



Habitat selection and abundance of West Indian manatees *Trichechus manatus* at the margins of their expanding range

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ABSTRACT: Habitat selection and abundances at range margins during geographic expansion may influence movement into new areas, shaping the trajectory of climate-driven changes in species distribution. The West Indian manatee is an ideal species to study how habitat selection influences range expansion because its presence has rapidly increased during the past 2 decades in the northern Gulf of Mexico (nGoM), a region outside its historical range. We estimated the habitat selection and abundances of manatees in coastal Alabama waters along the nGoM coast using resource selection functions and N-mixture models, respectively. Warm season (May–Nov) manatee abundances were estimated at 25 and 34 manatees at any given time in coastal Alabama waters in 2010 and 2019, respectively. Manatees primarily used the Mobile-Tensaw River Delta and Dog River areas, selecting nearshore shallow water habitats proximate to submerged aquatic vegetation. Distance to boat ramps and human population density had stronger effects on opportunistic sighting data but remained important for tagged data, indicating that manatee habitat selection overlapped with humans. Temperature strongly predicted manatee sightings; most sightings occurred when temperatures were >20°C. Our data indicate that the key interacting factors likely to moderate manatee range expansion, and therefore be important to management and conservation of this species, include increased sea temperature, availability of nearshore habitat with submerged aquatic vegetation, and regional manatee population dynamics. As environmental conditions at the range margins continue to become more favorable to manatees and areas within the range core decline in quality, areas at the range margins may become increasingly important.

KEY WORDS: Climate change · Habitat selection · Range shift · Tropicalization · Biotelemetry · Citizen science data · N-mixture models · Northern Gulf of Mexico

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1. INTRODUCTION

A primary way populations cope with climate and other environmental changes is through shifting their geographic ranges to new, typically adjacent, areas that support their environmental requirements (Thomas 2010, Travis et al. 2013). Populations at the

margins of their geographic ranges are well positioned to respond in this way because range shifts and expansions most frequently occur through dispersal or seasonal migrations to previously less favorable regions (Thomas 2010, Travis et al. 2013, Bright Ross et al. 2021, Cloyed et al. 2021b). These geographic range shifts are often driven by climate change and

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other anthropogenic factors that lead to altered habitat quality and availability (Mac Nally et al. 2009, Johnston & Caretti 2017). For example, many species ranges have shifted to higher latitudes or altitudes in the past several decades as they track favorable habitats and environmental conditions that are changing with the climate (Thomas 2010, Bright Ross et al. 2021, Cloyed et al. 2021b). As species shift into new ranges, their abundances in these areas are expected to increase through time until they reach the carrying capacity of that habitat, causing changes in intra- and interspecific interactions that can alter habitat selection, i.e. preferential selection of certain habitats over others, during the process of range expansion (Svenning et al. 2014). Quantifying the habitat selection and abundance of populations that are actively expanding their range will be essential for understanding range expansions driven by climate change and other environmental disturbances.

Habitat selection outside historical ranges will contribute to the dynamics and direction of climate-driven range expansions (Saura et al. 2014, Sullivan & Franco 2018, Platts et al. 2019). Selection of preferred habitats can act as steppingstones into new ranges (Saura et al. 2014, Laforge et al. 2016, Platts et al. 2019) as individuals explore and use new habitat patches that meet some of their environmental needs at or just beyond the range margins (Laforge et al. 2016, Lancaster 2020). Although habitat selection in newly occupied areas will likely be similar to historical regions, climate change will likely reshuffle ecological communities in non-analogous ways compared to historical communities (Williams & Jackson 2007, Williams et al. 2007). Populations may need to adapt to new conditions, whether relating to the thermal environment, resource availability, community structure, or their niche dynamics, as they undergo range expansion (Sullivan & Franco 2018, Cloyed et al. 2019a, Lancaster 2020, Martin et al. 2021). For example, populations may vary their niche breadth at expansion fronts (Hill et al. 1999, Oliver et al. 2009, Myles-Gonzalez et al. 2015, Walsh & Tucker 2020, Martin et al. 2021). In some circumstances, populations with wider niches (i.e. more generalist) may do better at range margins because they are more likely to use novel habitats and resources (Myles-Gonzalez et al. 2015, Walsh & Tucker 2020, Martin et al. 2021). In other circumstances, populations with narrower niches (i.e. more specialist) may better exploit minimally available resources (Hill et al. 1999, Oliver et al. 2009), a scenario that could be common at range margins. These niche dynamics at expansion fronts can aid or possibly hinder range expansion and affect

how different species will respond to climate change and other local perturbations that may affect populations at the margins of their range.

The West Indian manatee *Trichechus manatus* (hereafter manatee) is an ideal species to investigate habitat use at the margin of its range. Manatees are a tropical and subtropical species whose core population in the USA is in peninsular Florida (Runge et al. 2017). During previous geologic eras when climates were warmer, manatee range extended farther north than it is currently (Williams & Domning 2004, Domning 2005). While manatee sightings outside of peninsular Florida were rarely historically reported (Gunter 1941, Powell & Rathbun 1984), manatee sightings outside of Florida have rapidly increased during the last 2 decades and correspond with favorable seasonal water temperatures (Fertl et al. 2005, Pabody et al. 2009, Cummings et al. 2014, Hieb et al. 2017). While some manatees annually migrate long distances from refuge sites to warm season habitats (Deutsch et al. 2003, Cloyed et al. 2021b), they cannot tolerate temperatures $<20^{\circ}\text{C}$ and are typically constrained to warm water refugia in peninsular Florida during winter (Irvine 1983, Bossart et al. 2003). Today, manatees are routinely documented in the northern Gulf of Mexico (nGOM) between Apalachicola, Florida, and Lake Pontchartrain, Louisiana, generally arriving in the nGOM between April and June as water temperatures rise and returning to peninsular Florida between September and November to overwinter (Hieb et al. 2017, Cloyed et al. 2021b). Under current climate change scenarios, environmental conditions, particularly sea surface temperature, in the nGOM are potentially becoming more favorable for manatees (Fodrie & Heck 2011). These changes in the nGOM are occurring concomitantly with changes in manatee abundances and resources at the core of their range, including an unusual mortality event for manatees on the east coast of Florida, ongoing during the writing of this manuscript in 2021 (Hostetler et al. 2018, Lapointe et al. 2020). The complex situation in which climate change makes peripheral habitats like the nGOM more favorable while ecological dynamics in peninsular Florida are becoming less favorable (Runge et al. 2017, Littles et al. 2019) may lead to more individuals using habitat at the margins of their range (Cloyed et al. 2021b).

We examined the abundance and habitat selection of manatees in and around Mobile Bay, Alabama, a known migratory endpoint for manatees at the periphery of their range in the nGOM (Cloyed et al. 2021b). We estimated abundance seasonally and

through time using data from aerial surveys flown in 2010 and 2019–2020. We used resource selection functions (RSFs) to define habitat selection by tagged and sighted manatees using GPS telemetry and a citizen-sourced sighting database, respectively. To determine annual patterns of when manatees use coastal Alabama waters, we analyzed how season and air temperature affected the probability of manatee occurrence using the sighting database (Carmichael 2021). These are the first analyses to quantify manatee abundance and habitat selection in the USA outside of Florida. Results will provide an important baseline to compare habitat selection to other regions within the core (i.e. peninsular Florida and the Caribbean) and margins (i.e. nGOM, central Atlantic coast, USA) of the species' range to determine how selection may change in the nGOM as manatee density increases and the region becomes increasingly suitable for manatees and similar tropical or subtropical species.

