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Coastal habitat change and marine megafauna behavior: Florida manatees encountering reduced food provisions in a prominent winter refuge

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ABSTRACT: A decline in submerged aquatic vegetation (SAV) within Florida's spring-fed thermal refuges raises questions about how these systems support winter foraging of Florida manatees *Trichechus manatus latirostris*. We analyzed telemetry data for 12 manatees over 7 yr to assess their use of Kings Bay, a winter refuge with diminished SAV. After accounting for the effect of water temperature, we hypothesized that the number of trips out of Kings Bay would increase and the time wintering manatees spent in Kings Bay would decrease. Trips out of and into Kings Bay were also compared to assess potential influences on exiting or entering. There were no detectable differences in the number of trips out of the bay or overall time manatees spent in Kings Bay across winters. The percentage of time water temperatures were below 20°C was the single best predictor of increased time spent in Kings Bay. Trips out of Kings Bay were more likely than trips into the bay to occur after 12:00 h and during a high but ebbing tide. Nine manatees tracked for longer than 75 d in winter spent 7 to 57 % of their time in the Gulf of Mexico, and 3 of these manatees spent 7 to 65 % of the winter >80 km from the mouth of Kings Bay. Results suggest the low amount of SAV in Kings Bay does not obviate its use by manatees, though there are likely tradeoffs for manatees regularly foraging elsewhere. Accounting for movements of Florida manatees through a network of habitats may improve management strategies and facilitate desirable conservation outcomes.

KEY WORDS: *Trichechus manatus latirostris* · Kings Bay · Telemetry · Forage · Florida springs · Thermal refuge

1. INTRODUCTION

Many marine and coastal ecosystems are changing due to climate change, habitat degradation, or other anthropogenic stressors (Lotze et al. 2006, Waycott et al. 2009, Hoegh-Guldberg & Bruno 2010). While fluctuating resources and climatic conditions have led to gradual shifts in patterns of habitat use for some coastal and nearshore marine mammals (Hartel et al. 2015), many others are unable to adapt quickly enough to avoid sharp population declines or otherwise subtle but deleterious effects on survival, growth, and reproduction (Davidson et al. 2012). Indeed, the slow growth, low fecundity, and coastal range of marine mammals make them especially vulnerable to extinction (Davidson et al. 2012). Sirenians (manatees and dugongs), comprising the only herbivorous marine mammals, are facing climate- and hu-

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man-induced reductions in habitat because there are often concomitant limitations on their ability to find and forage on suitable benthic vegetation (Davidson et al. 2012, Estes et al. 2016, Marsh et al. 2017). Thus, there is a critical need to protect essential habitats whenever possible (Davidson et al. 2012, Marsh et al. 2017) and to understand how sirenians, and other marine megafauna, may respond to reductions in habitat when such losses do occur (Preen & Marsh 1995, Hartel et al. 2015, Estes et al. 2016). To best accommodate coastal species encountering these changes, management plans must be adaptive to anticipate potential range shifts and altered patterns of habitat use (Hartel et al. 2015).

We focused on the recovering population of Florida manatees *Trichechus manatus latirostris*. The estimated Florida manatee population in 2011 and 2012, based on statewide surveys and modeling to adjust raw counts, was greater than 6000 individuals (Martin et al. 2015), with some regions (e.g. the Northwest Florida management unit) exhibiting exponential increases over the last 20 yr (Kleen & Breland 2014, Littles et al. 2016, Sattelberger et al. 2017). These trends, among other considerations, led to the recent downlisting of West Indian manatees from endangered to threatened in the US Code of Federal Regulations (50 CFR 17, CFR 2017). Our goal was to evaluate whether and how vegetation declines in a prominent winter refuge have affected habitat use. Ideally, results will help inform ongoing management for this species.

Florida manatees traverse waters along the Florida coastline year-round, and along the Gulf of Mexico coast, they have been predominantly sighted in estuaries and nearshore seagrass meadows (Powell & Rathbun 1984, Kochman et al. 1985, Fertl et al. 2005). Manatees in the Northwest Florida management unit exist near the upper end of the latitudinal range for the genus, and they exhibit temperature-mediated seasonal movements in response to cooler temperatures (Hartman 1979). This type of temperature-driven movement between habitats has also been observed in dugongs *Dugong dugon* (Holley 2006, Marsh et al. 2011), which highlights the importance of multiple habitats in sustaining healthy sirenian populations (Castelblanco-Martínez et al. 2009, Alvarez-Aléman et al. 2017, Haase et al. 2017). In warmer months, Florida manatees often disperse widely to breed and forage on submerged aquatic vegetation (SAV) (Campbell & Irvine 1977, Hartman 1979, Powell & Rathbun 1984, Rathbun et al. 1990, Deutsch et al. 2003). When coastal water temperatures drop below 20°C, manatees often cluster near natural springs or warm-water plumes emanating from coastal power stations (Irvine & Campbell 1978, Hartman 1979, Kleen & Breland 2014). During these periods, manatees may feed on nearby freshwater and estuarine SAV, as shown by analyses of stable isotopes in plant and animal tissues (Reich & Worthy 2006, Alves-Stanley et al. 2010). Manatees may also leave springs to forage in nearshore seagrass beds (Rathbun et al. 1990). Thus, an ideal habitat for wintering manatees would provide both warm water and ample SAV in close proximity to minimize bioenergetic expenditures. Unfortunately, many of Florida's coastal bays inhabited by manatees have been degraded, with stark declines in SAV. The decrease in native macrophyte coverage is likely the result of several interacting factors including, for example, changes in salinity regimes due to varying precipitation patterns and lower groundwater levels, freshwater withdrawals, tropical storms, sea level rise, and the proliferation of macroalgae (Hoyer et al. 2004, Frazer et al. 2006, Heffernan et al. 2010, Hudon et al. 2014, Florida Springs Institute 2016). Substantial declines in native SAV and increased dominance of nuisance algae and invasive species, like the cyanobacterium *Lyngbya* sp. and *Myriophyllum spicatum*, are commonplace (Tomasko et al. 1996, Hauxwell et al. 2004, Caccia & Boyer 2007, Camp et al. 2014). The loss of suitable SAV near warm-water sites may be causing manatees to leave winter refuges more frequently or for longer durations, resulting in prolonged exposure to cold temperatures. To investigate this issue, we analyzed telemetry data for Florida manatees wintering in a system that provides ample thermal refuge but limited food.

