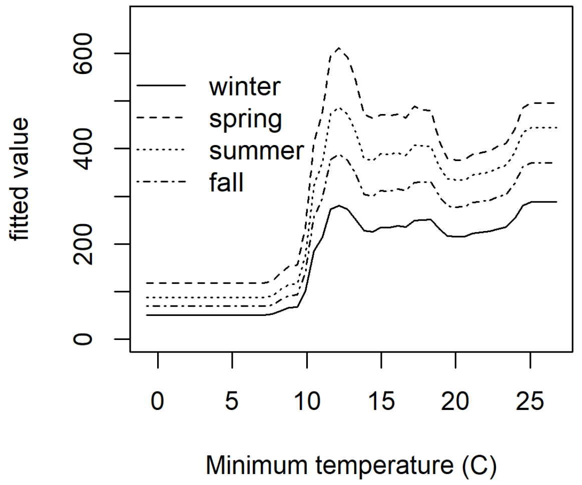

FIGURE 6
Interaction plot for the effect of temperature in each season in the boosted regression tree analysis for manatee counts. Y axes are model predicted counts. (Readers should use caution when interpreting model predictions outside of the observed data (e.g. cold temperatures in summer).

and others over large seagrass flats; based on behavior data for these coordinates, deep holes were used for resting and large seagrass beds were used for foraging. Most sightings were widely dispersed over seagrass areas and did not show significant aggregation. During the Initial Die-Off period, the hotspots increased in size and moved away from deep holes toward seagrass beds. In the Secondary Die-Off period there were fewer hotspots and were closer to the remaining seagrass beds which receded to shallower depths closer to the shore. Only a few small hotspots occurred near remnant seagrass beds during the Post Die-Off.

We found that manatees preferred to be in seagrass based on the proportion of manatees seen over seagrass beds compared to the proportion of open water within the study area. Non-significant sightings also shifted towards seagrass beds and the shoreline. In the Post-Die-Off period, only a few very small hotspots were identified, with most sightings being non-significant but still occurring closer to the shorelines. In the Banana River, manatees were observed at various depths, with a trend of mean depth becoming shallower and significant changes noted after 2011 (Figure 9). In Mosquito Lagoon, the overall mean depth of occurrence trended shallower. In NBR Manatees selected areas with seagrass at a higher proportion starting with the Initial Die-Off, when available seagrass had drastically declined (Figure 10).

Behavior and calves

In the NBR, feeding and resting were the two most common behaviors for all years and seasons, followed by travel which was higher in fall and winter (Figure 11). Starting during the Initial Die-Off feeding increased and at higher proportions, except for 2018, 2019 and 2021. Resting was highest in 2018 and 2019. In ML, feeding and resting were the two most common behaviors for all years and seasons, followed by travel which was higher in winter. From 2016-2018, feeding declined then markedly increased. Resting declined in 2021 and 2022. Cavorting was observed in all areas and seasons but in relatively low values. In NBR the proportion of calves

TABLE 2 **Posterior parameter estimates for the hierarchical Bayesian model used to estimate the summer abundance of manatee using the Northern Banana River.**

	Mean	SD	2.50%	50%	97.50%	Rhat	Samples
Abundance-intercept $_{\text{NBR}}$	5.61	0.25	5.11	5.60	6.11	1.00	356810
abundance-intercept $_{\text{ML}}$	7.43	0.51	6.27	7.49	8.29	1.00	122016
$\beta_{\text{seagrass NBR}}$	0.00	0.01	-0.02	0.00	0.02	1.00	5602626
$\beta_{\text{seagrass ML}}$	-0.02	0.02	-0.05	-0.02	0.02	1.00	200831
observation-intercept	0.71	0.07	0.56	0.71	0.82	1.00	4611
β_{clarity}	-0.67	0.19	-1.06	-0.66	-0.30	1.00	11152
$\beta_{\text{present NBR}}$	0.18	0.08	0.03	0.17	0.35	1.00	96552
$\beta_{\text{present ML}}$	0.10	0.10	0.00	0.07	0.37	1.00	49512
SD $\gamma_{y\ \text{NBR}}$	0.71	0.10	0.55	0.70	0.94	1.00	2587586
SD $\gamma_{y\ \text{ML}}$	0.25	0.23	0.01	0.19	0.82	1.00	62150
SD$\psi_{y\ \text{NBR}}$	0.68	0.10	0.50	0.67	0.90	1.00	20878
SD$\psi_{y\ \text{ML}}$	0.87	0.23	0.52	0.84	1.40	1.00	18483
BPV for N in NBR	0.50	0.50	0.00	1.00	1.00	1.00	29723260
BPV for N in ML	0.50	0.50	0.00	1.00	1.00	1.00	24253309
BPV for Count in NBR	0.45	0.50	0.00	0.00	1.00	1.00	12611316
BPV for Count in ML	0.50	0.50	0.00	1.00	1.00	1.00	21922408