2. MATERIALS AND METHODS

2.1. Study site

Mobile Bay, Alabama, is a freshwater-dominated estuary influenced by the Mobile-Tensaw Delta, the third largest freshwater discharge among watersheds in the USA (US Census Bureau 2012b). This freshwater discharge and the associated salinity gradient create a complex network of submerged aquatic vegetation (SAV) communities, including seagrasses and other SAV such as *Eichhornia crassipes*, *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Ceratophyllum demersum*, that manatees feed on in other parts of their range (Fertl et al. 2005, Reich & Worthy 2006, Alves-Stanley et al. 2010). In addition to these SAV communities, Mobile Bay has extensive *Spartina alterniflora* marshes, oyster shell deposits, and shallow non-vegetated bottoms. Mobile Bay has a subtropical climate with average minimum and maximum temperatures during January (~10°C) and July (~28°C), respectively, and ~160 d with minimum temperatures >20°C (National Data Buoy Center 1971). Additionally, Mobile Bay and the surrounding waters along the Alabama coast have considerable ship traffic because the city of Mobile is a major port, and the Intracoastal Waterway runs east–west through the southern portion of the bay. Manatees are known to use these ship channels during migration and when moving among habitats (Cloyed et al. 2019b).

2.2. Manatee abundance data

We flew aerial surveys between June and November 2010, as part of the National Resource Damage Assessment (NRDA) following the *Deepwater Horizon* oil spill, and in 2019 (Mar, May, Jul, Sep) and 2020 (Jan). The 2010 surveys were flown in Sikorsky S-76 helicopters at an altitude of 180 to 220 m and airspeed of ~160 km h⁻¹, while 2019–2020 surveys were flown using a Cessna 172 or 182 single-engine aircraft flown at an altitude of ~150 to 229 m and airspeed of ~130 to 185 km h⁻¹. Differences in detection between the aircraft types are unknown for this study but are expected to be minimized by the combination of the helicopter potentially being louder but also having a greater range of visibility, normalizing directional effects on detection relative to the fixed-wing aircraft. Both types of aircraft have been widely used for manatee surveys in the past, and the effect of aircraft type was found to be negligible, particularly in low-density areas (Rathbun 1988, Lefebvre & Kochman 1991, Morales-Vela et al. 2000). All surveys followed the coastline of Mobile Bay and major rivers and subembayments in surrounding coastal Alabama waters (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m696p151_supp.pdf). Two observers conducted each survey to increase the accuracy of observations. Start and end times and GPS track lines were recorded for each survey along with general weather and sighting conditions for survey areas (Miller et al. 1998). For each manatee sighting, observers recorded GPS location, number of calves and adults, manatee behavior and direction of travel (when possible), air temperature, wind speed and direction, and sea state (Beaufort scale). Our aerial surveys followed the same methods as those used in the state of Florida to perform abundance estimates, making our data comparable to well-established methods of manatee abundance estimates (Martin et al. 2015, Hostetler et al. 2018).

2.3. Manatee location data

2.3.1. Telemetry data

We collected manatee movement data via GPS satellite telemetry using established methods for capturing and tagging manatees (Bonde et al. 2012). As previously described in Cloyed et al. (2019), we captured 10 manatees during 4 health assessments in September 2009, August 2010, August 2012, and September 2014 (Table S1). Manatees were located

via an aerial observer, captured in a net deployed from a specialized boat, and brought aboard the boat to undergo a veterinary health assessment before being outfitted with a floating tow-behind tagging platform (Telonics; Bonde et al. 2012). Each tag was attached to the peduncle with a belt and tether following standard tagging procedures for manatees (Deutsch et al. 1998, Weigle et al. 2001). Each tagged manatee was released where it was captured, typically within 1 h. Tags were designed to break if they became entangled, and when possible, lost tags were reattached opportunistically at a later date by snorkeling or during a subsequent capture event. Tags were removed and replaced at the end of their battery life. We programmed tags to record GPS locations every 15 or 30 min, and locations were downloaded following tag recovery, which was high (98% recovery rate) because manatees use shallow coastal systems and lost tags were easily located.

Continuous tagging duration ranged from 2 wk to 13 mo, and non-continuous tagging (i.e. an individual tagged more than once) duration ranged from 4 to 22 mo. We monitored manatee locations using Argos services and conducted focal observations of tagged manatees ~1 to 3 times per 2 wk (Deutsch et al. 1998, Weigle et al. 2001). Data were directly downloaded from the tagging platform and included standard GPS locations or quick-fix pseudorange positions accurate within 10 or 75 m, respectively. Location data were plotted in ArcMap 10.3 to verify accuracy, and locations on land were removed (0.00006%). All work with live manatees was performed under US Fish and Wildlife Service permits MA107933-1 and MA37808A-0; Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries, annual permits; and University of South Alabama IACUC protocols 581568 and 1038636.

2.3.2. Sighting data

We used manatee locations from sighting data reported to the Dauphin Island Sea Lab's Manatee Sighting Network (DISL/MSN), a citizen science program in the nGOM (Pabody et al. 2009). Sightings were compiled from opportunistic citizen science reports and targeted research efforts. Opportunistic publicly reported sightings were collected during 2007 to 2020 as previously described (Pabody et al. 2009, Hieb et al. 2017) and included, at a minimum, the date, location, and number of manatees per sighting. Reported sightings that did not provide location infor-

mation were excluded from the dataset. Duplicate sightings, which we defined as occurring when multiple observers reported the same number of manatees at the same location, date, and time (within 30 min), were also removed from the dataset.

2.4. Environmental data

To link animal locations to habitat attributes, we used a base map of the study site for animal location and habitat selection analyses from a high-resolution vector of the study area in the UTM zone 16N projection. This dataset was created by combining digitized recent aerial photography of coastal Alabama waterbodies (<https://maps.cityofmobile.org/GIS/DownloadData.html>), the National Hydrography Dataset (<https://pubs.er.usgs.gov/publication/fs10699>), and a high-resolution orthoimagery (<https://www.usgs.gov/search?keywords=High%20Resolution%20Orthoimagery>). To determine which habitat attributes were most important to manatees, we extracted the following environmental and habitat attribute data: distance to nearest SAV patch (d.SAV; m), size of nearest SAV patch (s.SAV; m²), distance to land (d.land; m), proportion of land within a 1 km radius (p.land), water depth (depth; m), distance to boat ramp (d.boat; m), and population density (p.den; people km⁻²). We included d.SAV and s.SAV because aquatic vegetation is the primary dietary resource for manatees in the nGOM. Locations and sizes of SAV patches were obtained from the literature (Fig. S2) (https://www.mobilebaynep.com/images/uploads/library/SAV_2016.pdf). We included d.land and depth because manatees in peninsular Florida frequently use shallow waters (<3 m) close to the shoreline (Weigle et al. 2001, Flamm et al. 2005, Ross 2007, Littles et al. 2019). Shoreline locations and depths were obtained from NOAA's National Geophysical Data Center coastal digital elevation models for Mobile Bay and Pascagoula (Fig. S2) (Taylor et al. 2008, Amante et al. 2011). As manatees frequently use inshore waters, including creeks and rivers, we estimated the proportion of land within a 1 km radius to determine how much manatees use these types of habitats. The proportion of land within a 1 km radius was measured in QGIS by creating a 1 km buffer around each tagged or sighted manatee location and calculating the proportion of the buffer that overlapped with land. Values for p.land that were closer to 1 represent rivers and inlets that are primarily surrounded by land, values around 0.5 represent coastal areas that are ~50% surrounded by land, and values closer to 0

represent open water. Finally, we included d.boat and p.den to estimate how much manatee habitat selection overlaps with human use and determine how human activities might affect reported manatee locations in the sighting dataset. The population density of census blocks for Mobile and Baldwin counties in Alabama were obtained from the 2010 census (US Census Bureau 2012a). Distances to land (d.land), SAV (d.SAV), and boat ramps (d.boat) were calculated and rasterized in QGIS.

