West Indian manatee movements reveal novel occupancy and distribution patterns in the northern Gulf of Mexico

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Abstract

Since the 1980s, West Indian manatees (*Trichechus manatus*) have been reported more frequently along the northern Gulf of Mexico (GOM) coast in areas that were recently considered to be outside the species' normal areas of occupancy. The ecological importance of the northern GOM region to manatees is currently unclear, but knowledge of the spatial ecology, population linkages, and habitat associations of individuals occupying the fringes of their known range is vital to bring context and improve understanding of demographic trends and potential threats to the species, rangewide. We tracked regional-scale movements of 13 manatees documented in Mobile Bay, AL using satellite telemetry and mark-recapture methods. We determined movement and occupancy patterns including origins, seasonal dispersal and site fidelity, and functional movement modes of those individuals during the tracking period. Focal manatees moved along the GOM coast between Tampa Bay, FL and Lake Pontchartrain, LA, and consistently returned to discrete locations in both the northern GOM and within the species' core range in peninsular FL. Functional movement model fits confirmed that most relatively long-range seasonal movements were migratory in nature, suggesting that consistently occupied migratory endpoints contain relatively important seasonal habitat for manatees and diminishing the possibility that tracked manatees were nomads or transient within the study area. These results provide evidence of shifting seasonal manatee distribution in the US, and highlight repeatedly used locations that may increase in importance to the species if manatee abundance in the northern GOM increases.

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Introduction

West Indian manatees (*Trichechus manatus*) are large aquatic mammals that inhabit coastal areas in portions of the Atlantic, Caribbean, and Gulf of Mexico (GOM) (Lefebvre *et al.*, 2001). In the temperate United States (US), distribution of the Florida (FL) manatee (*T. m. latirostris*) varies seasonally relative to water temperature. During winter, manatees are constrained to a few areas within the state of FL that offer essential warm-water habitat, including coastal power plants and natural springs where water temperature remains above manatees' physiological threshold of about 20°C and aggregations of up to hundreds of animals may form (Irvine & Campbell, 1978; Bossart *et al.*, 2003; Laist & Reynolds, 2005; Laist *et al.*, 2013). Manatees depart winter resource-sharing aggregations in springtime, and disperse to inhabit coastal areas for the duration of warm weather (Hartman, 1979; Powell & Rathbun, 1984; Deutsch *et al.*, 2003). Although wintertime manatee distribution in FL is well documented, less is known about warm season dispersal and migratory movements, destinations, and resulting distributions during the warm season, particularly for manatees on the northern GOM coast (Fertl *et al.*, 2005).

On the northern GOM coast west of peninsular FL, reported manatee sightings were once sporadic but have increased in recent years, especially during warm months (Powell & Rathbun, 1984; Fertl *et al.*, 2005; Pabody *et al.*, 2009). Wintertime manatee sighting reports there are less common, and sightings made from Dec–Feb often culminate in death of the animal from starvation or cold stress (Fertl *et al.*, 2005; Hieb *et al.*, 2016). The sighting reports have been valuable to establish manatee presence in numerous localities throughout the region (Pabody *et al.*, 2009; Hieb *et al.*, 2016). Causes for the increase in sightings are not entirely clear (Fertl *et al.*, 2005), but it does suggest that the northern GOM is becoming a regular seasonal destination for manatees, and raises broad questions about current spatio-temporal patterns of manatee use in this region and the potential value of the area to the species in the future. But, there has been little directed research on the spatial ecology of manatees in the region to offer any insight on the ecological importance of the region to the species.

Resolving spatio-temporal movement and occupancy patterns of manatees in locations outside of core population areas will clarify links of those individuals to the FL manatee population, define the value of the region to the US manatee population, and inform management of this endangered species in understudied portions of its US range. Our objectives were to quantify patterns of broad-scale movement distance and timing, repeatedly occupied places, and functional movement strategies of manatees occurring in the northern GOM. To do that, we tracked the movements of 13 manatees targeted in Mobile Bay AL, an estuary on the northern GOM west of FL where manatee sighting and stranding reports date to 1912 and have increased in recent years (Fertl *et al.*, 2005; Pabody *et al.*, 2009). Data from this study will clarify and improve current

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understanding of sources, movement patterns, and locations of potentially important habitat for manatees in the northern GOM. This will immediately improve knowledge of manatee spatial ecology rangewide and highlight the potential value of the northern GOM region to manatees in the US, directly contributing to US endangered species management research goals. The resulting data will also contribute a baseline for manatee population assessment in the northern GOM.

Methods

Animal tracking

We applied satellite tracking equipment to individual manatees in Mobile Bay, AL during Sep 2009, Aug 2010, and Aug 2012. Animals were located by an aerial observer surveying in areas of known manatee use. The observer directed a boat capture crew to an animal's location, and the focal manatee was encircled by net and drawn into the capture boat. Animals were held out of water for up to one hour for fitting of telemetry equipment and a health assessment, released at the capture location, and observed post-release to verify resumption of normal behavior. Satellite telemetry equipment consisted of a floating unit programmed to fix and store a GPS reading every 30 minutes (manufactured by Telonics Inc., Mesa, Arizona, USA). The Telonics tag was attached to a nylon tether with a predetermined failure strength matched to animal size. The other end of the tether was attached to a belt fitted around the animal's peduncle, to allow a tow-behind tag configuration, following common methods (e.g. Deutsch *et al.*, 1998; Weigle *et al.*, 2001). The peduncle belt included an embedded acoustic transmitter (model CHP-87-L manufactured by Sonotronics Inc., Tucson, Arizona, USA) as an additional method of locating the animal. Stored GPS locations were retrieved upon tag recovery, either after unplanned tag detachment or after an in-place tag exchange for regular maintenance. Procedures for working with live animals were approved by the University of South Alabama and the Sea to Shore Alliance Institutional Animal Care and Use Committee (Protocols #581568 and #S2S-2010-03).

Tagged and belted manatees were also tracked actively and passively using portable and moored hydrophones to detect the belt acoustic transmitters. This method was useful to detect manatees that lost satellite tags due to tether breakage or tag malfunctions, mitigating the extent of movement data gaps for those individuals (Aven *et al.*, 2015). Portable hydrophones were used *ad hoc* to search specific areas of interest for previously tagged individuals, and moored data-logging hydrophones were deployed in areas of known manatee use in Mobile Bay, AL and in Apalachicola, FL.

Manatee photo-identification data were collected either by research personnel or opportunistically by members of the public who submitted photographs and sighting information

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to researchers (Pabody *et al.*, 2009; Hieb *et al.*, 2016). Photo-identification efforts were concentrated around Mobile Bay, AL, and photographs submitted by the public included locations in Louisiana (LA), Mississippi (MS), AL, and FL. Photographs containing uniquely distinguishing features, typically scar or mutilation patterns, were compared to existing manatee images collected throughout the southeastern US by cooperating researchers at the United States Geological Survey (USGS) Sirenia Project and the Florida Fish and Wildlife Conservation Commission (FWC) using established methods (Beck & Reid, 1995).

Movement analysis

Manatee tagging and photo-identification efforts originated in Mobile Bay, AL, and we operationally defined a broader study area from the observed range of the tracked animals. We delineated ten geographically distinct subranges ("zones") within the study area based on the highest density areas of pooled manatee locations, and we additionally included Lake Pontchartrain, Louisiana as a distinct zone representing the westernmost boundary of observed manatee movements (Figure 1). We named each zone based on a significant regional-scale geographic feature (primary bay, river, lake or associated municipality) contained within. We used this spatial stratification schema for two primary reasons: 1) the associated major geographic features are already well-aligned with local and regional wildlife management units, and 2) herbivore movements occurring on the timescales considered in this study (days to years) are best represented on the corresponding spatial scales of the animal's home range to annual range (Owen-Smith *et al.*, 2010). Thus the scale of our regional "zones" (tens to hundreds of km in diameter) was applicable to resolve within-season home range use patterns as well as regional-scale migratory movements.