Abundance-intercept is mean abundance in each water body, βseagrass is the effect of seagrass on abundance in each water body, βclarity is the effect of water clarity on detection, βpresent is the linear effect of days since start of summer on the availability for each water body, SD are the standard deviations of the random effects, and BPV are the Bayesian p-values (posterior predictive checks) calculated for 4 levels of the model.

Values give the mean, standard deviation (SD) and quantiles for the posterior distributions. Rhat values are the Gelman-Rubin convergence diagnostic, and Samples the estimated number of effective samples from the Markov chain Monte Carlo simulations.

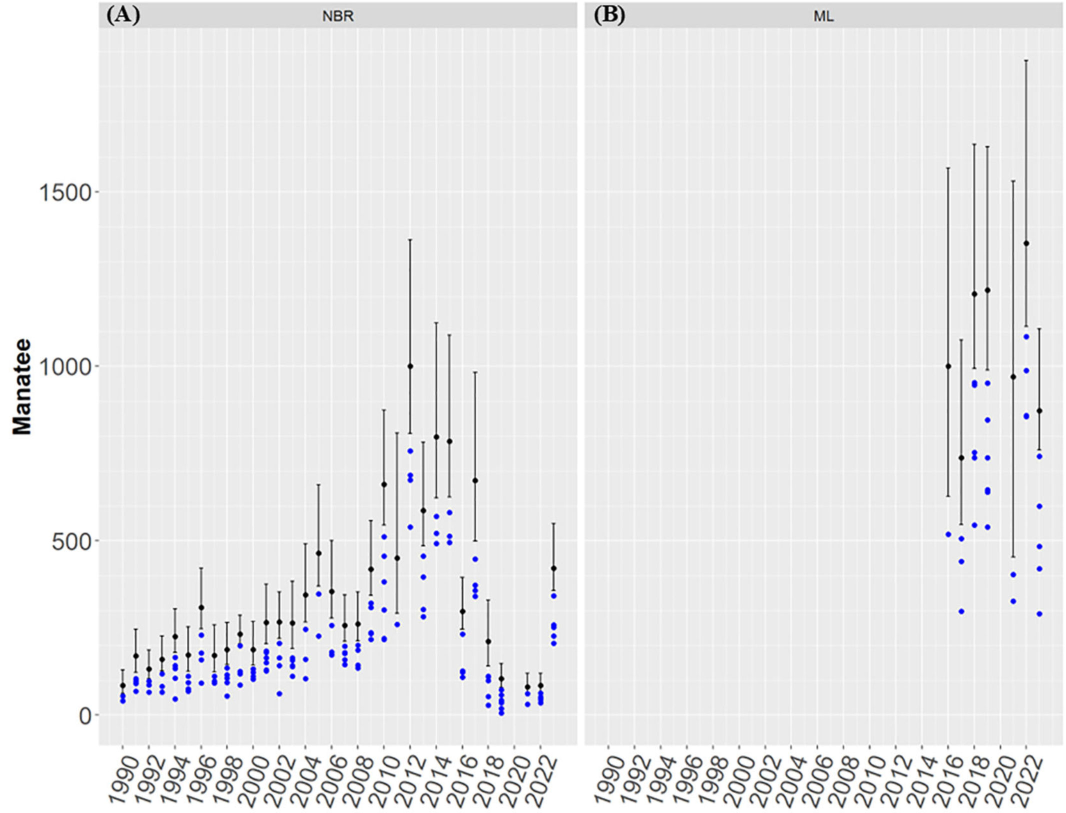

FIGURE 7
The predicted abundance of manatees with 95% credible intervals (black) in the **(A)** Northern Banana River (NBR) and **(B)** Mosquito Lagoon, from the Bayesian hierarchical model. The observed summer manatee counts are shown in blue.

in counts was just under 10% during Pre-Die-Off and Initial Die-off, but sharply declined during Secondary Die-Off and Post-Die-Off periods to under 3%. In ML the values declined from 5.7% during the Secondary Die-Off to 2.6% in Post Die-Off (Figure 12; Table 1).