2.5. Statistical analyses

2.5.1. Abundance estimates

We used binomial mixture models to estimate abundances from aerial surveys (Royle 2004, Martin et al. 2011). Specifically, we used a beta-binomial mixture model created for use with manatee aerial survey data that incorporates a beta distribution, allowing for correlation among sightings, because manatees may occur in groups (see Martin et al. 2011 for greater detail). Briefly, the number of individuals per site, i , was assumed to follow a Poisson distribution, with the probability of detecting a manatee following a binomial distribution (Martin et al. 2011). We used a goodness-of-fit test to assess the fit of these models, where values near 0.5 suggest good fit and values closer to 1 or 0 suggest poor fit (Martin et al. 2011). Our study region was divided into 6 sites for the abundance estimates: delta (all waters north of the open bay), north bay, south bay, west rivers (all rivers that feed into the western side of Mobile Bay), east rivers (all rivers, including the Intracoastal Waterway that feed into the eastern side of Mobile Bay), and Perdido Bay (including the waters around Orange Beach and Gulf Shores) (see Fig. 1). We included the log water area of each site as an offset in the model to account for the variation in size of each site (Martin et al. 2011). We treated each survey flown throughout each season, warm (May–Nov) and cold (Dec–April), as independent observations. This approach assumes that the abundance of manatees remains constant throughout the survey period. Manatees move into and out of the area to other sites, particularly as they seasonally migrate to the Florida peninsula (Cloyed et al. 2021b), and it is likely that the abundance of manatees increases through the summer before decreasing during the fall as manatees migrate back to Florida. Our statistical analysis should capture this variation, and abundances

throughout the season should fall within this estimated range. Our results should therefore be interpreted as the abundance of manatees at any given point in time during the season. We used these models to estimate total abundances, average abundance per site, detection probability, and correlation of sightings, which is a measure of dependence among sightings (Martin et al. 2011), for each year and for the warm season in 2010 and 2019. This approach resulted in 42 and 38 replicates for all of 2010 and the warm season in 2010, respectively, and 10 and 6 replicates for all of 2019 and the warm season in 2019–2020, respectively.

2.5.2. Utilization distributions

To determine the home and core ranges of manatees in coastal Alabama waters, we calculated the 95% (home range) and 50% (core range) utilization distributions (UDs) for both tagged and sighted manatees using kernel density estimates (Fieberg 2007, Kie et al. 2010). These resulting UD's represent where 95 and 50% of manatee locations occurred in coastal Alabama waters (sightings and tag locations outside this area were not considered in the UD's). Output grid cells were 1 km² to allow for fine-scale spatial resolution of the tagged dataset. We calculated appropriate bandwidths, or smoothing parameters, using a rule-based ad hoc method (Kie 2013). All UD's were calculated and mapped using QGIS.

2.5.3. RSFs

To quantify habitat selection, we used RSFs, which employed a use–availability framework (Boyce & McDonald 1999, Keating & Cherry 2004). For the use–availability framework, we combined locations used by manatees in the tagged and sighted datasets with availability data by selecting random point locations within the study site (i.e. unused) (Boyce & McDonald 1999, Keating & Cherry 2004). Each location was treated as a Bernoulli trial (used and unused), such that the RSF represents the probability that a manatee would use a particular location and associated habitat attributes (Boyce & McDonald 1999, Keating & Cherry 2004). We used a binomial logistic generalized linear model with a logit link function, $\text{logit}(\gamma_{i,d})$, where γ is the observed binary response by manatee i on Julian Day d for tagged manatees, and $\text{logit}(\gamma_{j,k})$, where γ is the observed binary response for sighting

j in year k . For the tagged dataset, to account for variation among individuals, we included a random effect for individual manatees and nested Julian Day by individual (Gillies et al. 2006). For the sighted manatee dataset, we included year as a continuous random effect because the number of sightings increased through time (Gillies et al. 2006). For modeling both the tagged and the sighted datasets, we included the following habitat variables in the global model: d.SAV (m), s.SAV (m²), d.land (m), p.land, depth (m), d.boat (m), and p.den (people km⁻²). We checked for collinearity among variables using the variance inflation factor (VIF) in the car package in R (Fox & Weisberg 2019). VIF values <5 indicate no collinearity among variables (Zuur 2009).

For each dataset, we started with a global model that included all habitat attribute variables and used Akaike's information criterion (AIC) for model selection, where lower AIC values indicate better-fitting models (Burnham et al. 2011, Symonds & Moussalli 2011). Beginning with the global model, we removed habitat attribute variables one at a time, and if the resulting model AIC value was greater than the previous model, the variable was replaced in subsequent models (Burnham et al. 2011, Symonds & Moussalli 2011). When the resulting AIC value was less than the previous model, the variable was not replaced in subsequent models (Burnham et al. 2011, Symonds & Moussalli 2011). To measure the relative strength of each model, we calculated normalized Akaike weights, w_i , for each model i , where:

$$w_i = \frac{e^{-0.5 \times \Delta AIC_i}}{\sum_r e^{-0.5 \times \Delta AIC_i}} \quad (1)$$

provides a probability that the given model is the best-fitting model: $w > 0.9$ indicates strong model support over others, and $w > 0.1$ indicates some model support and should be considered in the analysis (Burnham et al. 2011, Symonds & Moussalli 2011).

We validated the predictive performance of our models in 2 ways. First, we used areas under the curve (AUCs) for the receiver operating characteristic (ROC) and precision–recall (PR) curves for the best-fitting models (Boyce et al. 2002). ROC AUC values >0.7 and <0.9 are considered to have useful predictive capacity, and AUC values >0.9 are considered to have high predictive capacity (Boyce et al. 2002). We include the AUC of the PR curve to accommodate manatee locations within very localized areas of the study site; the PR curve often handles rare or localized data better than the ROC curve, and higher values suggest better predictive capacity (Sofaer et al. 2019). Second, we used 5-fold cross-validation,

where the study area was divided into 144 blocks, each measuring 2.905 km², which was determined based on the spatial autocorrelation of the environmental covariates using `spatialAutoRange()` in the R package `blockCV` (Valavi et al. 2019). We iteratively tested the RSFs by withholding 1 fold (20% of the data) and testing the remaining 4. We then compared the AUC for both the ROC and the PR curves for all 5 models from the tagged and sighted datasets.