To estimate minimum distances necessarily traversed by manatees traveling between zones, we used GIS tools to delineate a continuous aquatic path following the contours of the GOM coast, in keeping with most tracked manatee movements, excluding minor diversions such as inlets and rivers. This was useful to standardize and compare regional-scale manatee movements.

We used daily manatee locations to calculate residence and movement metrics for each focal animal. For satellite-tracked manatees, we calculated 1) residence time (days) of each zone occupation instance, and 2) number of occupations (i.e., number of return visits) to each zone. Because of occasional gaps in tracking data, we implemented the following rules to classify zone residence times. If an animal's location was unknown for less than 25 days, and occupied the same zone before and after that data gap, we assumed that the animal remained in the same zone, such that the calculated zone residence time included the duration of the data gap. If an animal's location was unknown for more than 25 days or if an animal had a data gap of fewer than 25 days

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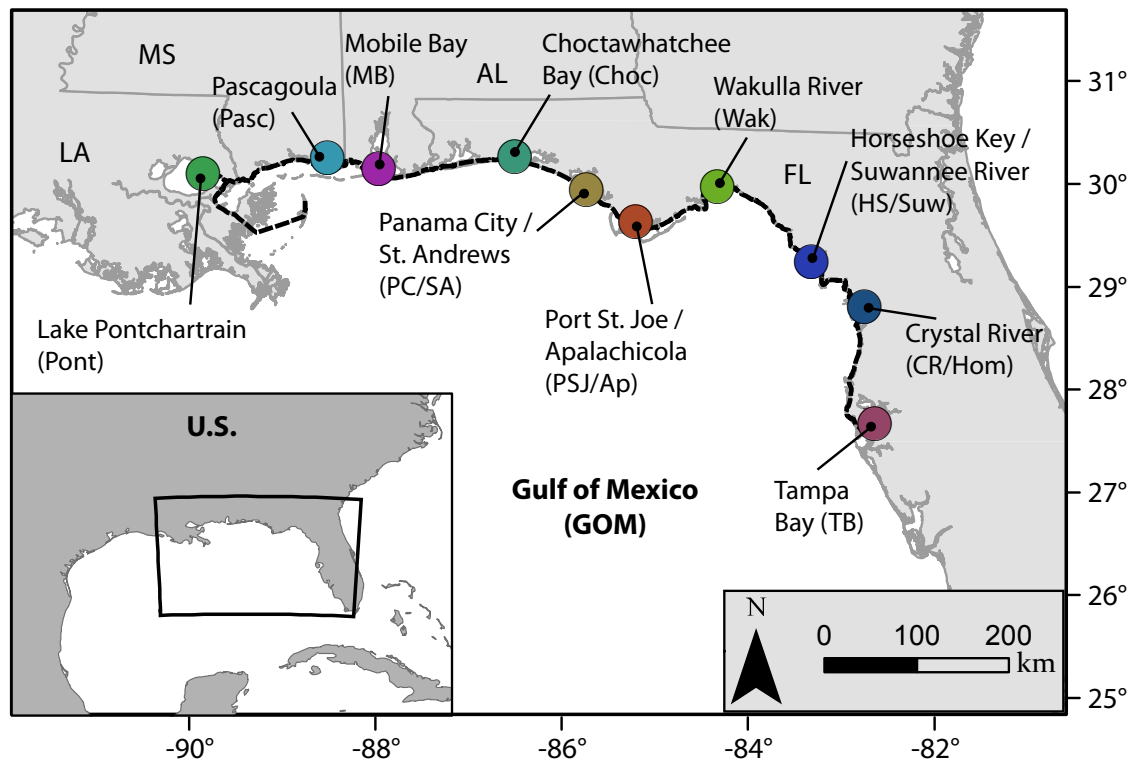
Figure 1 – Study area along the northern Gulf of Mexico coast, subdivided into "zones" signified by colored dots centered on areas of highest use by focal manatees. The shortest possible path of manatee travel between zones is shown by the dashed line.

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but moved from one zone to another during the data gap, zone residence time calculations excluded the gap period if it was between Apr–Nov. For satellite tracked animals with data gaps during the cold season (Dec–Mar), the previous rule was relaxed so as to bridge gaps of up to 90 days. This was equivalent to making the assumption that the animal did not depart the winter aggregation site during the data gap. We classified each zone occupation instance based on zone residence time (if known) as: "transient" if a focal animal remained in a zone for fewer than seven days, "stopover" if occupancy lasted 7 to 25 consecutive days, and "endpoint" if occupied for 25 or more consecutive days (the latter consistent with Deutsch *et al.* 2003). We calculated the number of times manatees occupied each zone as a stopover or as a migratory endpoint, and defined "site fidelity" as repeated occupation of the same zone in different years. We did not consider transient use of a zone to contribute to site fidelity.

To classify and contextualize manatee movement patterns relative to several animal movement scenarios known in nature, we modeled the net displacement (ND) of satellite-tracked manatees through time using a suite of non-linear models derived from the logistic function (Bunnefeld *et al.*, 2011; Beatty *et al.*, 2013). We calculated the linear ND of manatee daily locations from the study origin, defined as a reference point within Mobile Bay, AL (longitude -88.0318, latitude 30.6284), in kilometers using the great circle distance (Haversine formula). The candidate movement models included ecologically meaningful parameters that were interpretable as movement timing and distance attributes including onset and duration of movements and maximum distance from origin (Bunnefeld *et al.*, 2011; Beatty *et al.*, 2013) (Figure 2). That suite of candidate models included:

1. Stationary: no movement away from the origin

2. Nomadic: constant movement away from origin (no apparent endpoint)

3. Dispersal: movement from origin to an endpoint without return to origin, also called "ranging" (sensu Dingle & Drake 2007)

4. Simple migration: movement from origin to an endpoint, temporary occupation of endpoint, eventual return to origin

5. Mixed migration (MM): movement from origin to an endpoint, temporary occupation of endpoint, then movement and occupation of another endpoint before eventual return to origin (three places occupied)

6. MM with offset: as "mixed migration" above, with addition of a constant term allowing for an offset from the origin point (included to account for animals that were not near the predefined origin at the beginning of the modeled time period).