Kings Bay, a coastal embayment along the central Gulf coast of peninsular Florida, affords a unique opportunity to evaluate winter habitat use by manatees. Increasing numbers of manatees use its multiple springs as thermal refuges (Kleen & Breland 2014, Littles et al. 2016, Sattelberger et al. 2017). The abundance of SAV has significantly declined in Kings Bay, with the most recent surface water management plan noting a decline in biomass since 1994 and a decrease of roughly 72 % between 2006 and 2013 (Fig. 1) (SWFWMD 2015). Vegetation decline has been perpetuated by increased manatee grazing (Hauxwell et al. 2004), water quality issues (Florida Springs Institute 2016), growth of nuisance algae (Heffernan et al. 2010, Hudon et al. 2014), and stress from increased salinity (Frazer et al. 2006). Historical data indicate clearly that Florida manatees have consistently relied on Kings Bay and nearby offshore areas as a source of food throughout the year and as

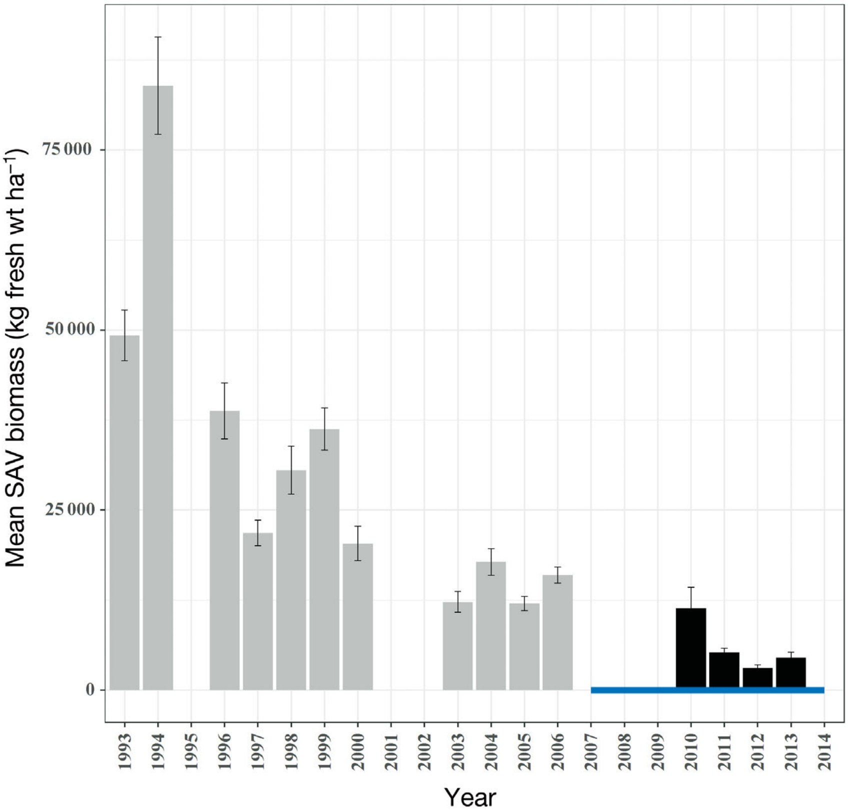

Fig. 1. Change in mean (± SE) above-ground biomass of submerged aquatic vegetation (SAV) within Kings Bay, with the blue horizontal line depicting years of manatee tracking data in the current study and bars overlapping that timeframe in black. Adapted from SWFWMD (2015, their Fig. 26)

a warm-water refuge during winter (Hartman 1979, Etheridge et al. 1985, Packard & Wetterqvist 1986, Berger 2007). Documenting movements of manatees between Kings Bay and the nearshore environment was a key first step in determining whether the loss of 1 potentially supplementary function (i.e. source of forage) has influenced Kings Bay's primary role as a thermal refuge. Continuous reductions in SAV prompt questions regarding the relative importance of wintering grounds that can provide both food and shelter from harsh conditions. We analyzed tracking data from manatees bearing satellite tags during 7 consecutive winters and explored patterns in movements related to sex, size class, time of day, and tidal stage. After accounting for interannual temperature variability, we hypothesized there would be an increase in the number of manatee trips out of Kings Bay and a decrease in the overall amount of time manatees spent inside of Kings Bay during winter. If wintering Florida manatees are truly dependent on Kings Bay vegetation for food, such findings would correspond with the downward trend in available SAV in the bay.

2. MATERIALS AND METHODS

2.1. Study area

Kings Bay is a spring-fed, tidally influenced waterbody covering approximately 1.75 km^2 within the Crystal River National Wildlife Refuge, near the city of Crystal River in Citrus County, Florida, USA. It forms the headwaters of Crystal River, which flows westward for approximately 11 km before discharging into the Gulf of Mexico (Frazer et al. 2001). The bay attracts large numbers of Florida manatees, with Kleen & Breland (2014) documenting use by at least 500 to 600 manatees in the winters between 2010 and 2012. Over 41 named springs and spring complexes provide warm water (approximately 23°C) year-round, while water temperatures near the mouth of the bay can drop to below 10°C during winter (Hartman 1979, Kochman et al. 1985, Vanasse Hangen Brustlin 2009, Chen 2014). Historically, manatees grazed on several species of SAV found in the bay (e.g. *Vallisneria americana*, *Ceratophyllum demersum*, *Potamogeton* sp., *Hydrilla verticillata*, and *Najas guadalupensis*) (Hauxwell et al. 2004, Jacoby et al. 2014) in addition to feeding on seagrasses offshore. We defined a study region bounded by latitudes of 28.60° and 29.04° N, which contained Kings Bay, Crystal River, 3 additional spring-fed rivers (i.e. Withlacoochee, Homosassa, and Chassahowitzka rivers), 1 power plant, and the adjacent waters in the Gulf of Mexico (Fig. 2).

2.2. Manatee trajectories

The US Geological Survey (USGS) Sirenia Project provided telemetry information for 18 manatees that had been tagged between 2007 and 2014 as part of a study on manatee movement in the northern Gulf of Mexico. Experienced personnel either captured the manatee before tagging it or attached a tag to a free-swimming animal (Bonde et al. 2012). Tags consisted of a belt enclosing the manatee's peduncle and a nylon tether attached to a floating cylindrical housing (Rathbun et al. 1990, Reid et al. 1995). The sex and total length of captured manatees were recorded as

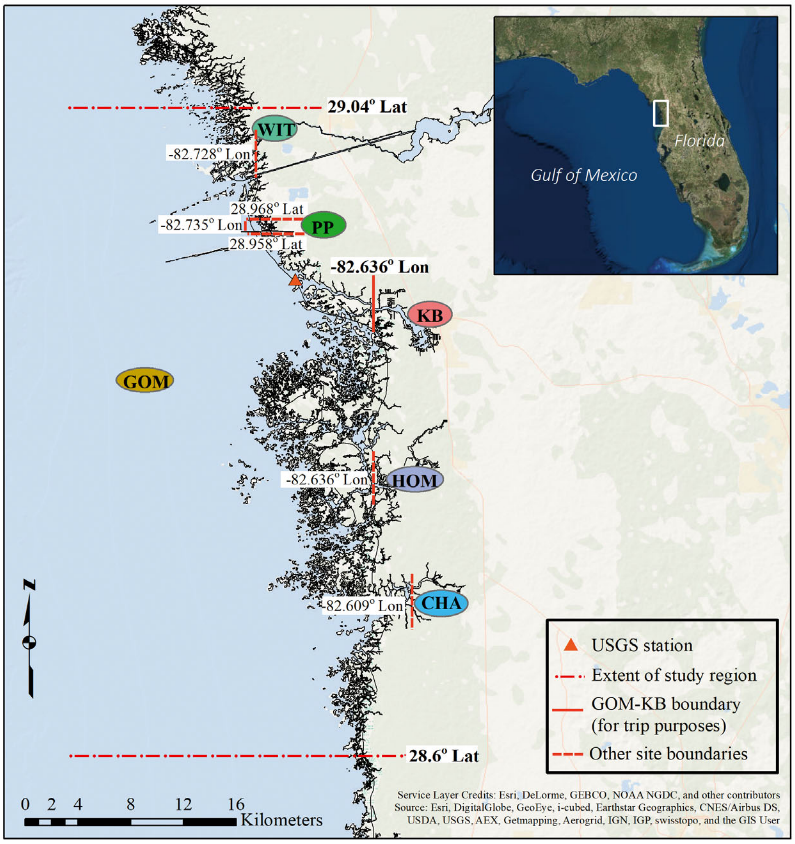

Fig. 2. Study region, delineated by latitudes. KB: Kings Bay, including the boundary for identifying trips into and out of the bay and additional spatial boundaries for other sites in the study region; US Geological Survey (USGS) station: site for records of water elevations and temperatures (Site 285531082412600); GOM: Gulf of Mexico; PP: Crystal River power plant; HOM: Homosassa River; CHA: Chassahowitzka River; WIT: Withlacoochee River