2.5.4. Temperature modeling

To understand how temperature drives manatee presence in coastal Alabama waters, we obtained daily mean air temperature (°C) data from 2008 to 2019 from the National Data Buoy Center, Stn DPIA1, located at Dauphin Island, Alabama (https://www.ndbc.noaa.gov/station_page.php?station=dpia1). In this analysis, we used only data from sighted manatees because we have a greater temporal scope for sighted manatees compared to data from tagged manatees, allowing the analysis of year-round trends. We recorded manatee presence if a manatee was sighted and reported to DISL/MSN anywhere within coastal Alabama waters, and each day of the year ($n = 365$) was treated as a Bernoulli trial in which manatees were or were not sighted. To quantify the probability of a manatee sighting depending on season and temperature, we divided the year into 4 seasons: winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and autumn (Sep–Nov). We used 4 seasons in this analysis compared to the warm and cold season for abundance because we have considerably more sighting data than aerial survey data and can therefore examine the sighting data at a finer temporal resolution. To examine the relationship between the probability of sightings and temperature, we used a binomial generalized linear model with a logit link. All statistical analyses were performed in R version 4.0.4 (R Core Team 2020).

3. RESULTS

3.1. Manatee abundance

Manatee abundances, detection probabilities, and correlations among sightings were higher in 2019 than in 2010 (Table 1). There were 19 and 23 manatee sightings during aerial surveys in 2010 and 2019, respectively. The beta-binomial mixture models estimated total manatee abundances of 27

Table 1. Estimated manatee abundances (total N), average per site (shown in Fig. 1), detection estimates (p), correlation among sightings (ρ), and goodness-of-fit test estimated from an N-mixture beta-binomial model. Values in parentheses are 95 % credible intervals

Year	Season	Total N	Average per site	p	ρ	Fit
2010	All	26.63 (9.00, 42.00)	4.44 (1.50, 7.00)	0.02 (0.01, 0.06)	0.15 (0.01, 0.50)	0.56
	Warm	26.52 (9.00, 42.00)	4.42 (1.50, 7.00)	0.03 (0.01, 0.07)	0.14 (0.02, 0.50)	
2019	All	37.01 (17.00, 42.00)	6.17 (2.17, 7.00)	0.06 (0.02, 0.13)	0.53 (0.26, 0.80)	0.53
	Warm	35.70 (14.00, 42.00)	5.95 (2.17, 7.00)	0.11 (0.03, 0.23)	0.51 (0.23, 0.79)	

($\pm 95\%$ CIs 9.00–42.00) and 37 (17.00–42.00) for 2010 and 2019, respectively, with the majority of manatees (26 [9.57–42.00] and 35 [15.57–42.00]) estimated during the warm season (Table 1). Models for year-round and warm season data had good fits in both years (Table 1), with the average number of manatees per site ranging from 10 to 29 for year-round data and from 8 to 18 for warm season data (Table 1).

3.2. UDs

The core and home ranges of manatees were similar when estimated using tagged and sighted datasets (Fig. 1). The 50 % UDs of tagged and sighted manatees were in the Mobile-Tensaw River Delta, including 2 core areas in the southwestern and southeastern parts of the delta, and the Dog River system (Fig. 1). For sighted manatees, the 50 % UD additionally included a small area of Perdido Pass (Fig. 1B). The 95 % UDs for manatees included areas surrounding the 50 % UDs in the delta, the Dog River system, and some areas of Perdido Bay as well as additional areas in tributaries of Mobile Bay, along the northeastern shoreline of Mobile Bay, and in parts of Mississippi Sound (Fig. 1). The 95 % UDs for sighted manatees included additional areas in southern Mobile Bay and along the Gulf of Mexico coast (Fig. 1B).

3.3. RSFs

The best-fitting RSF for tagged manatees was the global model that included d.SAV, s.SAV, d.land,

p.land, depth, and d.boat, but the model that did not include p.den had a similar AIC weight (Figs. 2A & 3; Table S2). The 3 strongest predictors for resource selection in the tagged manatee dataset were, in order, d.SAV, d.land, and depth (Figs. 2A & 3; Table S2). Many tagged manatee locations were recorded inside or within 100 m of SAV patches (Fig. 3A, Fig. S2; Table S2), <1000 m from shore (Fig. 3C), and in shallow water (<5 m; Fig. 3G, Fig. S3; Table S2). Similar to d.SAV and d.land, tagged manatees were likely to select habitats closer to boat ramps (Figs. 2A & 3E; Table S2) and with a high proportion of land

within a 1 km radius (Figs. 2A & 3D; Table S2). The area under the ROC curve was 0.886, and the area under the PR curve was 0.981 (Fig. S4A), indicating that models are robust at inferring manatee habitat selection. The 5-fold cross-validation also revealed no major differences in the AUCs across the study site, and all AUC values were >0.90 (Fig. S5). The VIF for the best-fitting RSF on tagged manatees was <2.00 for all variables, indicating there were no issues with collinearity among variables.

The best-fitting RSF for sighted manatees was the global model that included d.SAV, s.SAV, d.land, p.land, depth, d.boat, and p.den (Figs. 2B & 4; Table S3). Unlike the RSF for tagged manatees, this model had an AIC weight >0.9, indicating strong support over all other models (Table S3). Most manatees were sighted near or at the shore (Figs. 2B & 4C; Table S3), near or within SAV patches (Figs. 2B & 4A,B, Fig. S2; Table S3), and in shallow water (Figs. 2B & 4G, Fig. S3; Table S3). Manatees were more likely to be sighted near a boat ramp (Figs. 2B & 4E; Table S3), and although a weaker effect than d.land and d.SAV, the effect was stronger compared to the tagged manatee dataset. Manatees were also more likely to be sighted near areas with higher human population densities (Figs. 2B & 4F; Table S3). The 3 strongest predictors for resource selection in the sighted manatee dataset were the same as the tagged dataset, but the order differed slightly: d.land, d.SAV, and depth (Figs. 2B & 4; Table S3). The VIF for the best-fitting RSF on sighted manatees was <2.50 for all variables, indicating there were no issues with collinearity among variables.

Other important factors contributed to the best-fitting RSF of sighted manatees. While both s.SAV and p.land were not significant predictors of resource