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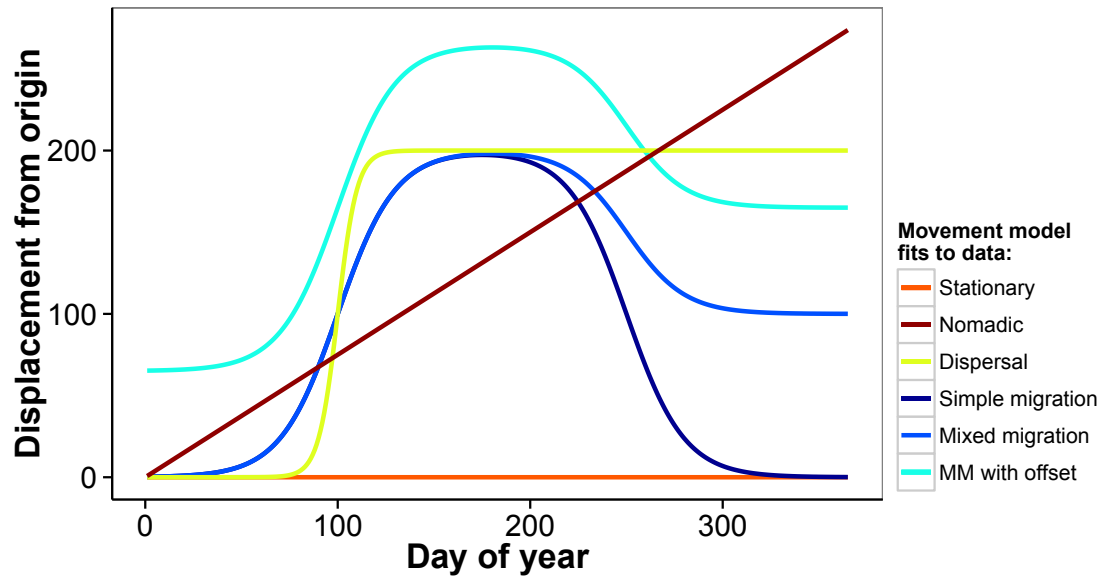
Figure 2 – Expected animal movement patterns simulated from each of the six deterministic functional movement model scenarios (following Bunnefeld *et al.*, 2011).

We fit the movement models first to each animal-year dataset (Jul 01–Jun 30) for individuals with at least 140 days of tracking data within that one-year period. Then we fit the movement models to pooled location data (all tracked animals, all years). Pooled models included a random effect of individual animal, to account for individual-level autocorrelation. We estimated model parameters using Markov Chain Monte Carlo simulation in Jags 3.4 (Plummer, 2003), implemented in the R software (R Core Team, 2016). We evaluated relative fit among the candidate movement models using the Deviance Information Criterion (DIC) score to identify the most parsimonious candidate.

Results

We collected location data for 13 manatees that moved between the north-central GOM and peninsular FL. Between 2009 and 2014, we captured nine manatees in Mobile Bay, AL and satellite tracked eight of those (two females, six males). We collected a mean (± std. dev.) of 364 ± 149 non-continuous days of satellite tracking data per animal, resulting in sufficient data to resolve regional scale movements for seven tagged manatees (one female, six males; Figure 3). There were occasional temporal data gaps in satellite tracking data due to tag detachment or malfunction. During some of those gaps, we were able to partially resolve focal animal movements using supplemental photo-identification or hydrophone data.

    Photo-identifications were made from photographs of manatees taken between 1978 and

Table 1 – Captured and satellite-tracked manatees (top) and manatees tracked by other means (bottom), including identification code, year-month of capture, morphological data, tracking duration (days, non-continuous), and number of mark-recapture encounters. CMA001/CR123, captured in Sep 2009, was not satellite-tracked. Two captured manatees (TMA004, TMA005) were recaptured and tracked a second time after their initial tracking period ended.

Animal ID	Capture date	Sex	Length (cm)	Weight (kg)	Tracking duration (days)	Hydrophone (days)	Photo-ID (n)
Satellite-tracked							
TMA001	Sep 2009	F	275	464	450	33	6
TMA002	Sep 2009	M	300	530	359	—	—
TMA003/CR267	Aug 2010	M	306	619	379	—	3
TMA004/CR581	Aug 2010	M	304	551	553	7	1
	Aug 2012		303	586*			
TMA005/CR633	Aug 2010	M	285	467	366	1	2
	Aug 2012		294	478*			
TMA006/TB439	Aug 2012	M	306	587*	345	1	1
TMA008	Aug 2012	F	230	265*	35	27	—
TMA010	Aug 2012	M	290	499*	421	—	—
Other Tracking							
CR054	—	F	—	—	—	—	23
CMA001/CR123	—	F	335	742	—	—	91
CR224	—	M	—	—	—	—	7
TB186	—	M	—	—	—	—	29
TB294	—	M	—	—	—	—	9

*Estimated weight based on animal length and girth (K. Rigney, FWC, pers. comm.)

2014. Using photo-identification we documented 10 manatees that occurred in both Mobile Bay and at a known FL wintering site in multiple years. Of those 10, five were previously satellite-tracked manatees with detached or nonfunctional satellite tracking equipment (Figure 3) and the other five were non-satellite tracked individuals (Figure 4). Hydrophone identifications of five previously satellite-tracked manatees (that retained the belt with acoustic transmitter) were made in Mobile Bay ($n = 63$), Apalachicola, FL ($n = 4$) and Crystal River, FL ($n = 2$).

Manatees moved along the GOM coast as far northeast as Lake Pontchartrain, LA and southwest to Tampa Bay, FL (Figure 3, Figure 4). The longest within-year movement covered 1150 km from Tampa Bay, FL to Lake Pontchartrain, LA (TMA006, Spring 2013) (Table 2, Figure 3), and the shortest was 113 km from Crystal River, FL to Suwanee River, FL (TMA010, 2013 and 2014). Mean (± std. dev.) one-way travel distance was 695 ± 235 km (median: 737 km), and during this study, all focal animals made at least one movement of 737 km (at a minimum) from the Mobile Bay, AL capture zone to Crystal River, FL (or further) during the
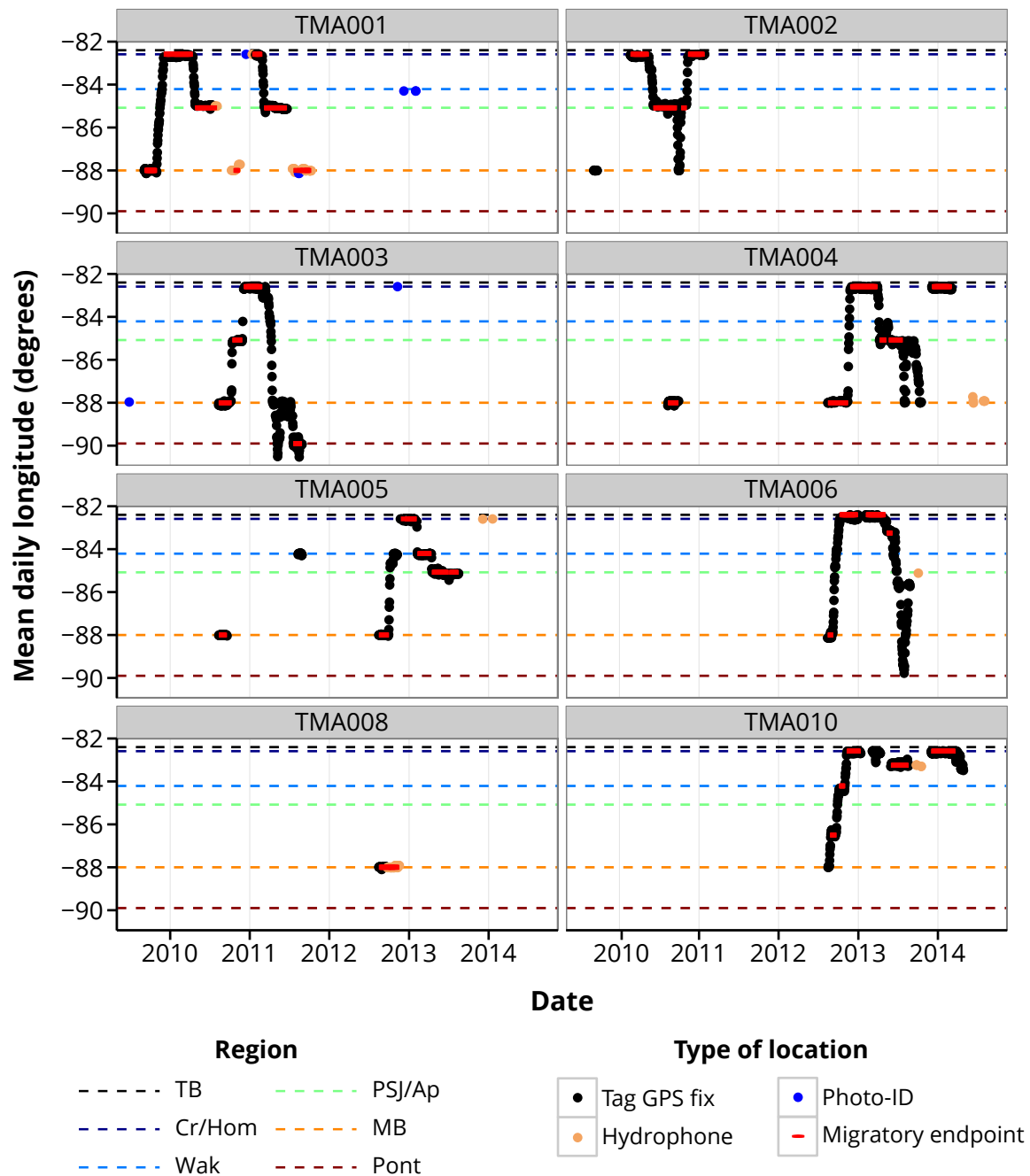
Figure 3 – Mean daily locations (longitude) from 2009 through 2014 for satellite-tracked manatees (including non-satellite detections of those animals occuring after Sep 2009). Panel labels correspond to individual animal ID code. Dashed colored lines represent geographically distinct zones along the northern GOM coast. Migratory endpoint occupations (zone residence ≥ 25 days) are denoted with red bars extending the duration of occupancy.