Discussion

Factors influencing abundance

Long-term monitoring of long-lived animals is recognized as crucial for informing conservation and management (White, 2019). Our 34-year study quantified manatee abundance that varied across changing seagrass conditions. For almost 30 years, we regularly counted hundreds to a thousand animals within the NBR during spring and summer surveys prior to the seagrass die-off. These numbers represented some of the largest aggregations of manatees within the IRL system and were similar to winter aggregations at the nearby powerplant (Laist et al., 2013; Reynolds and Scolardi, 2016). During the die-offs, the NBR experienced a 95% loss of seagrass habitat. During this same period, manatee abundance initially increased despite decreasing seagrass cover and then manatee abundance dropped to historic lows. This pattern was likely driven by traditional site fidelity to the NBR as a spring aggregation area, and a search for forage, as seagrasses in nearly all other areas of the IRL except ML had already collapsed (Breininger et al., 2017; Morris et al., 2022).

While we did not perform regular manatee surveys in ML prior to the Initial Die-Off, our field observations and occasional aerial surveys by others indicated relatively low manatee numbers in ML (Martin et al., 2015; Reynolds and Scolardi, 2016), 2.8 per flight (Edwards and Ackerman, 2016) and only 28% of 57 tagged manatee visited ML and on average spent less than 4% of their time in ML (Deutsch and Barlas, 2016). After the Initial Die-Off, we found hundreds to a thousand manatees in ML despite this area previously having low numbers. The markedly large increase in manatee use of the ML, during the Secondary Die-Off, contrasted with the NBR numbers which dropped to historic lows. Ultimately, seagrass in ML recovered faster than other IRL basins, including the NBR, in part due to it being surrounded by conservation-managed natural areas. From this we can reasonably infer that individual manatees shifted their foraging distribution from NBR to ML.

Using a machine learning approach (BRT), we identified important factors explaining manatee counts, including Die-Off periods, season, water clarity, minimum air temperature, an increasing trend in the state's population, and changes in seagrass cover in Banana River Lagoon. The Die-Off period had the largest effect on manatee counts. The effects of season and temperature were consistent with seasonal movements between winter refugia and seagrass beds, patterns known to occur across the manatee range (Deutsch et al., 2003; Stith et al., 2006; Haase et al., 2023). The