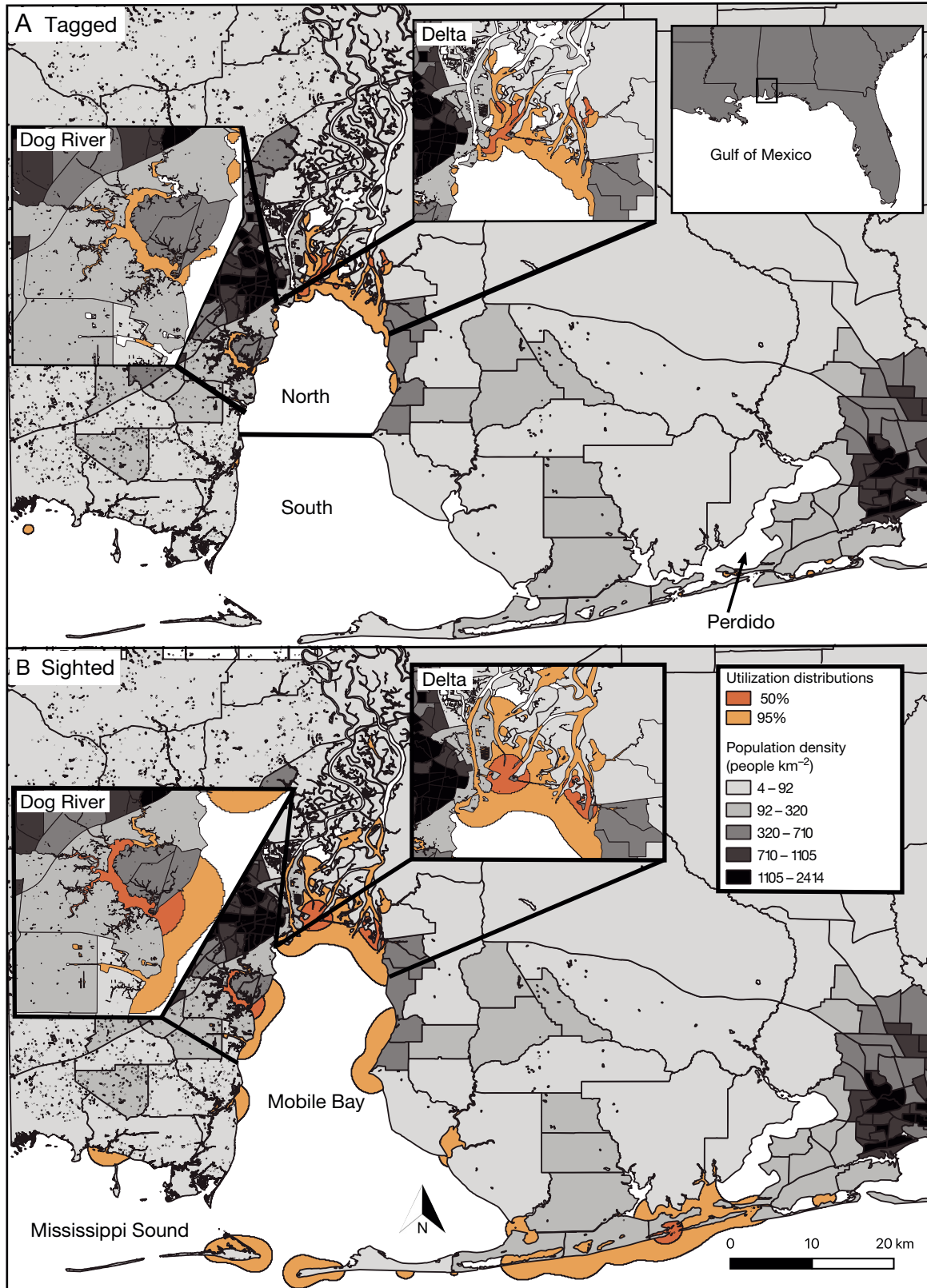


Fig. 1. Utilization distributions (95%, home range; 50%, core range) of (A) tagged and (B) sighted manatees, with enlarged views (insets) for the Mobile-Tensaw River Delta (delta) and Dog River. Population density for surrounding watersheds is shown for 2010 census blocks. The north, south, and Perdido Bay sites for the abundance estimates are labeled in (A); the delta is shown in the inset; the west rivers include all tributaries flowing into the western bay below the delta; and the east rivers include all tributaries flowing into the eastern bay, including the Intracoastal Waterway between Mobile and Perdido bays

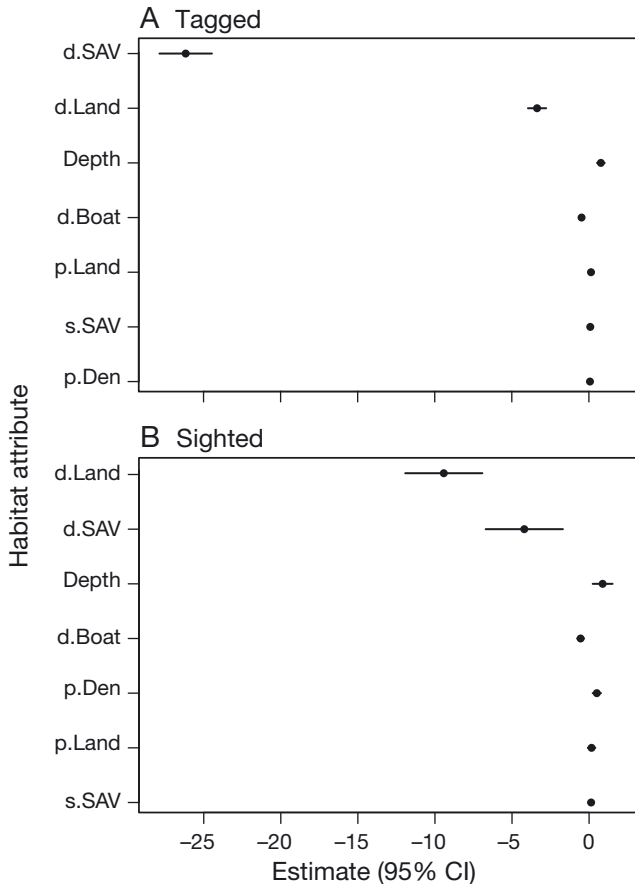


Fig. 2. Scaled coefficient estimates for the resource selection functions for (A) tagged and (B) sighted manatees. d.SAV: distance to submerged aquatic vegetation (SAV; m); s.SAV: size of nearest SAV patch (m^2); d.Land distance to shoreline (m); p.Land: proportion of land within a 1 km radius; Depth: water depth (m); p.Den: human population density of nearest census block (people km^{-2}); d.Boat: distance to boat ramp (m)

selection in the sighted dataset, they were both included in the best-fitting model, and in general, manatee sightings increased with the size of the nearest SAV patch and proportion of land within a 1 km radius (Figs. 2B & 4B,D; Table S4). The area under the ROC curve was 0.834, and the area under the PR curve was 0.908 (Fig. S4B), indicating that models are robust in inferring manatee habitat selection. The 5-fold cross-validation also revealed no major differences in the AUCs across the study site, and all AUC values were >0.75 and most were >0.85 (Fig. S6).

3.4. Temperature effects on sightings

Temperature had a strong and seasonally variable effect on the probability of sighting manatees in coastal Alabama waters (Fig. 5; Table 2). Manatees

were most likely to be sighted during summer when temperatures were high, but the probability of sightings did not change with temperature during the summer (Fig. 5; Table 2). The probability of manatee sightings decreased in autumn, and sightings decreased with temperature (Fig. 5). The probability of sightings was higher in autumn compared to similar temperatures during the spring (Fig. 5). When air temperatures rose above $\sim 20^\circ C$ during the spring, the probability of manatee sightings increased drastically (Fig. 5). Manatees were unlikely to be sighted during the winter, and temperature had little effect on the probability of sightings during that period (Fig. 5).

4. DISCUSSION

We estimated West Indian manatee abundance and habitat selection at the margins of their range in the USA for the first time. Although relatively small compared to the USA manatee population in the core range in Florida, the seasonal population of manatees in coastal Alabama waters may be growing. Our estimates of manatee abundance were slightly higher in 2019 than in 2010; however, the 95% CIs between the 2 years overlapped. We did not survey the center of Mobile Bay; therefore our estimates may be conservative, although our tagging and sighting data indicate manatees do not frequently use this area. Furthermore, many coastal Alabama waters are turbid, which may lead to an undercount in waters where visibility was low. However, areas with the most turbid waters include the delta and rivers on the western side of Mobile Bay, which are where the highest number of sightings occurred. This increase in manatee abundance between 2010 and 2019 in Alabama waters is consistent with the increased estimated abundances among core populations of Florida manatees in recent years (Martin et al. 2015, Hostetler et al. 2018). Our results are additionally supported by the increased opportunistic sightings in coastal Alabama waters during the previous several decades (Pabody et al. 2009, Hieb et al. 2017) and the overall trend that manatees in the USA are increasingly using habitats outside peninsular Florida (Fertl et al. 2005, Cummings et al. 2014, Hieb et al. 2017).