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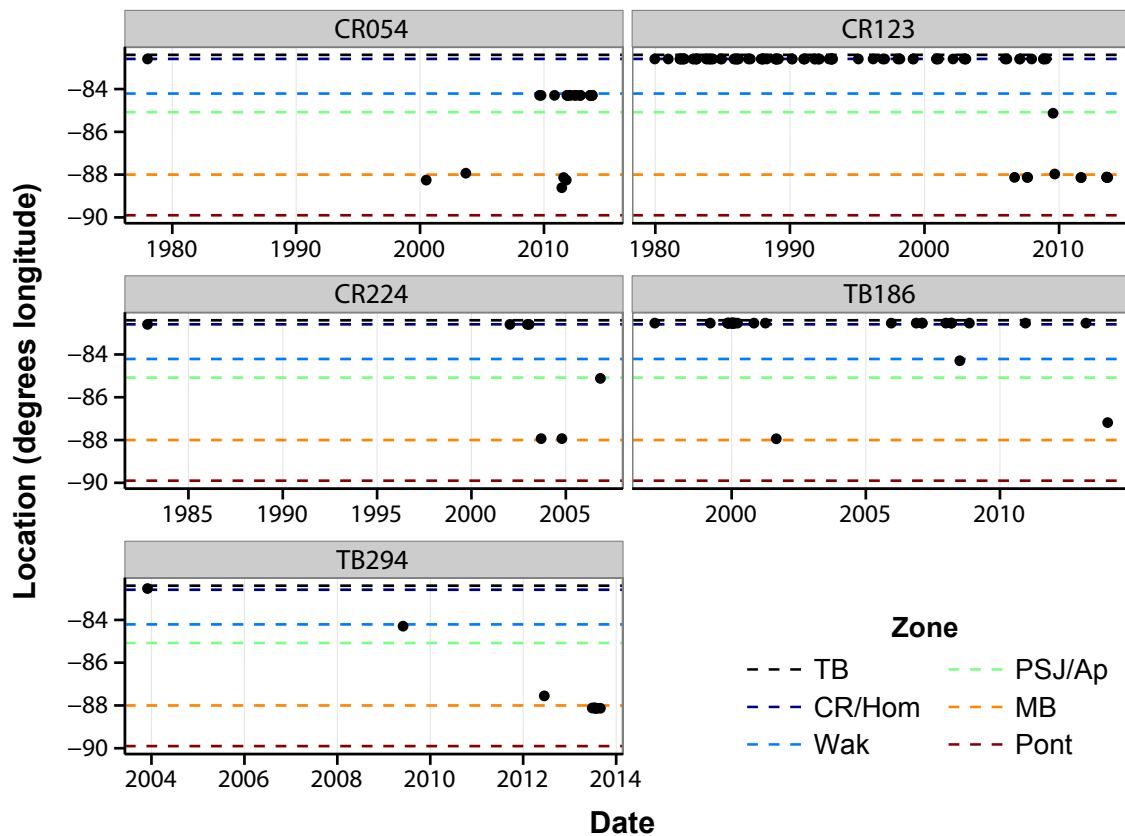
Figure 4 – Location (longitude) of photo-identified manatees for the extent of their tracking history. Panel labels correspond to individual animal ID code. Dashed colored lines represent geographically distinct zones along the northern GOM coast.

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Table 2 – Coastal travel distances between the Mobile Bay, AL zone and the center of the other regional zones (Figure 1).

| Zone	Coastal travel distance to Mobile Bay (km)
Lake Pontchartrain, LA (Pont)	223
Pascagoula, MS (Pasc)	67
Mobile Bay, AL (MB)	—
Choctawhatchee Bay, FL (Choc)	169
Panama City / St. Andrews, FL (PC/SA)	255
Port St. Joe / Apalachicola, FL (PSJ/Ap)	334
Wakulla River, FL (Wak)	469
Horseshoe Key / Suwannee River, FL (HS/Suw)	624
Crystal River / Homosassa Spring, FL (CR/Hom)	737
Tampa Bay, FL (TB)	927

study period. One animal captured and tagged in Mobile Bay during 2012 lost its satellite tag in Mobile Bay within weeks of capture and was not subsequently retagged (TMA008; Table 1), data from that individual were excluded from dispersal results.

Zone occupancy and site fidelity

Each zone was used by at least one satellite-tracked animal as a migratory endpoint, a stopover, or both (Figure 5). Mobile Bay, AL, Apalachicola, FL, and Crystal River, FL were the most frequently used migratory endpoints. Pascagoula, MS and Panama City, FL were not used as migratory endpoints. Tampa Bay, FL was used by only one satellite-tracked manatee (TMA006, migratory endpoint) and by one photo-identified manatee (TB186).

The timing of migratory endpoint occupancy showed seasonal trends. Focal manatees used Crystal River, FL most heavily during winter (Dec–Mar), Apalachicola, FL during spring and summer (Apr–Aug) and Mobile Bay, AL in late summer and fall (Sep–Nov) (Figure 6). All photo-identifications of focal animals in Apalachicola, FL or further west were made when manatees were in the area between May and Oct, except one photo-identification of a manatee carcass (TB186, Pensacola, FL, Jan 2014). Most photo-identifications of focal animals made east of Apalachicola, FL occurred at known wintering sites between Nov and Apr.

Mobile Bay and Wakulla, FL were the most frequently used stopover zones. Mobile Bay was used as a stopover most frequently from Jul–Sep, but peak use of Wakulla as a stopover occurred during the months of Mar and Oct (Figure 6).