the tracking period for each animal). We then linked successive relocations for each animal between December and February (i.e. winter) to create a winter trajectory, while periods between March and November were evaluated as separate non-winter trajectories (R package adehabitatLT, Calenge 2015; R version 3.3.2, R Development Core Team 2016). No animal was tracked continuously over the entire study period, but several were tracked over successive winters. The winter in each year was evaluated as a separate monitoring bout (i.e. continuous tracking record for a single manatee or winter year), from which we could evaluate trends across years. The total time tracked, during winter and non-winter (i.e. March through November) periods, was then used to estimate the proportion of time manatees spent in various locations within the study region. Subsequent analyses only included manatees that were tracked for at least 25 % of 1 winter (i.e. ≥22.5 d) and remained within the study region for at least 50 % of the time they were tracked.

We established 82.636° W longitude as the boundary for distinguishing the western extent of Kings Bay and subsequent trips into and out of the bay. Although there is no specified boundary between the 2 systems, this arbitrary boundary is close to the confluence of the Salt and Crystal rivers, and so Kings Bay, as defined, includes the upper portion of Crystal River. Moving the boundary slightly east or west did not change the calculated number of trips out of the bay. For each manatee, we estimated the proportion of the total tracked time that was spent in rivers within the broader study region and outside the study bounds to the north or south (i.e. other area). Longitudinal boundaries were identified to estimate the proportion of time manatees spent within adjacent spring-fed rivers and the waters surrounding the Crystal River power plant. We used the same Kings Bay longitudinal boundary for the Homosassa River, as the rivers are roughly parallel and discharge in close proximity to one another. The longitudinal boundaries for the Withlacoochee and Chassahowitzka rivers were defined at 82.728° and 82.609° W, respectively, to provide a similar demar-

they were tagged. For free-tagged animals, visual estimates and belt sizes were used to assign each manatee to a size class. The floating housing contained a GPS receiver (TMT-240, TMT-460, TMT-462, or TMT-464; Telonics, www.telonics.com) that recorded locations at 30 min intervals and transmitted those locations to the user via an Argos Data Collection and Location System (www.argos-system.org/). Data from the older tags (TMT-240) correctly ~~identified~~ 90 % of GPS locations within 15 m of the tag location, and the newer tags (TMT-460, TMT-462) were tested at known locations ~~to document that the median distance encompassing~~ 90 % of locations ~~was~~ 4 m when there was a clear view of the sky. Similar to other tracking studies using GPS technology (Rempel et al. 1995, Witt et al. 2010), obstructions, such as trees or docks, degraded the accuracy.

Manatee relocation data were screened to delete outliers (movement rate > 2.78 m s^{-1}, locations mapped over land or offshore, and locations falling outside cation of divergence from the main river stem. All of the aforementioned rivers have a combination of salt marsh, mangroves, and island habitat features where they discharge into the Gulf of Mexico, and the selected longitudinal boundaries demarcate the transition into a riverine system. Given the absence of water temperature data to distinguish the exact location and size of the warm-water plume from the power plant, manatee relocation information aided in delineating general longitudinal and latitudinal boundaries, as depicted in Fig. 2. A more comprehensive comparison of differences between rivers and the power plant would require additional considerations, including the location of spring sites, discharge volumes, distance to the Gulf, and metrics for water quality (i.e. salinity, temperature etc.), that were beyond the scope of this study.

2.3. Statistical models

Studies of large animal trajectories, including marine mammals, often include individuals tracked over several years, and mixed-effect models can account for the correlated variance structure when testing for significant main effects (Kuhn et al. 2009, Tosh et al. 2012, Curtice et al. 2015, Hamilton et al. 2017). We used a maximum likelihood approach applied to generalized linear mixed-effect models (glmer function in lme4 R package, Bates et al. 2015) in our analysis. We constructed additive models (i.e. no interactions), and manatee ID was a random effect in all models. In some cases, we tested alternate optimization functions (optimx R package, Nash & Varadhan 2011) and/or models were updated with 90 000 additional function evaluations to improve convergence. Multiple models were evaluated with Akaike's information criterion adjusted for small sample sizes (AICc) to identify the best ones (Symonds & Moussalli 2011). Based on models with explanatory power, post hoc Tukey's HSD analyses facilitated pairwise comparisons of factor levels (glht function in R package multcomp, Torsten et al. 2016). Figures were generated using various functions within the ggplot2 package (Wickham 2009).

2.4. Model covariates

We evaluated the potential effects of winter year (WYR), gender (SEX), water temperature (TEMP), manatee size (SIZE), tide stage (TIDE), time of day (6HR), and gage height (GAGE) relative to the North American Vertical Datum of 1988 (NAVD 88) on the number of hours spent in Kings Bay, number of aggregate trips out of the bay, and individual trips out of (versus into) Kings Bay (Table 1). These predic-

Table 1. Parameters for generalized linear mixed-effect models, i.e. the total hours manatees spent in Kings Bay over winter (Time), aggregate number of trips manatees made out of Kings Bay during winter (Trips), and trips out of (Trips-OUT) relative to trips into Kings Bay. The number of hours manatees were tracked in the study area during winter was included as an offset in both Time and Trips models. USGS: US Geological Survey; TL: total length; NAVD: North American Vertical Datum of 1988

Parameter (code)	Description	Model(s)
Winter year (WYR)	~~1 December through 28/29 February~~	Trips, Time
Water temperature (TEMP)	Average bottom water temperature recorded at the USGS monitoring station at Shell Island near the mouth of Crystal River (Site 285531082412600) while manatees were tracked within the study area	Trips, Time
Exposure to cold (tCOLD)	~~Percentage~~ of time an individual manatee's tracking bout was in the study area and daily maximum bottom water temperatures recorded near the mouth of Crystal River (USGS Site 285531082412600) did not exceed 20°C	Trips, Time
Size class (SIZE)	Subadults or small adults (250–280 cm TL) and medium or large adults (≥280 cm TL); classes were adapted from O'Shea et al. (1985)	Trips, Time
SEX	Male or female	Trips, Time
Maximum daily bottom water temperature (tMAX)	Daily maximum bottom water temperatures recorded near the mouth of Crystal River (USGS Site 285531082412600)	Trips-OUT
6-hour time span (6HR)	Factor representing the 6 h time frame during which a trip took place (i.e. 24:00–06:00, 06:00–12:00, 12:00–18:00, and 18:00–24:00 h)	Trips-OUT
Gage height (GAGE)	Gage height above NAVD 88 at the USGS monitoring station (USGS Site 285531082412600)	Trips-OUT
Tide stage (TIDE)	Factor variable denoting the tidal stage (i.e. slack, ebb, or flood)	Trips-OUT
Manatee ID	Random effect included in all models to account for the variation due to manatee individuals	All

tors may help explain manatee behavior under certain circumstances (Hartman 1979, Deutsch et al. 2003, Berger 2007), and we tested their potential relevance to wintering manatee movement decisions in Kings Bay.