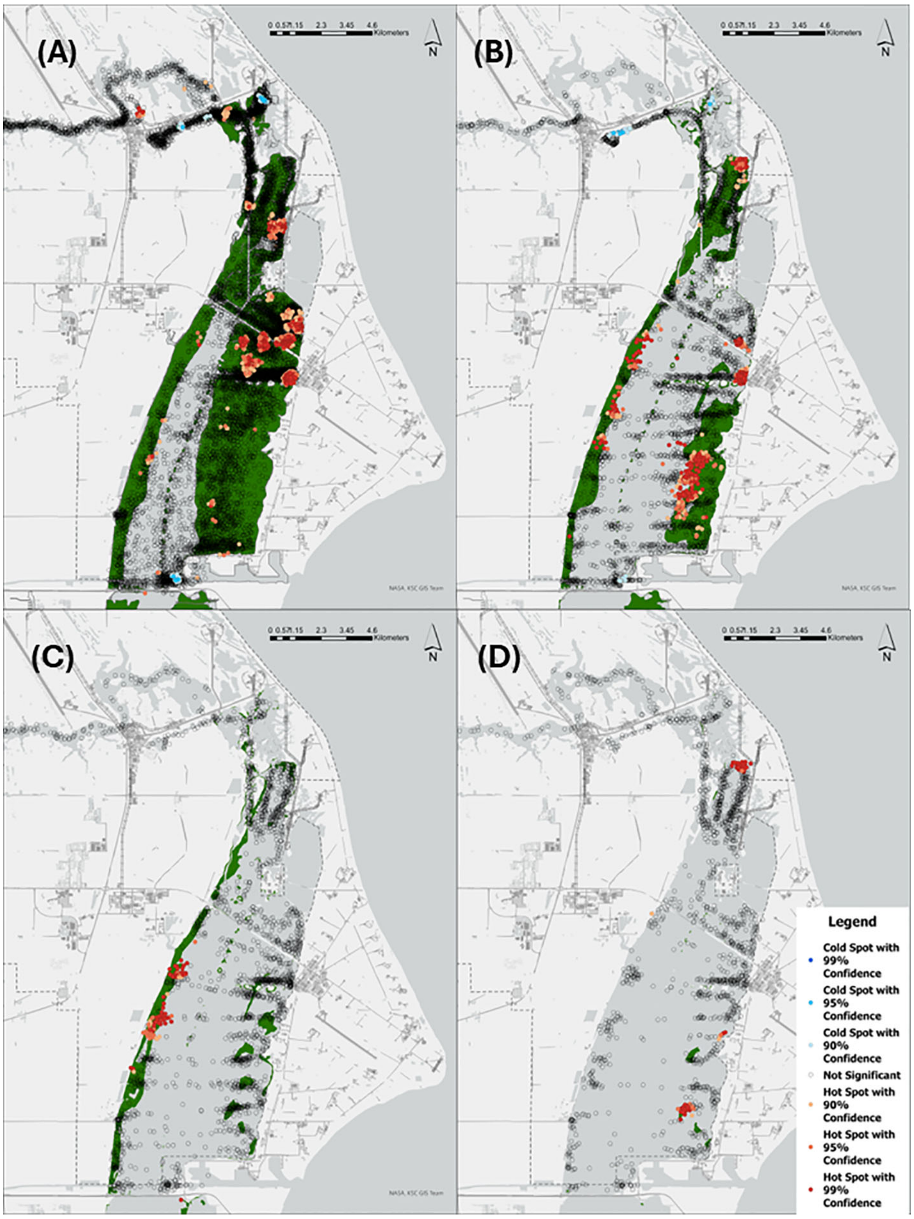

FIGURE 8
Optimized Hotspot Analysis of manatee distribution within the Northern Banana River comparing all sightings during Die-Off periods. **(A)** Pre-Die-Off (1990–2010), **(B)** Initial Die-Off (2011–2015), **(C)** Secondary Die-Off (2016–2022), **(D)** Post-Die-Off (2023–2024). Each circle represents a sighting location of a manatee. Red circles and blue circles indicate hot and cold spots respectively, with darker hues indicating higher confidence levels. Open black circle indicates non-significant sightings. Green coloration represents maximum mapped seagrass coverage during each period, Pre-Die-Off year = 2009, Initial Die-Off = 2015, Secondary Die-Off -2017 and Post-Die-off = 2023.

highest manatee counts typically were recorded in spring, coinciding with manatees departing winter ranges and thermal refugia, and the lowest counts were recorded in winter when animals move south or gather at thermal refugia. Manatees left KSC waters when air temperatures were below 10 °C, which was consistent with manatee intolerance to cold weather (Hardy et al., 2019). Decreased water clarity influenced counts partly because of decreased detection, especially during the peak bloom as murky water made manatees difficult to see. We note also that reduced light penetration caused by the bloom was determined to be a significant factor in the widespread seagrass die-off (Phlips et al., 2021; Morris et al., 2022). Seagrass cover was not very influential on counts until seagrass within the NBR was almost completely gone.

The hierarchical Bayesian summer abundance model refined our understanding of manatee use of the study areas by identifying factors that influenced the number of manatees using the system and those that influenced their availability and detection. It was important to account for factors that cause observation bias since unadjusted counts generally underestimate the size of populations (Martin et al., 2010; Williams et al., 2011; Hammond et al., 2021). The model confirmed our expectation that poor water clarity reduced detection (Martin et al., 2015). The increase in the