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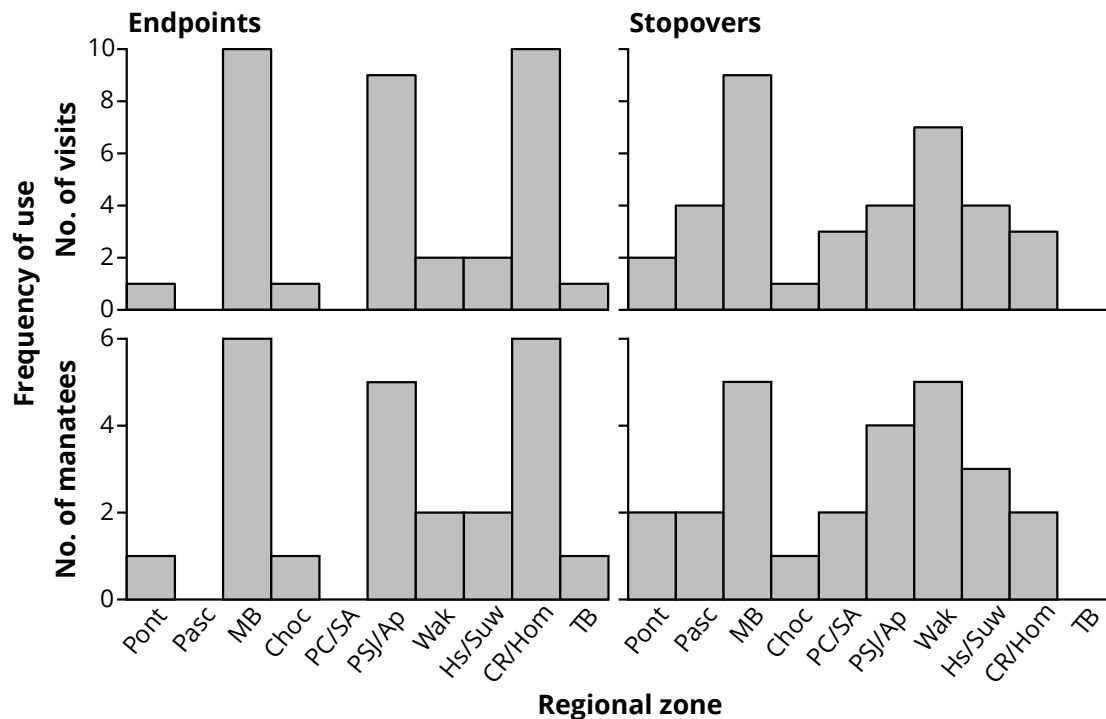
Figure 5 – Zone use by satellite-tracked manatees as migratory endpoints (left panels) and stopovers (right panels). Bars represents total number of visits to each zone by all focal individuals (top panels) and number of individuals using each zone (bottom panels).

Animal movement models

We obtained sufficient satellite tracking data (> 140 days) to fit annual movement models for nine individual-years (five tracked manatees for one year each, two for two years; Table 3). All nine of those movement datasets revealed a pattern of movement with three distinct endpoints punctuated by well-defined long-distance movements. Seven were best described by the "mixed migration" model and the remaining two (TMA001 Jul 2010–Jun 2011 and TMA004 Jul 2013–Jun 2014) were best described by the similar "mixed migration with offset" model (Figure 7). Parameter estimates of migration timing reflected seasonal patterns of movement away from the origin (Mobile Bay, AL) during fall and winter, extended occupation of a winter migratory endpoint, and movement back towards Mobile Bay during spring/summer, with an intermediate spring/summer migratory endpoint between the overwintering site and the ultimate summer destination (Table 3, Figure 7).

There was substantial variation in individual movement model parameter estimates corresponding to differences in migration phenology among individuals and years (Table 3). Among individual manatees, the autumn migration midpoint was estimated to be 05 Nov ± 25 days with migration duration of 39 ± 29 days (mean ± std.dev). Spring migration among