Potential differences among WYRs were assessed to determine whether the overall downward trend in the amount of available forage within Kings Bay (SWFWMD 2015) had any detectable effect on the rate at which manatees left the bay or the amount of time manatees spent in Kings Bay during winter. SEX was included in models because male manatees are known to exhibit more dispersed distributions and move greater distances during non-winter periods (Deutsch et al. 2003, Flamm et al. 2005), and it was unclear whether these non-winter forays might provide males with a mental map of alternative refuges that they could visit opportunistically to supplement needs during winter. We evaluated the potential effect of SIZE because late juvenile and subadult manatees have shown greater susceptibility to cold stress (O'Shea et al. 1985), so they could be more inclined to stay near thermal refuges to minimize heat loss in winter.

The movements of manatees may be influenced by several environmental factors. For example, manatees' poor ability to thermoregulate means that they seek warmer water when exposed to colder temperatures (Hartman 1979, Deutsch et al. 2003, Laist & Reynolds 2005); thus, we included 3 potential water temperature metrics in our models. Daily water temperatures from the USGS monitoring station at Shell Island near the mouth of Crystal River (Site 285531082412600; see Fig. 2) were used to estimate the average water temperatures (TEMP) manatees were exposed to during trips out of Kings Bay, the proportion of tracked time water temperatures were at or below 20°C (tCOLD), and the maximum daily water temperature (tMAX). Lastly, we tested for potential effects of 6HR, GAGE, and TIDE because these variables could differentiate between a manatee's decision to leave (versus return to) Kings Bay. For example, higher water elevation could provide access to forage that would be inaccessible at a low tide (Deutsch et al. 2003). Florida manatees might also move with the current, as has been observed for Antillean manatees (Deutsch et al. 2003), as a strategy for conserving energy. The potential effect of TIDE was explored by identifying daily high and low tides, rising tides, and falling tides from the gage height. Gage height was measured at 15 min intervals at the USGS monitoring station at Shell Island near the mouth of Crystal River (Site 285531082412600), and we used the reported gage height for consecutive time stamps to identify whether the water level increased (flood tide), decreased (ebb tide), or remained the same (slack tide). There would be a slight delay between when water started ebbing or flooding at the USGS water monitoring station at the mouth of the river and the selected demarcation line for trips into and out of the bay, approximately 0.5 km upriver. However, this was the best available data for providing an indication of water level and tide stage during manatee trips out of Kings Bay. We set the threshold of gage height change to 4 times the data accuracy of the monitoring station (i.e. ~12.2 mm) to differentiate slack tides from ebb and flood tides. We then graphed gage height against tide stage to confirm this threshold was sufficient to capture slack periods (typically 2–3 time steps before and after high and low tides), without encompassing other tide stages.

2.5. Time and Trips models

Estimates for the amount of time spent in Kings Bay and trips out of the bay were derived from tracking data. The number of hours in Kings Bay was estimated using the time stamps in trajectory files and relocations within Kings Bay. Time in Kings Bay was rounded to the nearest hour prior to running Poisson mixed models. A trip was defined as the crossing of the established longitudinal boundary in Kings Bay, and the date–time stamps from consecutive trips into and out of the Bay were used to estimate the duration of each trip. Trips less than 1 h on either side of the boundary were excluded to avoid arbitrarily inflating the number of trips. We calculated the total number of trips out of Kings Bay during each tracking bout.

For the total number of hours manatees spent in Kings Bay during winter (Time models) and number of aggregate trips out of Kings Bay (Trips models), we assumed a Poisson error distribution with a log link function and took the log of the total number of hours each manatee was tracked in the study area as an offset in both Time and Trips models. Time and Trips models included WYR, water temperature (TEMP or tCOLD), SEX, and SIZE as fixed effects. WYR was a fixed effect with levels corresponding to winters with tracking data, excluding years with only a single manatee bout. This approach resulted in up to 10 total parameters in the full models for manatee Time and aggregate Trips. Given the aforementioned predictors, we tested 17 different models for Time and Trips.

2.6. Trips-OUT models

We tested for significant differences in the predictors for a single trip out of Kings Bay (versus into Kings Bay) using binomial mixed models with a logit link. In binomial models, the response variable (trips) was coded 1 for a trip out of Kings Bay and 0 for a trip into the bay. Manatee trips were matched to the correct tidal stage using the date–time stamp at which a manatee crossed the boundary into or out of Kings Bay, rounded to the nearest 15 min time interval. We investigated patterns in trips out relative to 6HR by totaling the number of trips in successive 6 h intervals. This timeframe ensured that we did not parse the data among too many model covariates. Thus, models for trips out included up to 5 factors (i.e. tMAX, 6HR, GAGE, and TIDE), including the random effect for manatee ID (Table 1). This approach resulted in a final subset of 16 unique binomial models for detecting differences between trips out of Kings Bay and into the bay.

Table 2. Total number of days tracked during winter (December through February) and non-winter (March through November) for the 13 manatees that largely remained in the study area for at least 1 winter year (WYR). WYRs in **bold** indicate that there was at least 1 bout for which the manatee spent 50 % or more of the time tracked within the study area. See Fig. 3 for the proportion of overall tracked time each manatee spent in Kings Bay and adjacent river systems versus in other locations outside the study area. WYR(s) in **underlined bold** were ultimately excluded from models for the aggregate number of trips and overall time spent in Kings Bay because of insufficient sample size (TCR-07 2007, TCR-19 2010, and TPH-01 2009), failure to meet the minimum 25% tracking duration for a winter bout (TCR-07 2008), or zero observations (i.e. no time spent in Kings Bay during the specified winter; TCR-05 2010)

Manatee ID	Sex	Size class	Winter	Non-winter	WYR(s) tracked
TCR-05	Male	Subadult/small adult	29.7	133.9	**2011**
TCR-07	Male	Adult	100.4	83.8	**2007**, **2008**
TCR-10	Female	Adult	89.5	210.1	**2008**
TCR-13	Male	Adult	308.6	781.9	**2008**, 2009, 2010, 2011
TCR-19	Male	Adult	293.6	648.1	**2010**, **2011**, **2012**, **2013**
TCR-23	Male	Adult	86.3	103.6	**2013**
TCR-24	Female	Adult	111.1	274.8	**2013**, **2014**
TCR-25	Male	Adult	33.2	0.0	**2014**
TPH-01	Female	Adult	179.4	664.1	**2008**, **2009**
TPH-05	Female	Subadult/small adult	75.0	404.8	**2010**, **2011**
TPH-06	Female	Subadult/small adult	61.1	233.5	**2011**
TPH-09	Male	Adult	82.3	267.8	**2011**, 2012