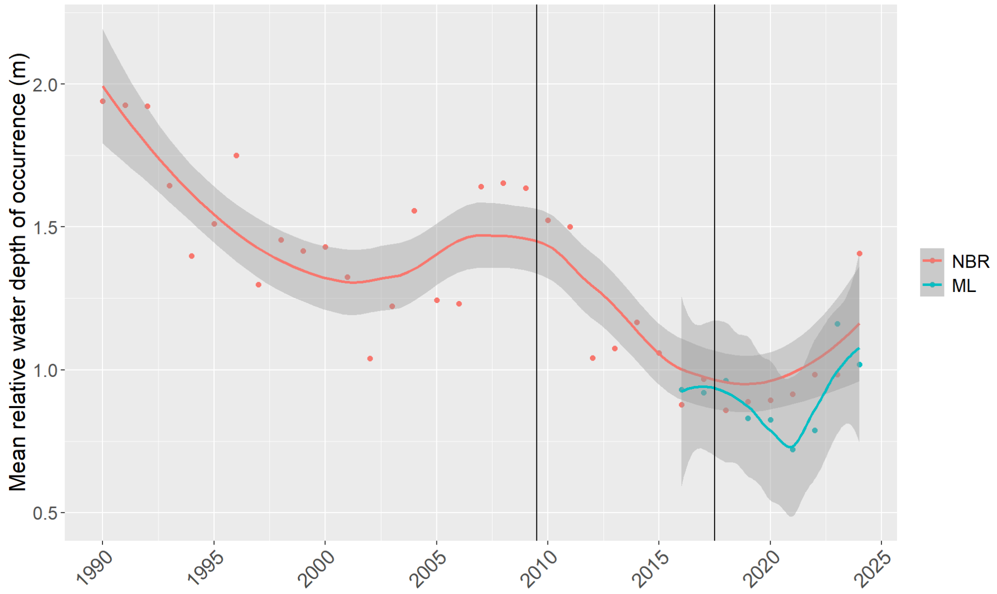

FIGURE 9
The annual mean relative depth of occurrence of all manatees observed in the Northern Banana River (NBR - Red) and Mosquito Lagoon (ML - Blue). Black vertical lines seagrass Die-Off.

fraction of individuals that were available for detection during summer surveys provides evidence that manatees used waterways beyond the study area. The increase in availability over the summer period may reflect a concentration of manatees within the high-quality seagrass of the NBR study area. Another factor may be that exclusion of boats provided better foraging conditions such as less disruption. Unexpectedly, the abundance model did not support a strong relationship between annual abundance and seagrass coverage. This could be due to a lag in effect, given that manatees traditionally returned to NBR where they reliably encountered abundant seagrass for decades and they possibly spent additional time foraging on remaining above and below ground biomass before abandoning the area (Provancha and Provancha, 1988, ProvanchaProvancha, 1989; Provancha and Hall, 1991; Deutsch et al., 2003). Manatee movements can respond asynchronously following environmental changes (Fonnesbeck et al., 2009; Langtimm, 2009). Increasing summer counts of manatees in the NBR over the first 25 years of the study mirrored a statewide increase in numbers during this period (Hostetler et al., 2018). Increased counts specifically within NBR also could have been

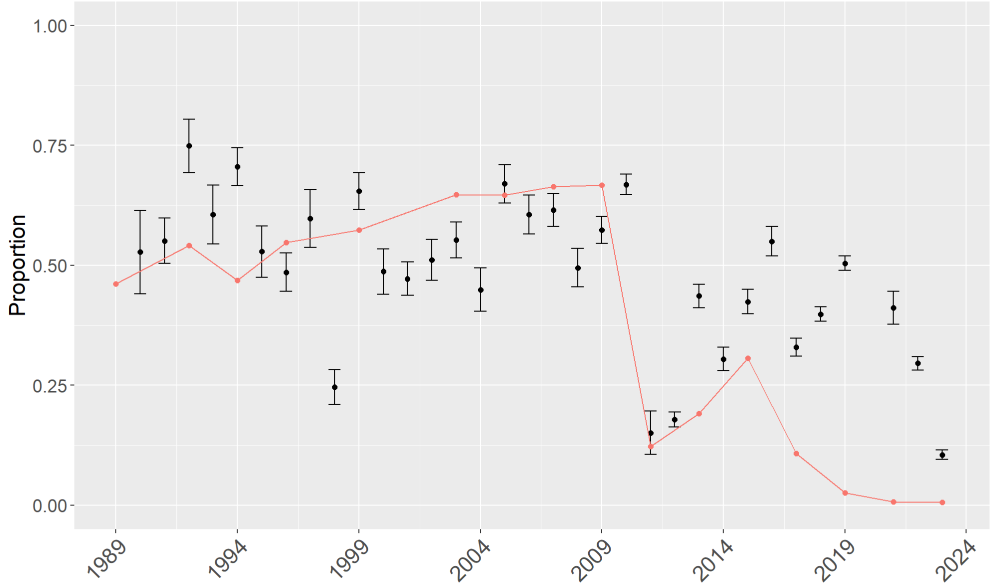

FIGURE 10
The mean annual proportion (with 95% confidence intervals) of manatees observed over seagrass in the Northern Banana River study area (black dots with bars) compared to the proportion of seagrass available (red dots and line) for each mapping year from St. John's River Water Management District, seagrass maps.