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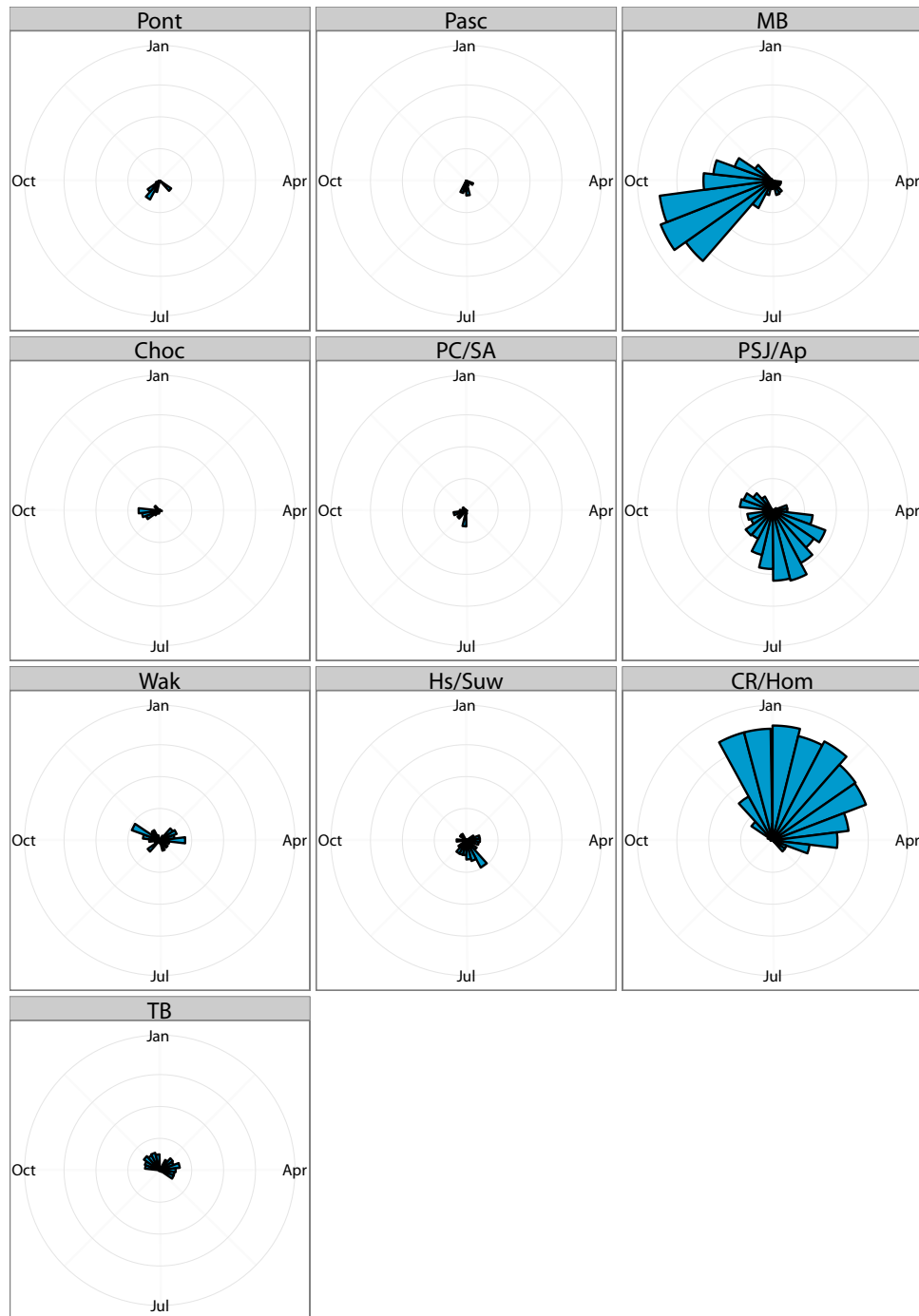
Figure 6 – Seasonality of daily manatee zone occupancy, pooled among animals over the duration of the study. Each panel depicts the calendar year starting in Jan (top) and moving clockwise; bar height indicates the total number of focal manatee-days in that zone during that two-week period.
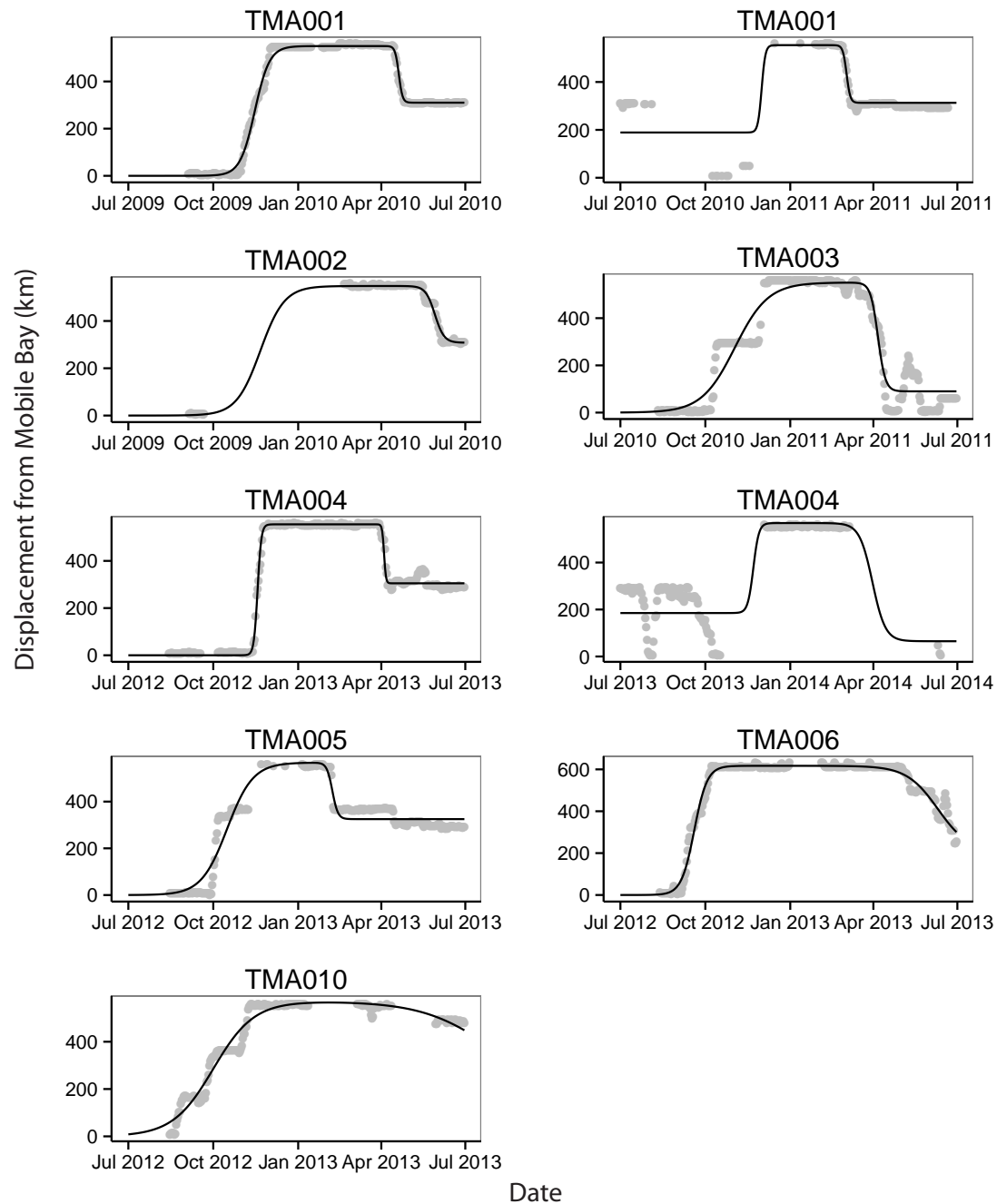
Figure 7 – Best-fitting movement model predictions from parameter estimates (black lines) plotted over observed mean daily locations (grey dots) for one-year periods (Jul–Jun) with at least 140 days of tracking data for that individual.

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Table 3 – Movement model parameter estimates of migration timing, including estimated midpoint of migration (day-month) and duration of travel (days) for autumn and spring migrations of individual tracked manatees with sufficient tracking data, and for pooled data (aggregated from all individuals and years), corresponding to Figure 7 and Figure 8.

Animal ID	Year	Days tracked	Autumn		Spring	
			Midpoint	Duration	Midpoint	Duration
TMA001	2009–2010		15 Nov	30	20 Apr	8
TMA001	2010–2011		30 Nov	9	03 Mar	10
TMA002	2009–2010		03 Nov	29	29 May	19
TMA003	2010–2011		02 Nov	74	06 Apr	17
TMA004	2012–2013		19 Nov	8	05 Apr	5
TMA004	2013–2014		08 Nov	14	21 Apr	62
TMA005	2012–2013		16 Oct	50	08 Feb	12
TMA006	2012–2013		20 Sep	29	26 Jun	85
TMA010	2012–2013		05 Oct	91	09 May	156
Best fit	Pooled		09 Nov	48	09 Apr	67

individual manatees was estimated to be centered on 24 Apr ± 52 days with duration of 35 ± 46 days.

Among movement model to pooled manatee location data (all individuals and years), the "mixed migration with offset" model fit the data best (Figure 8). Parameter estimates from the pooled model fit indicated a general pattern of movement away from Mobile Bay during fall and winter, a period of overwintering at a second migratory endpoint, and movement towards a third migratory endpoint in the direction of Mobile Bay during spring/summer. Parameter estimates of seasonal migration timing from the pooled model indicate that autumn migration to overwintering locations was centered on 09 Nov, and spring dispersal away from overwintering locations towards warm weather ranges was centered on 07 Apr (Table 3).

Discussion

This study tracked manatee movements along the northern GOM coast at least 469 km west and as far as nearly 700 km west of what was recently considered the "typical" warm-weather western limit to FL manatees' areas of occupancy (Wakulla River, FL; O'Shea & Kochman, 1990). Manatees showed site fidelity to discrete locations in the northern GOM region, and most large-scale movements were migratory in nature. Migration timing reflected general seasonal patterns, but there was variation in timing parameters. These results build upon previous studies documenting manatee sightings along the northern GOM coast by using telemetry to accurately track residence time and regional-scale movements, which allowed us to quantify the extent of