3. RESULTS

Twelve of the initial 18 animals tagged by USGS personnel over the span of this research had at least 1 continuous tracking bout longer than 22.5 d that was located within the study area for at least 50 % of the time, which met the criteria for inclusion in our analyses. The duration of tracking for these individuals, including periods spent outside the study area, spanned ~30 to 309 d during winters and 0 to 782 d during non-winter periods (Table 2). Individual trajectories from manatees spending winters in the Kings Bay region revealed several interesting aspects of habitat use. Of the 12 manatees, 5 moved beyond our study area for 7 to 65 % of the time during winter, when locations were pooled across tracking bouts (Fig. 3). Two of the individuals that spent the greatest percentage of winter elsewhere were tracked in the Wakulla River (i.e. TCR-13 and TPH-09), another known warm-water refuge for manatees. Including bouts for these 2 individuals, manatees that remained in the study area for at least 1 bout spent a greater proportion of their time, on average, in Kings Bay during winters (0.50 ± 0.26, mean ± SD) than during non-winter periods (0.10 ± 0.10). Two female manatees, TCR-24 and TPH-05, spent more time in the Homosassa River than in Kings Bay or the Gulf of Mexico during winter. The Withlacoochee and Chassahowitzka rivers were visited least frequently (winter and non-winter), with only 2 manatees visiting each site. Conversely, 11 of the 12 manatees visited the waters surrounding the power plant during 1 or both seasons, though none spent more than 15 % of their time at that location (Fig. 3).

Data from 14 separate tracking bouts for 11 manatees were used in linear models examining the number of hours manatees spent inside Kings Bay during winter. Of the 11 manatees included in analyses, 3 were subadults or small adults, 7 were medium-sized adults, and 1 was a large adult (TCR-24), so we pooled data for the 1 large adult with data for the medium adults. In addition, observations from WYRs 2007, 2009, and 2010 were excluded from statistical models because there was only information for a single bout during each of those winters. All observations were compared to those at the intercept, which represented observations for female adult manatees during WYR 2008.

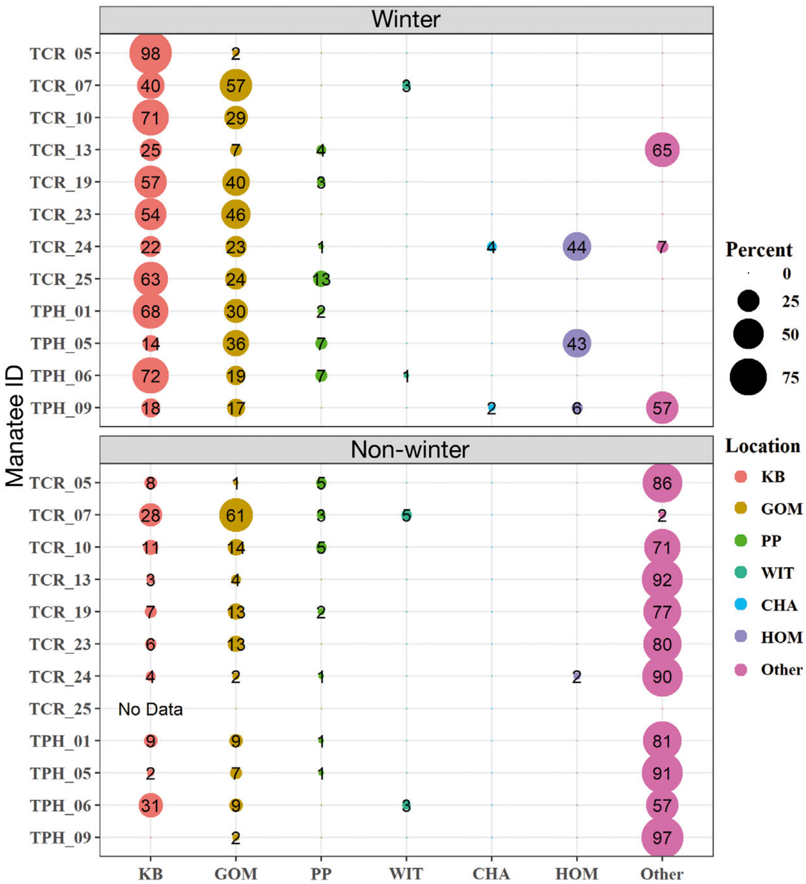

Fig. 3. Bubble plot depicting the percent of time each manatee spent outside the study area (other), in Kings Bay (KB), in the Gulf of Mexico (GOM), at the Crystal River power plant (PP), and in the Withlacoochee (WIT), Chassahowitzka (CHA), and Homosassa (HOM) rivers during winter and non-winter periods pooled across tracking bouts

~~Overall, AIC$_c$ scores indicated that models excluding sex, size, and mean bottom water temperature (TEMP) performed better than models including those parameters.~~ The proportion of time manatees ~~may have been exposed to cooler water tempera~~tures in the study area (tCOLD) was a better predictor than TEMP, and the best model to account for the number of hours wintering manatees spent in Kings Bay included tCOLD alone, with individual manatees as a random effect (Table 3). The proportion of each bout with exposure to cold was a highly significant factor ($p < 0.001$), and there was a positive linear relationship between tCOLD and the number of hours manatees spent in Kings Bay (Fig. 4). Incidentally, when we compared the average bottom water temperatures across winter years, not exclusive of tracking bouts, the mean ± SD temperatures in WYR 2011 (17.9 ± 2.1°C) and 2012 (18.6 ± 2.3°C) were higher than those recorded in WYR 2010 (15.1 ± 3.5°C), 2013 (17.1 ± 2.8°C), and 2014 (16.9 ± 2.0°C), though we had insufficient data to test statistically significant variation in time spent within Kings Bay among years.

Assessing patterns in the aggregate number of trips manatees made between Kings Bay and the Gulf of Mexico over the course of several winters was challenging due to variability in the duration of continuous records and behavior of individual manatees. In winters, bouts included in the analysis varied from 29 to 90 d (58.6 ± 27.0 d, mean ± SD) and represented between 461 and 3700 relocations. Even after accounting for the random effect of individuals in mixed models, there were no significant predictors of the total number of trips manatees made out of Kings Bay, with the null model having the lowest AIC$_c$ value (Table 3).

The best binomial trip model for the probability of a single trip out of (versus into) Kings Bay included time of day, gage height, and tide stage as predictors (Table 3). The probability of a trip out of Kings Bay, compared with a trip into the bay, was significantly greater between 12:00 and 24:00 h, during ebb tides, and at relatively higher water elevation (Fig. 5). Post hoc Tukey's comparisons confirmed a significantly greater probability for a trip out of Kings Bay during ebb tides, when compared with slack ($p < 0.01$) and flood ($p < 0.05$) tides, though there was no significant difference between slack and flood tides. For context, the percentages of ebb, flood, and slack tides over the winter tracking periods in this study were 47, 37, and 16%, respectively. Post hoc analysis for the timing of trips out of Kings Bay, relative to those into the bay, revealed a significantly higher probability for a trip out to occur between 12:00 and 24:00 h ($p < 0.001$), ~~whereas there was no detectable difference in the probability of trips out versus in during 00:00 to 12:00 h or 12:00 to 24:00 h~~. Visualizing these results for all individual manatees clearly showed that most manatees made more trips out of Kings Bay between 12:00 and 24:00 h and trips into the bay between 24:00 and 12:00 h (Fig. 6).