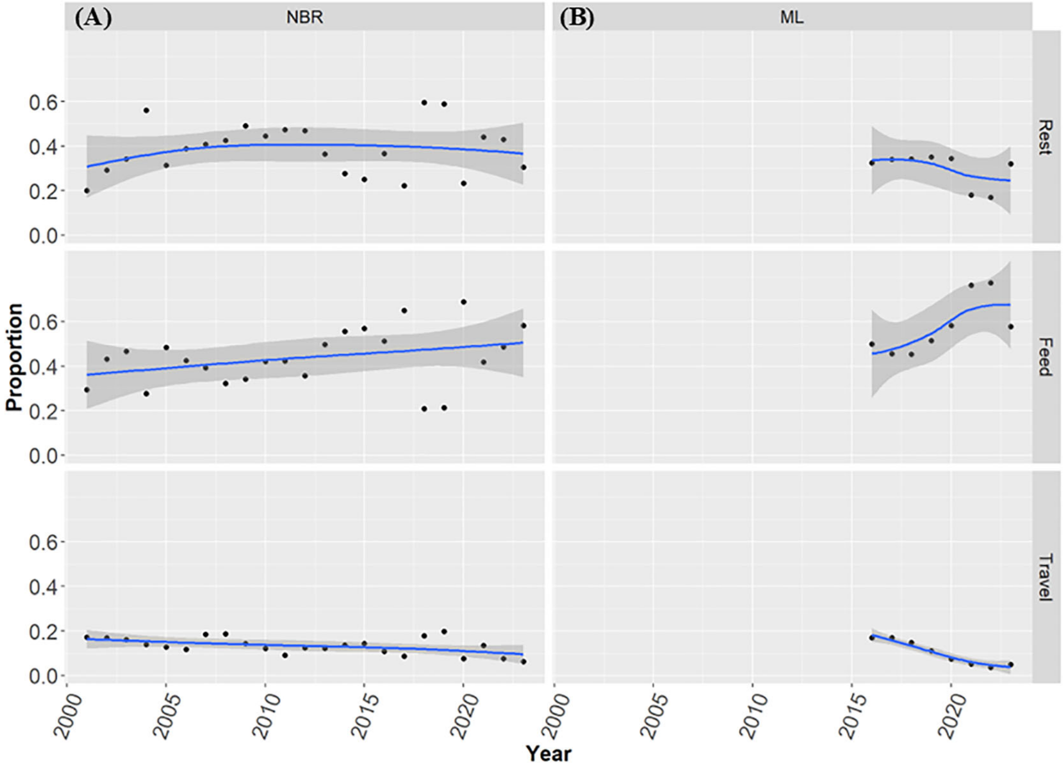

FIGURE 11
The proportion of adult behavior observed by year in **(A)** Northern Banana River 2000–2024 and **(B)** Mosquito Lagoon 2016-2024. Black dot actual values and blue line represents the smoothed estimate (loess locally weighted regression of degree 2) with shading to indicates a 95% confidence interval.

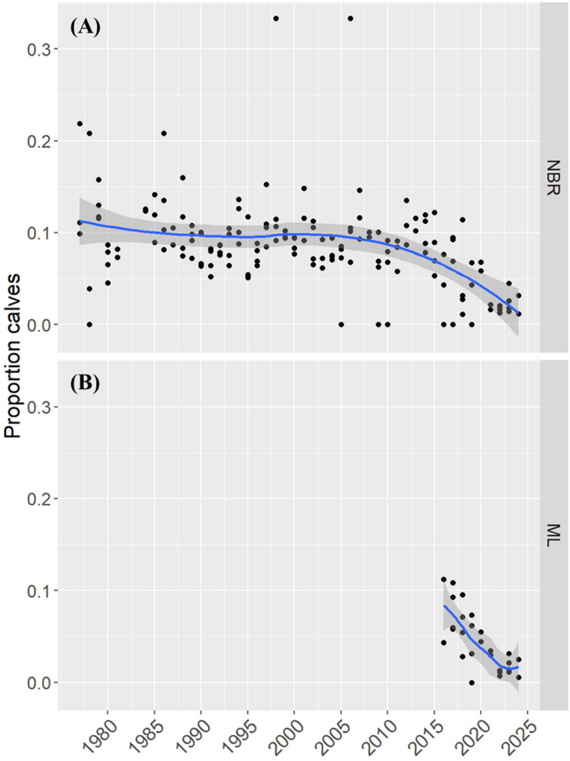

FIGURE 12
Mean annual proportion of calves observed during surveys for the **(A)** Northern Banana River (NBR) and **(B)** Mosquito Lagoon (ML) survey areas. The blue line represents the smoothed estimate (loess locally weighted regression of degree 2) with shading to indicate a 95% confidence interval.