It is also possible, but less likely, that the higher abundance estimates in 2019 may be due to other non-mutually exclusive reasons. First, the 2010 aerial surveys were performed using helicopters as was protocol for the NRDA response. Fewer observations would be expected in 2010 if manatees avoided heli-

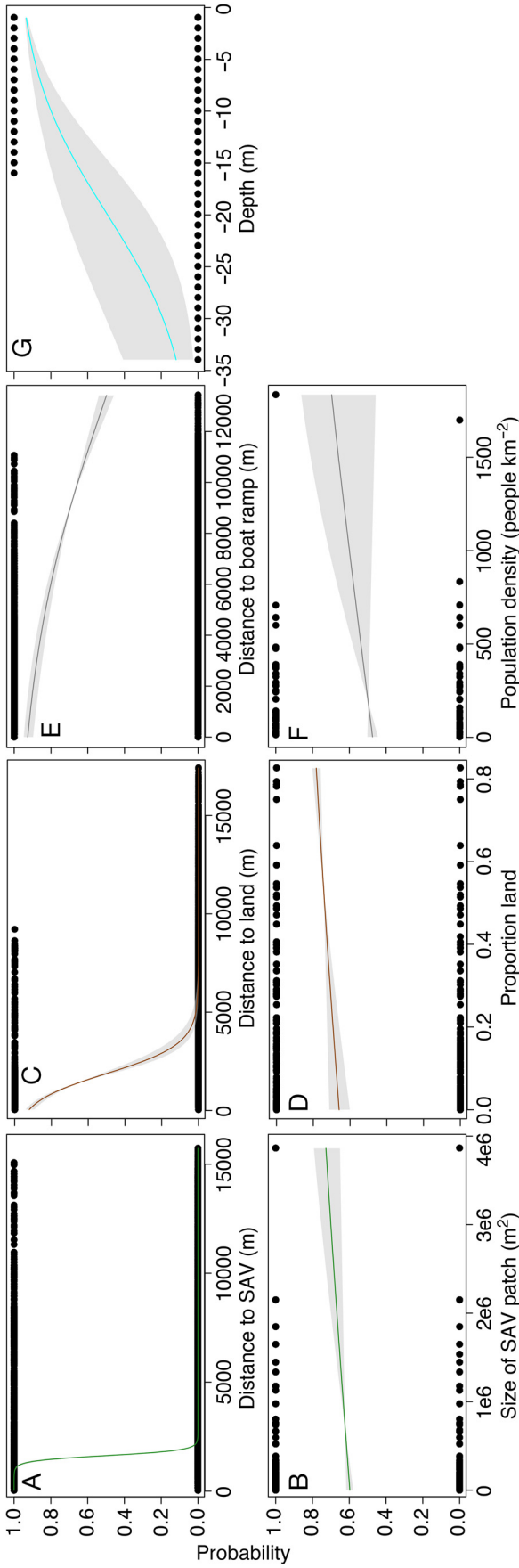


Fig. 3. Resource selection functions for tagged manatees. (A) Distance to nearest submerged aquatic vegetation (SAV) patch, (B) size of nearest SAV patch, (C) distance to land, (D) proportion of land within a 1 km radius, (E) distance to boat ramp, (F) human population density of nearest census block, and (G) water depth at manatee location. Grey shading depicts 95% confidence bands. Dots represent unused (○) and used (●) locations

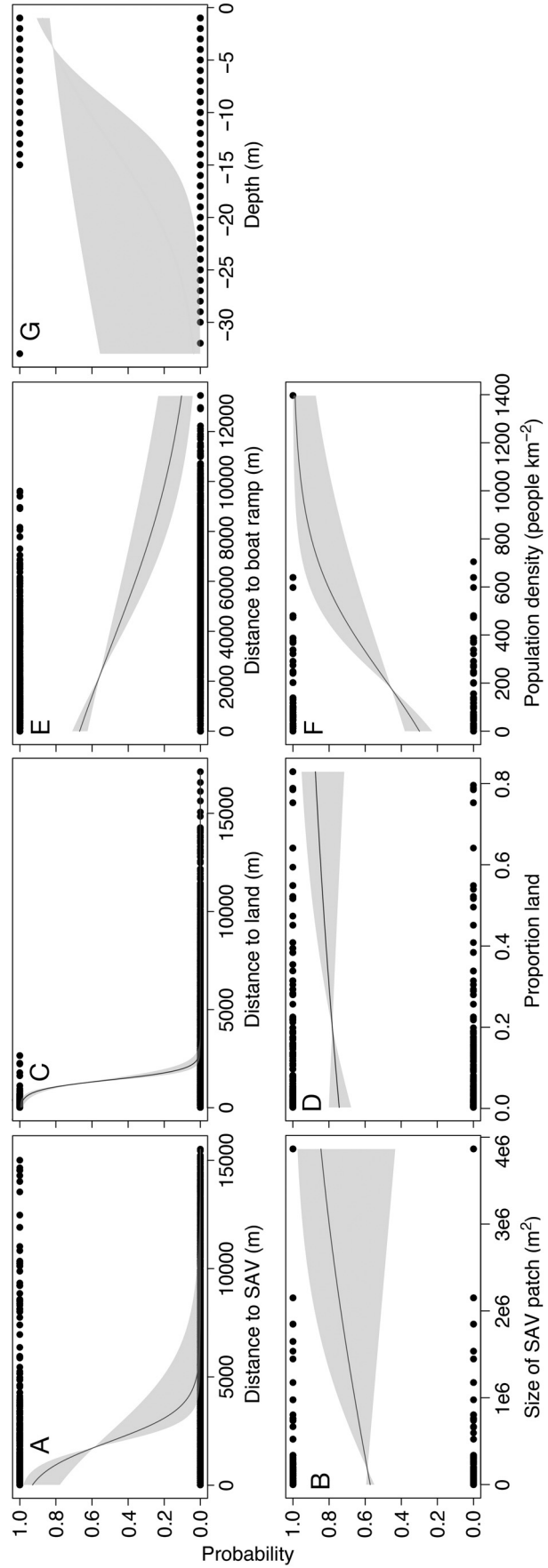


Fig. 4. Same as Fig. 3 but for sighted manatees

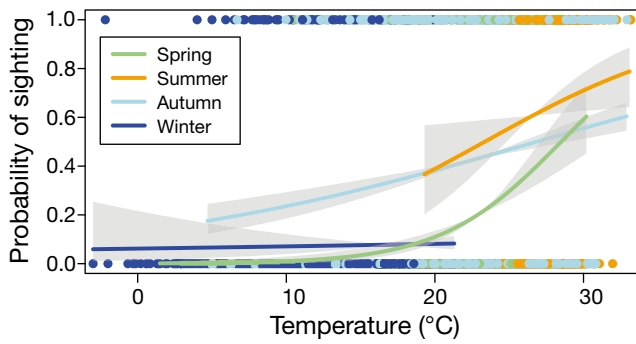


Fig. 5. Probability of manatee sightings with air temperature among seasons. Grey shading depicts 95% confidence bands

copters. Previous studies, however, have found helicopters to either have no meaningful effect or increase detection during surveys (Rathbun 1988, Lefebvre & Kochman 1991). Additionally, manatees were not observed to avoid or respond to the helicopters during this study (R. H. Carmichael & M. Ross pers. obs.). Hence, aircraft effects are an unlikely explanation for the different abundance estimates between years. Second, the 2010 surveys were initiated in response to the 2010 *Deepwater Horizon* oil spill, which could have affected manatee numbers in the area. During 2010, however, DISL/MSN did not observe a significant decrease in sightings (Hieb et al. 2017); the timing and direction of manatee migration during and following the spill (which was opposite the timing and direction of oil in the region) likely minimized potential effects on manatees, and a study done in nearby Choctawhatchee Bay, Florida (~145 km east), estimated that between 46 and 107 manatees occupied the region during the oil spill, which is much higher than our estimate of ~26 (Martin et al. 2014). While the effects of these external factors cannot be excluded from consideration, if they influenced our estimates, it was likely small compared to the corresponding decadal effects of increasing abundance throughout the range.