Table 3. Comparison of models applied to data on the number of hours manatees spent in Kings Bay (Time), total trips taken out of the bay (Trips), and trips out of Kings Bay compared with trips into the bay (Trips-OUT). While results are only presented for the top 10 models, all combinations of fixed effects were tested, including those testing each fixed effect individually. All models included individual manatees as a random effect. *k*: number of parameters in the model; AIC_c: Akaike's information criterion (AIC) corrected for small sample sizes; ΔAIC_c: change in AIC or AIC_c relative to the best model (i.e. lowest AIC or AIC_c); *w*: relative weight of evidence for each model; LL: log-likelihood; ~: explanatory variable; all other abbreviations as per Table 1

Parameter/Candidate models	*k*	AIC_c	ΔAIC_c	*w*	LL
Time					
~ tCOLD	3	187.41	0.00	0.52	–89.50
~ TEMP	3	189.26	1.85	0.21	–90.43
~ SEX + tCOLD	4	189.95	2.54	0.15	–88.75
~ SIZE + tCOLD	4	190.77	3.36	0.10	–89.16
~ SEX + SIZE + tCOLD	5	193.34	5.93	0.03	–87.92
~ WYR	6	203.88	16.47	0.00	–89.94
~ SIZE + WYR	7	208.68	21.27	0.00	–88.01
~ tCOLD +WYR	7	210.12	22.71	0.00	–88.73
~ SEX + WYR	7	210.92	23.51	0.00	–89.13
~ SEX + SIZE + WYR	8	211.41	24.00	0.00	–83.31
Trips					
~ 1 (NULL)	2	86.34	0.00	0.52	–40.62
~ tCOLD	3	89.18	2.84	0.12	–40.39
~ SIZE	3	89.46	3.12	0.11	–40.53
~ TEMP	3	89.63	3.29	0.10	–40.62
~ SEX	3	89.64	3.30	0.10	–40.62
~ SIZE + tCOLD	4	93.02	6.68	0.02	–40.29
~ SEX + tCOLD	4	93.22	6.88	0.02	–40.39
~ SEX + SIZE	4	93.50	7.16	0.01	–40.53
~ WYR	6	98.05	11.71	0.00	–37.02
~ SEX + SIZE + tCOLD	5	98.07	11.73	0.00	–40.28
Trips-OUT					
~ GAGE + TIDE + 6HR	8	440.85	0.00	0.41	–212.25
~ GAGE + TIDE + tMAX + 6HR	9	441.30	0.45	0.33	–211.43
~ TIDE + 6HR	7	442.94	2.09	0.14	–214.33
~ TIDE + tMAX + 6HR	8	443.51	2.66	0.11	–213.58
~ GAGE + 6HR	6	451.68	10.83	0.00	–219.74
~ 6HR	5	452.02	11.17	0.00	–220.93
~ GAGE + tMAX + 6HR	7	452.23	11.38	0.00	–218.98
~ tMAX + 6HR	6	452.65	11.80	0.00	–220.22
~ GAGE	3	570.28	129.43	0.00	–282.11
~ GAGE + tMAX	4	570.96	130.12	0.00	–281.43

4. DISCUSSION

Sirenians, and coastal species around the world, are facing changes in habitat due to climate-driven and other anthropogenic influences (Lotze et al. 2006, Waycott et al. 2009, Hoegh-Guldberg & Bruno 2010, Marsh et al. 2011, 2017). Although the recent downlisting of West Indian manatees suggests this population is recovering (CFR 17, Runge et al. 2017), significant changes in their wintering grounds may affect within-season movements and habitat use by the growing population. While studies have documented manatees in Kings Bay throughout the year (Hartman 1979, Kochman et al. 1985, Packard & Wetterqvist 1986, Berger 2007, Kleen & Breland 2014), many of these same studies indicate non-winter use is intermittent at best. Nearly all the manatees tracked in this study were tagged because of their individual histories as warm-season migrants to the northern Gulf of Mexico. Therefore, our results indicating limited use of Kings Bay during non-winter periods were not surprising. Manatees primarily visit Kings Bay during winter, when its abundant warm-water springs provide thermal refuge (Berger 2007, Sattelberger et al. 2017). Similar to water levels that restrict Antillean manatee movements during the dry season (Castelblanco-Martínez et al. 2009), temperatures at this northern limit of the genus largely restrict the winter range of Florida manatees (Kochman et al. 1985, Laist & Reynolds 2005).

As wintering Florida manatees also have an option to forage in nearshore seagrass beds, this study serves as a first step in understanding whether reductions in Kings Bay vegetation pose any long-term risks to a recovering manatee population. There was no detectable increase in the number of trips out of Kings Bay or the amount of time spent in the bay over the course of this study, even though SAV has clearly declined. Results suggest that manatees in this region have not changed these aspects of their behavior in response to observed SAV loss and are likely not dependent on Kings Bay SAV for sustenance during winter. Results from a previous study of finer-scale manatee movements in northwestern peninsular Florida, conducted during the winter of 1981, indicated that 3 manatees tracked over 7 d spent an overwhelming majority of their time within Kings Bay but also made frequent departures to feed on vegetation in Crystal River during high tides that occurred around dusk (Rathbun et al. 1990). Some manatees tracked over the course of the current study spent a considerable amount of time in Kings Bay throughout the winter, but all individuals

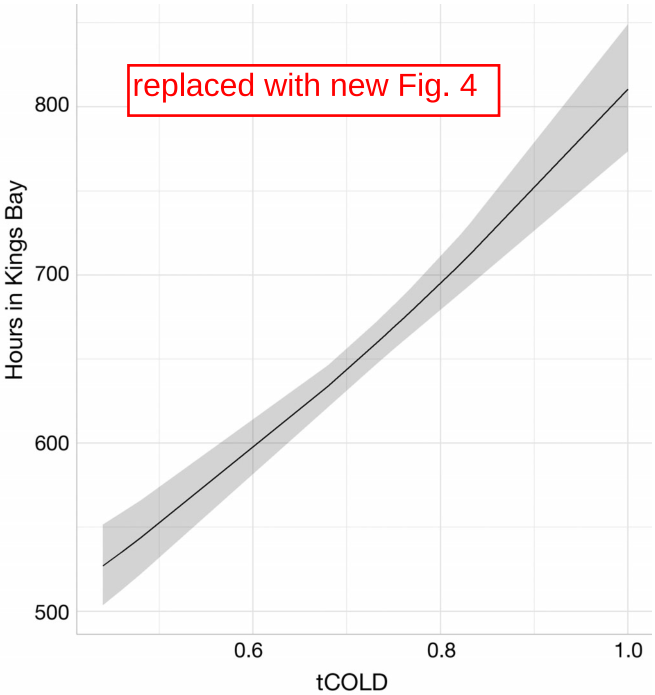

Fig. 4. Predictions from the best generalized linear mixed-effects ~~model for the num~~ber of hours spent in Kings Bay (KB), with ~~percentage~~ of time exposed to cold (tCOLD) over ~~each tracking bout as a fixed effect and manatee ID as a ran~~dom effect. The model-predicted number of hours in KB ~~given tCOLD is depicted (line), with shading representing the 95% CI~~

also made forays into the Gulf of Mexico and many visited adjacent rivers. Given potentially greater risks from cold exposure and boat strikes when manatees leave designated sanctuaries (Buckingham et al. 1999, Wirsing & Heithaus 2012, Sattelberger et al. 2017), understanding how availability of forage in thermal refuges affects movement patterns can help manage related threats.