driven by increasing human disturbance and boat use outside of the sanctuary. Given the appropriate data, the abundance model could be used to investigate how environmental factors influence population changes across many basins in the IRL with different food availability, distance to thermal refugia, boating activity, and sources of freshwater.

Local spatial variation, behavior, and calves

The location and intensity of hotspots differed between the periods. During the Pre-Die-Off, manatees were found resting in historically known hotspots along the edges of seagrass beds adjacent to deeper water (4–10 m), such as manmade dredge holes and boat channels (Provancha and Provancha, 1988). Manatees outside of aggregations were widely dispersed over seagrass areas and were feeding. After the Initial Die-Off period, manatees appeared to abandon these historical hotspots and spend more time foraging, being widely distributed over shallow areas, having a few small hotspots near the remnant seagrass beds that had receded shoreward (Morris et al., 2022). Accessing shallow areas requires significant energy and risk of exposure to boat traffic for these large animals; they were often seen with their entire dorsum out of the water.

The decrease in the proportion of calves after the Initial and Secondary Die-Offs was expected as the Unusual Mortality Event was associated with large-scale manatee starvation that was deemed an IRL-specific, episodic catastrophe within the species' range. Reduced reproductive output for large mammals is often a response to food stress (Ward et al., 2009; Harvey Sky et al., 2024). Calf production is thought to be dependent and correlated with adult survival. Calf survival is difficult to measure as calves do not accumulate the boat scars often used for individual recognition (Runge et al., 2017). Further study is required to determine if calf numbers rebound.

A hypothesis from population risk analyses (Runge et al., 2017) is that surviving animals will avoid areas that have insufficient food resulting in a long-term reduction in realized regional carrying capacity due to altered behavior (Provancha et al., 2012). Our most recent data suggests that manatees are returning to the NBR as seagrass rebounds, suggesting an ability to adapt to changing environmental conditions.

Summary and conclusions

Our long-term study confirmed that the NBR continued to have very large manatee aggregations, comparable to those in winter refugia, until a catastrophic algal bloom and seagrass die-off occurred across the IRL system. Recently, both seagrass cover and manatee numbers have been increasing in the NBR, suggesting that this basin might return to being an important hub within the IRL due to its proximity to winter refugia, protection from boating disturbance, and usually abundant seagrass. Our data showed that large numbers of manatees eventually moved to ML during the Initial Die-Off. The importance of ML may continue given that algal blooms are increasing in the IRL, indicating the need to regularly update conservation measures as environmental conditions are rarely static. Additionally, the continued aerial monitoring of the Banana River and surrounding waters is especially important to identify key habitats and emerging threats to manatees. This study exemplifies the importance of long-term monitoring for trends in abundance to compare to environmental conditions or episodic environmental stressors such as persistent algal blooms and seagrass die-offs.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

DS: Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Supervision, Writing – original draft, Writing – review & editing, Validation, Methodology. JP: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. ES: Data curation, Formal analysis, Methodology, Validation, Writing – original draft, Writing – review & editing, Conceptualization. DB: Formal analysis, Validation, Writing – original draft, Writing – review & editing, Conceptualization. RC: Data curation, Investigation, Software, Validation, Writing – original draft, Writing – review & editing. RL: Data curation, Investigation, Validation, Writing – review & editing. ER: Investigation, Validation, Writing – review & editing. BA: Investigation, Validation, Writing – review & editing.

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Conflict of interest

Authors DS, JP, ES, DB, RC, RL, ER, and BA were employed by the company Herndon Solutions Group, LLC.

The authors ES, DB declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

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SUPPLEMENTARY FIGURE 1

Number of manatees observed by individual flight during surveys of the KSC portions of the Northern Banana River (NBR - Blue) and Mosquito Lagoon (ML – orange) from 2016 to 2024.

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