The findings suggest that our data will be useful to determine if the abundances of a core population

affect abundances at habitat margins and whether demographic changes have the potential to interact with environmental attributes to mediate habitat selection. For example, during the study period, 47 manatees that use Alabama coastal waters have been individually identified by their distinct scar patterns (Beck & Reid 1995, E. E. Hieb & R. H. Carmichael pers. obs.), further consistent with our estimates of 25 to 37 manatees using these waters at any given time during the warm season. Of those 47 known individuals, 29 have been documented from Crystal River, 16 from the Tampa Bay area, and 2 from the east coast of Florida. If all the manatees in the nGOM originated from the Florida peninsula and the Crystal River population is the primary source population for most manatees that migrated to the nGOM during the time of this study (Cloyed et al. 2021b), our abundance estimates could mean that ~8.5% of manatees from northwestern Florida are Alabama migrants ($N = 270; [(29/47) \times 37]/270$) (Martin et al. 2015, Hostetler et al. 2018). If western peninsular Florida as a whole is considered a potential source population, our abundance estimates suggest Alabama migrants may represent ~0.7% of that group ($N = 4810; [(45/47) \times 37]/4810$) (Martin et al. 2015, Hostetler et al. 2018). To better estimate the proportion of manatees that migrate to coastal Alabama waters, more manatees need to be tracked to the subregions of the Florida peninsula or other areas they use during the cold season, and reliable population estimates of those areas are needed. These data will be useful to determine if the abundances of a core population affect abundances at habitat margins and whether demographic changes have the potential to interact with environmental attributes to mediate habitat selection.

Within coastal Alabama waters, the UD and RSFs indicated that manatees primarily used 1 or 2 sites during the warm season. The UD and RSFs for sighted and tagged manatees showed manatees particularly used parts of the Mobile-Tensaw Delta and the Dog River system. Both the delta and Dog River are inshore shallow water sites with many large SAV

Table 2. Coefficient estimates for the probability of sighting manatees relative to temperature for each season

Season	Intercept			Slope		
	Estimate (±SE)	z	p	Estimate (±SE)	z	p
Spring	-7.026 ± 0.979	-7.302	<0.001	0.246 ± 0.043	5.763	<0.001
Summer	-3.149 ± 1.526	-1.018	0.309	0.135 ± 0.057	1.434	0.152
Autumn	-1.874 ± 0.274	-6.842	<0.001	0.070 ± 0.012	5.771	<0.001
Winter	-2.718 ± 0.743	-1.800	<0.072	0.014 ± 0.031	-1.751	0.080

patches (https://www.mobilebaynep.com/images/uploads/library/SAV_2016.pdf), and RSFs of both sighted and tagged manatees found that distances to SAV and land as well as water depth were the 3 strongest variables in predicting resource use. The delta had the largest SAV patches (https://www.mobilebaynep.com/images/uploads/library/SAV_2016.pdf), and the resource selection models also indicated that the size of the nearest SAV patch was an important predictor. Hence, proximity to these very large SAV patches likely made these sites preferred. Furthermore, both sites contain freshwater or easy access to it, which is a physiological requirement for manatees (Ortiz et al. 1998). The population in Alabama is relatively small, so manatee habitats and resources are unlikely to be limited, and the areas where manatees spend most of their time are likely the most preferred areas for manatees. As indicated by the 95% UD, other areas of nearshore shallow habitats with SAV (smaller patches than the delta or Dog River) within coastal Alabama waters may become more frequently used if the population continues to grow and manatees need to use more available habitat. The consistency of results between tagged and sighted datasets, in both UD and RSF, provides strong support for these habitat use patterns and highlights the importance of food resource availability and water depth to habitat selection once thermal requirements are met. These data additionally provide corroboration that rigorously documented citizen science data can be useful and credible for demographic and resource use analyses.

Although the general types of habitats manatees use across their geographic range are similar, there are environmental differences between the nGOM and more tropical parts of their range that have important effects on manatee ecology. Across their geographic range, manatees select for nearshore shallow habitats that contain ample amounts of vegetation (Lefebvre et al. 1999, Morales-Vela et al. 2000, Weigle et al. 2001, Flamm et al. 2005, Castelblanco-Martínez et al. 2013), using creeks, inlets, and enclosed bays much more frequently than open waters (Morales-Vela et al. 2000, Gannon et al. 2007). Mobile Bay and adjacent waters of the subtropical nGOM have very different environmental characteristics from tropical habitats. Tropical areas and peninsular Florida have greater amounts of seagrass, an important food source for manatees in tropical areas, compared to the nGOM (Lefebvre et al. 1999, Castelblanco-Martínez et al. 2009, León-Pérez et al. 2019, Handley & Lockwood 2020). Other types of SAV such as *Eichhornia crassipes*, *Hydrilla verti-*

cillata, *Myriophyllum spicatum*, and *Ceratophyllum demersum* are more common in coastal Alabama waters, and manatees are known to feed on these species in other parts of their range but less preferably compared to seagrasses (Fertl et al. 2005, Reich & Worthy 2006, Alves-Stanley et al. 2010). Seagrasses are less common in the nGOM, so it is possible that manatees in Alabama coastal waters may be more generalist in their diet selection compared to populations in southern Florida and the Caribbean. For example, a study comparing diet between peninsular Florida and Puerto Rico found that manatees were less selective of seagrasses and more generalist in Florida, where seagrasses are comparatively less common and more types of SAV are available, than in Puerto Rico (Lefebvre et al. 1999), and manatees in northern and eastern Florida consume more non-seagrass SAV compared to more southern populations (Reich & Worthy 2006, Handley & Lockwood 2020). Seagrass coverage was estimated to have increased 40% in Mobile Bay between 2007 and 2015 (from 2264 to 3807 ha; Handley & Lockwood 2020). During most of those years, we had tagged manatees in the field, but we were unable to differentiate use of seagrass from other types of SAV in this study. Manatees may be tracking these environmental changes in the nGOM where tropicalization of vegetation and seagrass-associated species is occurring (Fodrie et al. 2010, Heck et al. 2015). Future work could determine whether manatees are preferentially using seagrass when it is available and tracking changing environmental conditions. This type of study would provide additional data to determine how species use habitats on a finer scale at their geographic margins and whether individuals are able to use habitats at expansion fronts because they act more as generalists or if those habitats are changing to better support the individuals using them.