Results of this study suggest no detectable shift in the use of Kings Bay corresponding with decreasing SAV. Earlier isotopic studies and anecdotal observations indicating a greater dependence on freshwater vegetation (e.g. Hartman 1979, Etheridge et al. 1985, Packard & Wetterqvist 1986, Reich & Worthy 2006) may have reflected opportunistic feeding behavior when freshwater SAV was more abundant. While exposure to cooler water temperatures prompted greater use of Kings Bay during winter, other factors, such as the number of boats in the water, social patterns, learning and memory, predator avoidance, and individual preferences, likely also play a role in dictating manatee movements (Buckingham et al. 1999, Sheppard et al. 2006, Berger 2007, Marsh et al. 2011, Wirsing & Heithaus 2012, Hays et al. 2016, Sattelberger et al. 2017).

Reduced SAV within Kings Bay has not negated its most critical function (i.e. warmth) for wintering manatees. As has been observed in numerous other studies (Kochman et al. 1985, Rathbun et al. 1990,

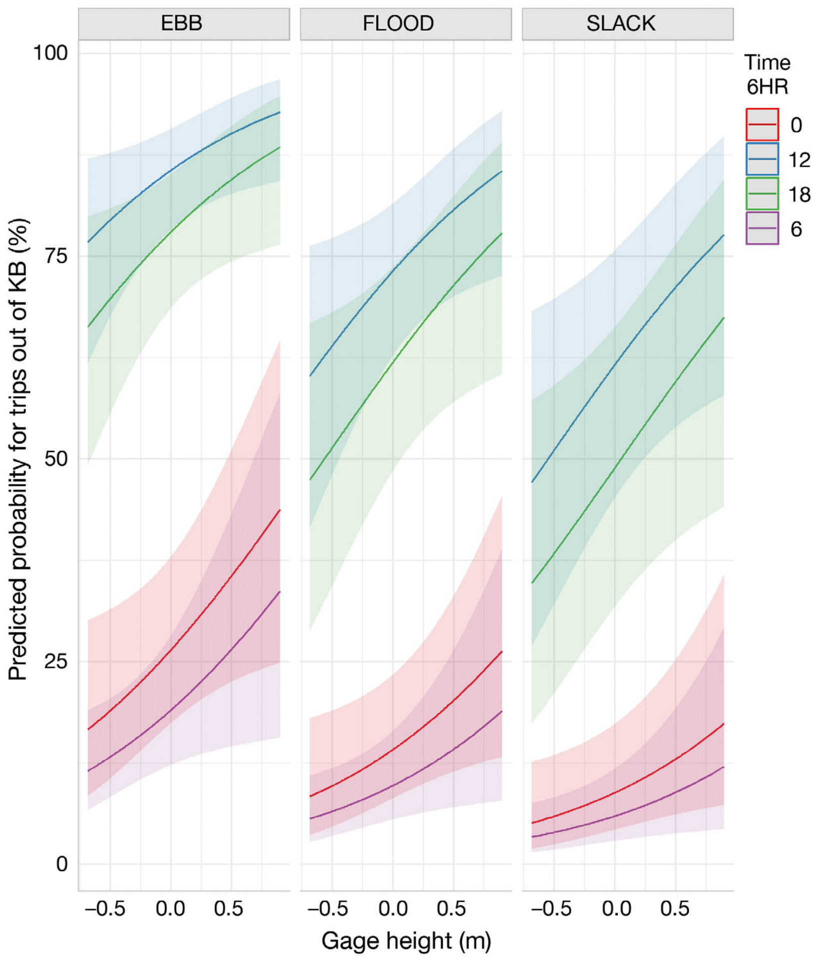

Fig. 5. Model coefficients and predictions from the best generalized linear mixed model comparing trips out of Kings Bay (KB) with those into the bay. Tide stage (TIDE), gage height (GAGE), and 6 h time period (6HR) were fixed effects, and manatee ID was included as a random effect. Panels depict the predicted probability for a trip out during the specified tide stage, given 6HR time period (solid lines) over the range of gage height relative to NAVD88 (*x*-axis). ~~For the 6th period,~~ 0 corresponds to cumulative trips taken over interval 24:00–06:00 h, 6 ≈ 06:00–12:00 h, 12 ≈ 12:00–18:00 h, and 18 ≈ 18:00–24:00 h. Shading denotes the 95% CI