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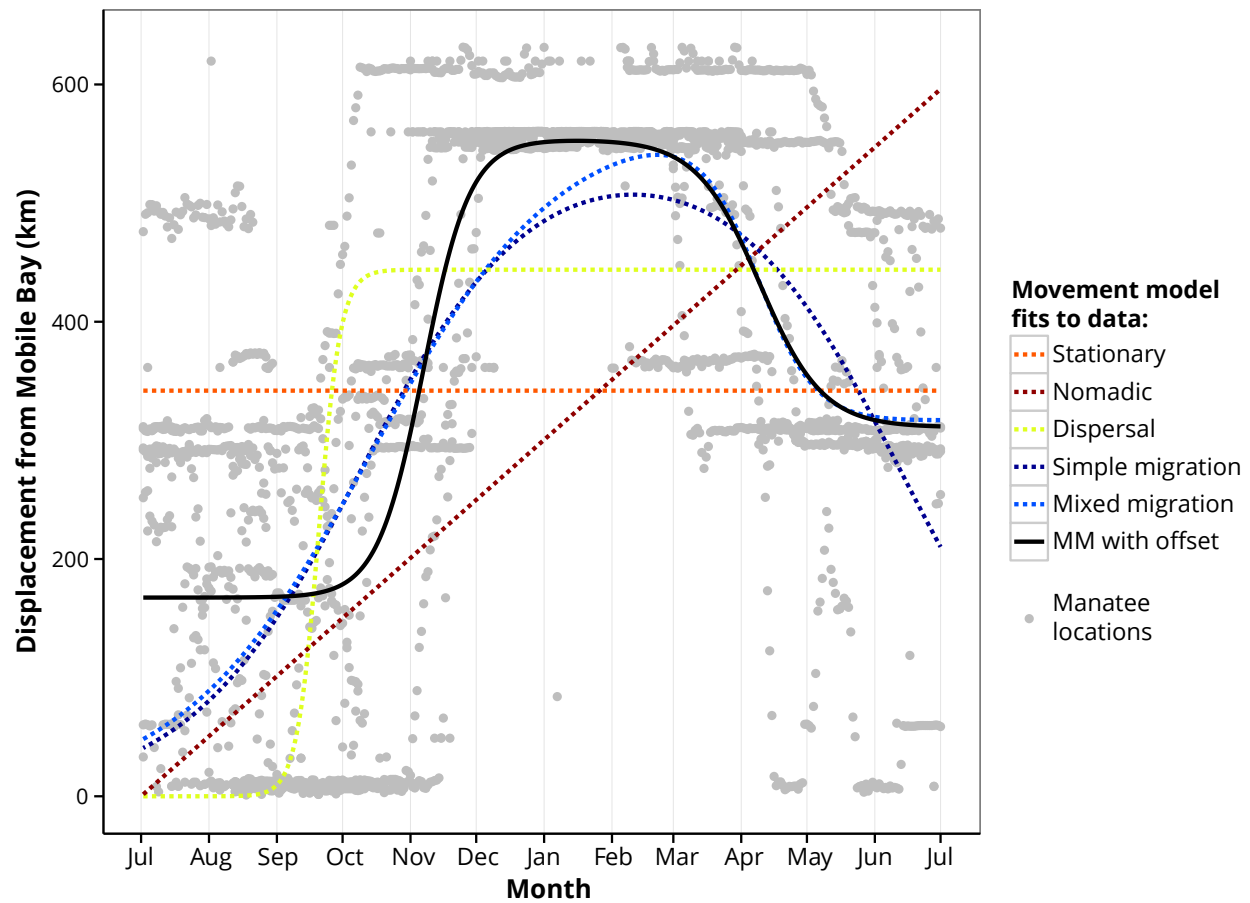
Figure 8 – Movement model fits (colored lines) and observed mean daily locations (grey dots) pooled among animals over the duration of the study. The best-fitting candidate model, mixed migration with offset, is plotted with a solid black line; fits for other candidate models are shown with dotted lines.

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use and the geographic linkages of tracked manatees in ways that revealed novel information about how manatees use the region.

Manatees migrating to and from the northern GOM may be the among the longest travelers on the continuum of migratory behavior exhibited by FL manatees or other extant Sirenians. Although the longest seasonal movement reported here (Crystal River, FL to Lake Pontchartrain, LA, 1150 km) was half as far as the longest tracked manatee movement ever reported (2300 km, Atlantic coast), average migration distances have been reported as 250–350 km (range 80–830 km) for manatees on FL's Atlantic coast, and up to 240 km for Antillean manatees (*T.m. manatus*) (Deutsch *et al.*, 2003; Castelblanco-Martínez *et al.*, 2013). A study of 70 tracked dugongs (*Dugong dugon*) reported movements averaging 244 km, up to 560 km among some individuals that made "macroscale" movements, with a high degree of variation in movement behavior among individuals (Sheppard *et al.*, 2006).

Movement model results indicated that functional movement patterns of tracked manatees were migratory in nature. This finding diminishes the possibility that those individuals used nomadic or other movement strategies within the region that could be interpreted as naive or exploratory movement, and suggests some perceived value in the migratory endpoints that were used. Focal manatees showed fidelity to the Apalachicola, FL and Mobile Bay, AL areas in particular as migratory endpoints during the warm season and to the Crystal River, FL area during cold months.

Systematically repeated use of distinct areas by wildlife suggests relatively high habitat quality at these locations, and site fidelity has also been related to breeding success for some species (Switzer, 1993; Hoover, 2003). Predictable migration patterns often emerge in herbivore populations when spatio-temporal variations in forage quality or quantity are driven by regular, predictable seasonal trends in rainfall, temperature, or light (Dingle & Drake, 2007; Mueller & Fagan, 2008). Hence, migratory endpoints defined by tracked manatee movements and occupancy likely offer relatively favorable and predictable conditions (i.e., freshwater inputs, high quality or quantity of forage) for at least a portion of the year (Dingle & Drake, 2007). Frequently used locations likely offer a favorable atmosphere for survival and reproduction (Dingle & Drake, 2007), and the Apalachicola and Mobile Bay areas in particular offer significant freshwater inputs and large quantities of fresh and brackish aquatic vegetation. Although attractive to manatees, those locations cannot be occupied year-round because of seasonal water temperature fluctuations that constrain migratory manatees to essential winter habitat locations in peninsular FL. The effects of this obligate wintertime range contraction on the potential magnitude and geographic extent of subsequent manatee seasonal dispersal are not understood. This situation is unique to manatees in the US, since manatees elsewhere in the world are generally not constrained by water temperature and are not known to form aggregations of the size seen at FL overwintering sites

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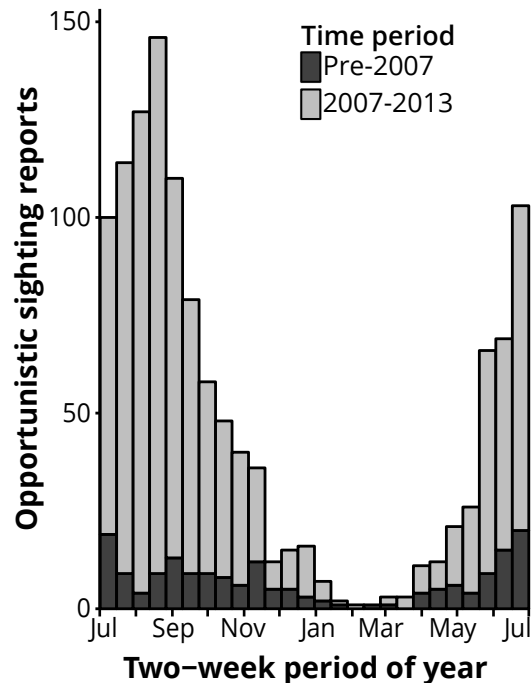
Figure 9 – Frequency of opportunistic manatee sighting reports near Mobile Bay, AL, in two-week intervals shaded by era (pre- or post-establishment of sighting network; Hieb *et al.* 2016).

(Rathbun *et al.*, 1995), prompting the question of how FL manatee manatee movement patterns and geographic distributions may be different without that constraint.