Increasing flexibility in resource use near the margins of their range may be a mechanism to facilitate range expansions (Lancaster 2020, Walsh & Tucker 2020, Martin et al. 2021). For many species, resource and dietary plasticity can aid survival in the novel environments encountered at the front of range expansions (Myles-Gonzalez et al. 2015, Lancaster 2020, Walsh & Tucker 2020, Martin et al. 2021). Habitat availability at and just beyond the margins of the range is crucial for enabling expansion (Saura et al. 2014, Platts et al. 2019), and resource generalists, because of their capability to use more habitat types and consume more types of forage, are more likely to find habitats and resources that meet their requirements. In some cases, populations have evolved to use habi-

tats more efficiently at the expansion front (Llewelyn et al. 2010, Gruber et al. 2017, Carbonell et al. 2021), and it is common for individuals in these populations to be bolder, test novel resources, and be more generalist (Myles-Gonzalez et al. 2015, Gruber et al. 2017, Martin et al. 2021). It is possible that individual manatees making the long migration from peninsular Florida to the nGOM fit this generalist behavioral type in that they are bolder, more likely to explore new habitats, and test potentially new dietary resources within them. This boldness, in turn, may be vertically transferred through the population via behavior and/or genetics (Mazué et al. 2015, Bubac et al. 2021). More work comparing diets between manatees in periphery and core habitat regions will help elucidate the patterns of resource use between these areas. Intraspecific behavioral differences have important consequences in ecological communities (Bolnick et al. 2011, Perkins et al. 2020, Cloyed et al. 2021a,c) and may have critical implications for the trajectory of range expansions and the conservation of species that respond to climate change and other local stressors through range shifts. Future work examining individual behavior and other intraspecific variation among many species and relationships to range expansions is warranted given the reshuffling of ecological communities that is occurring and will likely accelerate in future decades.

Many habitat areas used by manatees in the nGOM overlapped with human activities, and this overlap presents conservation issues for this species, which is threatened across its range and listed as endangered in multiple nGOM states. Waterfronts along the river systems and parts of Mobile Bay that make up the 50 and 95 % UDs for manatees are highly developed, and boaters and recreational fishermen frequently use the delta and other rivers and creeks that feed into Mobile Bay. The patterns of resource selection between tagged and sighted datasets revealed some of these effects. Population density of the nearest census block and distance to the nearest boat ramp, for example, influenced both the tagged and sighted datasets, indicating considerable overlap in the habitats that manatees select and those where humans recreate and reside, with a slightly stronger effect on the sighted dataset. Furthermore, d.land had a higher impact on the sighting data compared to the tagged data, which may be due to a high number of manatee sightings reported from people on land when waterfront homeowners see manatees from their yards and docks. This overlap in habitat use between manatees and humans provides a clear conservation concern (Wright et al. 1995, Flamm et al. 2005, Bauduin et al.

2013, de Oliveira Alves et al. 2013); boat collisions are a major source of mortality for manatees in Florida (Wright et al. 1995), and the first reported mortalities from boat collisions in the nGOM have occurred in the last decade (Hieb et al. 2017). Manatees in Alabama are known to use ship channels as they move among habitats and when entering and exiting the region during migration (Cloyed et al. 2019b). Boat collisions and other negative effects from human interactions will need to be monitored, particularly during warmer months, when more boats and manatees are likely to be present in coastal waters at the northern margin of their range, including the nGOM and Atlantic coasts.

The relationship between manatee sightings and water temperature corroborates the potential effects of climate change on manatee habitat selection, as manatee sightings in coastal Alabama waters were primarily driven by temperature. Manatee sightings were most likely to occur during summer, when temperatures were nearly always $>20^{\circ}\text{C}$, while during winter, manatees were unlikely to be sighted. This finding is not surprising, given the physiological constraints of manatees relative to temperature (Irvine 1983, Bossart et al. 2003). The seasonal difference between autumn and spring likely results from the timing of seasonal migration relative to temperature. Our data suggest manatees departed gradually as temperature declined, remaining in the area during autumn until air temperatures were sufficiently low to force manatees to migrate to seek warm water refuge sites (Laist & Reynolds 2005, Laist et al. 2013). Human behavior may have biased these results if people were outside more on warm days, but these patterns are supported by both sighting and tagged data, suggesting that any bias is minimal. The sudden increase in sighting probability with temperature in spring can similarly be explained by manatees remaining at warm water refugia outside Alabama until waters have sufficiently warmed to prompt seasonal migrations northward and arriving in the nGOM sometime after temperatures have reached 20°C (Deutsch et al. 2003, Laist & Reynolds 2005). Temperature is an important driver of when manatees are likely to be sighted in the nGOM, and increased temperatures associated with climate change will likely promote more manatees using the area and staying for longer periods of time, increasingly affecting the ecological communities associated with these habitats (Hieb et al. 2017). Species in other marine ecosystems such as cyanobacteria, fish, and cephalopods also have increased in abundance at higher latitude as temperature increased at those latitudes (Flombaum et al. 2013, Ruiz-Cooley et al.

2013, Payne et al. 2018). Our method comparing occurrence probabilities with temperature can be an effective way to determine how temperatures affect these patterns of spatial use at relatively higher latitude sites in a wide range of species.

Our study provides important information regarding habitat use during range expansion and the potential for habitats at range margins to meet the needs of species as environmental conditions in core ranges degrade or change. Manatees are known to travel farther west than Alabama along the nGOM coast (Cloyed et al. 2021b), and sites like Mobile Bay and Lake Pontchartrain in Louisiana act as steppingstones for manatees that are increasingly using waters outside their currently established range, providing a mechanism for range expansion in marine species (Saura et al. 2014, Cloyed et al. 2021b). Like climate change, other local stressors in peninsular Florida may also drive manatees to migrate and use nGOM habitats. In peninsular Florida, increased population abundances of manatees concurrent with habitat loss and degradation may result in a manatee population that is close to its carrying capacity. Habitat changes in the core parts of the manatee's range in the USA are likely to continue, and the combination of local stressors and climate change may drive more manatees to migrate and use nGOM habitats. For example, current pollutant inputs into several Florida estuaries have reduced the amount of SAV, possibly driving a historic number of manatee mortalities (Lapointe et al. 2020). The first documented mortality of a manatee previously only known from the USA Atlantic coast occurred in the nGOM in early 2021 during this ongoing unusual mortality event related to food resource limitation on the east coast of Florida. Habitat changes in the core parts of the manatee's range in the USA are likely to continue. Indirect effects of climate change, such as sea level rise and food limitation, as well as other anthropogenic stressors, like pollution, will necessarily lead to changes in habitat quality and availability for many species in the future. In the wake of these complex interactions, habitats at range margins may become increasingly important for a wide range of species but particularly for marine species and those in subtropical habitats undergoing tropicalization, for which climate change may make conditions in their current range less favorable and range margins more suitable.

Acknowledgements. This project was funded in part by the Alabama Division of Wildlife and Freshwater Fisheries under traditional Section 6 of the US Fish and Wildlife Service, the NRDA for the *Deepwater Horizon* oil spill, the

Northern Gulf Institute, Mobile Bay National Estuary Program, Seamen's Foundation, the University of South Alabama, and the Dauphin Island Sea Lab. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank Allen Aven for helping to conceive of this project, collect data, and generate some initial analyses. We also thank personnel at SeaWorld Orlando, Sea to Shore Alliance (currently at Clearwater Marine Aquarium Research Institute), and the University of Florida College of Veterinary Medicine; flight crews; DISL staff and volunteers, particularly Courtney Nelson Seely, Nicole Taylor, Rod Kellogg, and Katherine Frisch; and many others for field work assistance related to spotting, capturing, tagging, and tracking manatees. The authors declare no conflict of interest.

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Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA

Reviewed by: D. Gonzalez-Socoloske,
N. Castelblanco-Martínez and 1 anonymous referee

Submitted: January 11, 2022

Accepted: June 30, 2022

Proofs received from author(s): September 2, 2022