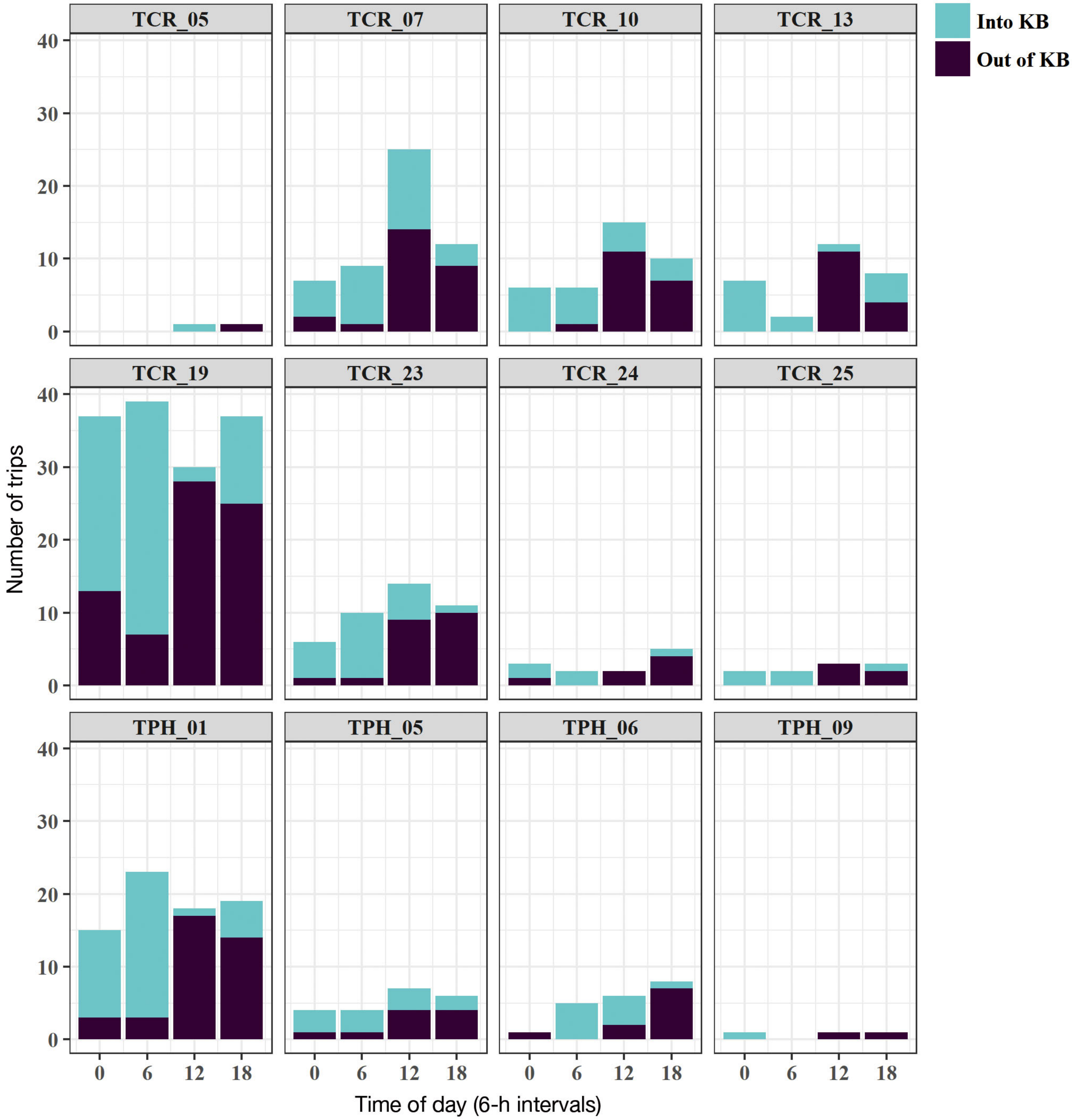

Fig. 6. Number of winter trips into and out of Kings Bay (KB) over 6 h time intervals (see Fig. 5 for details) for 12 manatees tracked from 2007 to 2014. Time reflects Eastern Standard Time, and bins reflect the number of trips that occurred over each time interval. TCR and TPH numbers indicate manatee IDs

Kleen & Breland 2014), Kings Bay springs continue to provide an important thermal resource for manatees along the west coast of Florida. We did not undertake a detailed analysis of finer-scale manatee movements within Kings Bay as part of this study. However, a recently published report comparing use of locales within Kings Bay during warm and cold periods within winter found that while manatees dispersed into surrounding habitats including offshore seagrass beds when Gulf water temperatures were greater than 17°C, the highest densities of manatees that remained in Kings Bay were always near springs (Slone et al. 2018). Sattelberger et al. (2017) also noted higher manatee abundance near springs during aerial surveys of Kings Bay conducted over 29yr. Results for manatees tracked in this study demonstrated that water temperature, and specifically the proportion of time manatees may have been exposed to temperatures below 20°C, had a significant effect on the amount of time spent in Kings Bay, with individuals spending more time in the bay when Gulf water was colder. While this result was not surprising, temperature was not the sole factor that determined manatee movement into and out of the bay. The decision to make a trip out of (versus entering) Kings Bay was related to a combination of factors, including gage height, time of day, and tide stage, while daily ~~average water temperature was not a significant influence.~~ There was a clear indication that manatees were timing trips out of the bay to move with the outgoing current, minimizing energetic expenditures, and when water levels were sufficiently high, perhaps to maximize access to ~~seagrass,~~ as has been observed for ~~dugongs~~ (Arraut et al. 2010). The greater probability for a trip out of Kings Bay after 12:00 h may reflect manatees' avoidance of humans and boats near spring sites (Buckingham et al. 1999, Berger 2007, Sattelberger et al. 2017) or correspond with warmer offshore water temperatures later in the day.

While an in-depth analysis of the potential bioenergetic consequences of diminishing SAV in Kings Bay was beyond the scope of this study our results do raise interesting questions regarding tradeoffs in traveling and foraging strategies that should be examined. Manatees in this study traveled frequently into the Gulf of Mexico, into adjacent rivers, and beyond the study area ~~at similar frequencies when comparing movements between winter years.~~ In addition, previous aerial surveys and tracking studies documented manatees using these same rivers during winter (Powell & Rathbun 1984, Rathbun et al. 1990, Kleen & Breland 2014). Given the extent of seagrass beds in the study area (Hale et al. 2004) and the presence of some SAV in nearby riverine systems, these excursions may be normal phenomena for wintering manatees that represent attempts to meet metabolic needs, especially during periods of moderate water temperatures that posed no immediate risk of cold stress. Unfortunately, habitats in most riverine systems face many of the same threats as Crystal River and Kings Bay, with the Homosassa River experiencing comparable declines in SAV (Hoyer et al. 2004, Frazer et al. 2011). A recent study of habitat use by wintering manatees in southwestern Florida (Haase et al. 2017) may offer important insights into how manatees choose between distinct habitat patches (i.e. foraging versus thermal). Haase et al. (2017) identified key factors, such as the distance between patches and the spatial configuration of patches of ~~fodder~~ and thermal refuges within locations, as important predictors in models of habitat selection. Given this context, future work to map specific manatee foraging sites used during winter in the northern Gulf of Mexico and their proximity to various thermal refuge sites might prove insightful. Understanding the extent to which sirenians rely on networks of habitats within coastal regions (Holley 2006, Castelblanco-Martínez et al. 2009, Haase et al. 2017) represents an important consideration when estimating carrying capacity and determining optimal management strategies to support the population's continued recovery.

The potential consequences of habitat loss and fragmentation are not unique to Florida manatees (Castelblanco-Martínez et al. 2009, 2012, Marsh et al. 2017), nor is this a new problem. In fact, a recent exploration of trophic cascades suggests that the extinction of Steller's sea cow *Hydrodamalis gigas* from the Commander Islands (located in the Bering Sea) was exacerbated, if not driven by, a decline in their primary foraging habitat (i.e. kelp forests) once sea otters were hunted to near extinction and sea urchin populations grew unchecked (Estes et al. 2016). Given the increasing numbers of Florida manatees utilizing Kings Bay in winter (Kleen & Breland 2014, Littles et al. 2016, Sattelberger et al. 2017), no foreseeable increase in SAV within the bay (Hauxwell et al. 2004, Jacoby et al. 2014), and potential effects from climate change (Marsh et al. 2017), frequent movements beyond Kings Bay may become more common for manatees in this region.

We relied primarily on telemetry tracking to investigate the extent to which winter forage might have affected manatee movements, and we acknowledge that assessing trends in movement out of Kings Bay was limited by the relatively small number of animals tracked, coupled with the same individuality that has been observed in other studies of manatees and dugongs (Etheridge et al. 1985, Deutsch et al. 2003, Nowacek et al. 2004, Sheppard et al. 2006). Complementary data sources could certainly aid in investigating bioenergetic tradeoffs associated with movement decisions between habitats. For example, Christiansen et al. (2016) used unmanned aerial surveys to estimate the surface area of humpback whales, then estimated body condition and bioenergetic costs of reproductive classes during the breeding season. Employing a similar approach could aid in sampling a greater proportion of the wintering Florida manatee population and detecting changes in body condition, for multiple size classes, over the entire season. In the case of Florida manatees, there is also a tremendous opportunity to leverage information collected during yearly health assessments (Bonde et al. 2012). While there has been no indication of a systemic decrease in body condition or health for manatees captured in Crystal River to date, the ongoing monitoring of this population can certainly help identify any changes, should they occur. As with any study of marine fauna, new and emerging technologies are likely to improve our understanding of physiological responses to environmental variables and implications for movement and other behaviors (Hays et al. 2016). However, there is no doubt that degradation of coastal habitats poses an ongoing risk to sirenians in general (Castelblanco-Martínez et al. 2012, Marsh et al. 2017) and Florida manatees in particular, with the latter contending to meet both a need for warmth and a need for food during critical winter periods (Laist & Reynolds 2005). Long-term conservation strategies for manatees, and other coastal fauna, will be enhanced by a holistic understanding of how animals respond and adapt to changes in their habitats.

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