In Mobile Bay, tracked manatee presence and occupancy was temporally consistent with peak periods of citizen-reported sightings of untagged manatees there (Jul–Sep) (Fertl *et al.* 2005; Pabody *et al.* 2009; Figure 9). The frequency of those reports increased since the 1990s (Bonde & Lefebvre, 2001; Fertl *et al.*, 2005), coinciding with substantial increases in cold-weather manatee aerial survey counts (signifying minimum local abundance) at major winter aggregation sites in northwest peninsular FL (Kleen & Breland, 2014). Manatees recently began using Wakulla Spring, northwest of peninsular FL, as a winter use site (Butler *et al.*, 2011; Figure 1). Thus, the number of manatees at the known overwintering sites nearest to our study area in the northern GOM is now likely higher than ever. Our results, along with recent sighting report increases and observed changes in manatee use of overwintering sites, suggest greater use of areas in the northern GOM previously thought to be outside their recent typical range.

Tracked manatees' relatively infrequent use of the Wakulla River, FL zone as a migratory endpoint may understate its true importance to migrating manatees. Wakulla Springs is a natural warm water source recently identified as being used by some manatees as a thermal refuge during winter (Butler *et al.*, 2011), making it the closest known manatee overwintering spot to Mobile Bay where this study originated. Although manatees in this study did not overwinter at Wakulla

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Springs, some used the Wakulla River zone as an early and late season stopover site in conjunction with migratory movements to and from overwintering sites. Wakulla River's central position between core manatee range in FL and more remote areas on the northern GOM coast, as well as the availability of warm water there, highlight that area's potential importance as a stepping stone connecting seasonal movements to and from other areas in the region.

Among migratory movements of focal manatees, there was substantial variation in the timing of onset and the duration of migration. Variation in regional-scale movement timing among individuals has been reported in other manatee tracking studies (Weigle *et al.*, 2001; Deutsch *et al.*, 2003). This variation could reflect plasticity in individual response to migration cues, or seasonal variation in abiotic variables correlated with migrations (e.g., water temperature), and may also be affected by animal gender. Male manatees typically travel farther and stay at endpoints for shorter durations than females during the warm season (Deutsch *et al.*, 2003; Flamm *et al.*, 2005). Although we could not make a robust comparison between genders within our data, we did see instances of fairly rapid movement between two widely separated locations by male manatees (e.g., TMA003 Spring 2011, TMA004 Fall 2013; Figure 7). Those instances may correspond to "patrolling" behavior, hypothesized to be for purposes of mate seeking, or as part of a mobile mating herd, described in Bengtson (1981). During this study, those movements were not frequent enough to affect model classification of the annual-scale movement pattern for those individuals.

Indicators of manatee presence in the northern GOM outside FL have increased since the 1990s. Increasing numbers of opportunistic public sighting reports in the northern GOM, especially in warm months (Bonde & Lefebvre, 2001; Fertl *et al.*, 2005; Hieb *et al.*, 2016), coincided with increases in manatee counts at winter aggregation sites in northwest peninsular FL (Butler *et al.*, 2011; Kleen & Breland, 2014). This study confirms that some FL manatees migrate west to locations further removed from known essential winter habitat than previously known, occupy the region for sustained periods, and often return year after year. Those lines of evidence together indicate that manatees are regular seasonal occupants of the northern GOM, and suggest that manatee use of the region is greater than it was before the 1990s.

Potential drivers of distribution change

Mechanisms driving the movement patterns reported here are unknown, but they are of interest to scientists and managers, especially since manatees making relatively long-range movements between wintering sites in peninsular FL and warm-season ranges on the northern GOM coast pass by apparently suitable habitat. Some speculation has been put forth on drivers that may cause manatee distribution changes (Edwards, 2013), but data to support those ideas as they relate to

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manatees in the northern GOM have been largely anecdotal.

Manatees and associated habitat within FL are under pressure from human activity, indirectly and directly, as the human population there grows. Watercraft interactions are a leading cause of adult manatee mortality in FL (Runge *et al.*, 2015). Manatees are known to flee from approaching boats, and manatee use of specific foraging patches and warm-water springs has been negatively correlated with high boat traffic (Nowacek *et al.*, 2004; Berger, 2007; Miksis-Olds *et al.*, 2007). Motorboats can directly cause long-term damage to seagrass beds by prop scarring, and eutrophication from coastal development has negatively affected seagrass abundance (Waycott *et al.*, 2009). There is potential for any or all of those anthropogenic effects to result in manatee avoidance of affected areas, which could in turn increase animal density in adjacent areas and thus alter distribution of manatees.

Climate change has altered animal and plant dispersal and phenology patterns worldwide (Parmesan & Yohe, 2003; Root *et al.*, 2003) and in the northern GOM (Fodrie *et al.*, 2010; Pinsky *et al.*, 2013). Increases in air and sea surface temperatures should decrease the amount of time within the year that manatees are constrained to essential winter habitat and increase the time available for warm-season travel. Sea level rise and decreasing rainfall may work together to alter distribution of submerged aquatic vegetation by increasing depth and salinity in areas that manatees use to forage (Short & Neckles, 1999). Climate-related changes may alter dispersal timing and distribution of suitable manatee habitat, and may result in altered movement and distribution patterns as animals emigrate from overwintering sites and seek out high quality habitat.

This study focused on longer-distance migrants, but juxtaposed with other studies of FL manatees, it is evident that there is a wide range of expression of dispersal and migratory behavior within the US manatee population. Within-population variation in dispersal and migration behavior is known in other species, and may provide an evolutionary benefit to the population. For example, salmonid "homing" (returning to natal streams) for reproduction is typical behavior for most of the population, but a small proportion exhibit "straying" behavior (migration to non-natal streams) where they reproduce with conspecifics of a different population (reviewed by Keefer & Caudill 2014). In a similar phenomenon seen in other migratory fish, sub-groups of a population form contingents that exhibit "exploratory" migrations with different spatio-temporal patterns from the majority of the population (Secor, 1999). Both of those migratory strategies are thought to increase the population's resistance and resilience to environmental change by hedging against stochastic variations in habitat quality, facilitating colonization of new locations, and reducing density-dependent effects (Secor, 1999).

The ultimate benefits of variable migration behavior within fish populations may also apply to FL manatees. Manatees in the northern GOM are relatively long-distance migrants, and the

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spatial separation between them and manatee subpopulations occupying core range areas in peninsular FL may help buffer the species as a whole against small scale perturbations. For example, recent localized mass mortality events from harmful algal blooms in FL (Florida Fish and Wildlife Conservation Commission, 2015) offer a stark reminder of why it may be important for manatees to be well-dispersed. The potential ultimate benefits may help explain why some manatees migrate hundreds of km annually to the northern GOM and pass by locations containing seemingly suitable habitat on that journey.

Conclusions

To achieve better understanding of manatee spatial ecology and thus better comply with US federal mandates for endangered species conservation, it is essential to define the distribution, movement patterns, and locations of important habitat throughout FL manatees' entire range. Those basic biogeographical data underpin comprehensive understanding of population and habitat units and provide context necessary to inform broad-scale management applications and protect biodiversity (Steen & Barrett, 2015). This study quantitatively defines geographic locations that are regularly and repeatedly used by migratory manatees in the northern GOM, findings that suggest that the region offers valuable habitat to migratory FL manatees and provide evidence of a recent change in seasonal manatee distribution. The mechanisms for the observed patterns are unknown, but may include the effects of species management and conservation efforts, anthropogenic causes, or climate changes, among others. Hence, further research is necessary to better define the drivers of the movement patterns reported here and the population distributions resulting from those movements. This study fills fundamental data gaps to support future work and provides baseline data on manatee seasonal movements and space use to assess future conservation and recovery actions (e.g., the currently debated reclassification of manatees from "endangered" to "threatened" under US law), stochastic events, or other perturbations to manatees in the GOM.

Acknowledgments

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