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Mapping spatial resources with GPS animal telemetry: foraging manatees locate seagrass beds in the Ten Thousand Islands, Florida, USA

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ABSTRACT: Turbid water conditions make the delineation and characterization of benthic habitats difficult by traditional *in situ* and remote sensing methods. Here, we develop and validate modeling and sampling methodology for detecting and characterizing seagrass beds by analyzing GPS telemetry records from radio-tagged manatees. Between October 2002 and October 2005, 14 manatees were tracked in the Ten Thousand Islands (TTI) in southwest Florida (USA) using Global Positioning System (GPS) tags. High density manatee use areas were found to occur off each island facing the open, nearshore waters of the Gulf of Mexico. We implemented a spatially stratified random sampling plan and used a camera-based sampling technique to observe and record bottom observations of seagrass and macroalgae presence and abundance. Five species of seagrass were identified in our study area: *Halodule wrightii*, *Thalassia testudinum*, *Syringodium filiforme*, *Halophila engelmannii*, and *Halophila decipiens*. A Bayesian model was developed to choose and parameterize a spatial process function that would describe the observed patterns of seagrass and macroalgae. The seagrasses were found in depths <2 m and in the higher manatee use strata, whereas macroalgae was found at moderate densities at all sampled depths and manatee use strata. The manatee spatial data showed a strong association with seagrass beds, a relationship that increased seagrass sampling efficiency. Our camera-based field sampling proved to be effective for assessing seagrass density and spatial coverage under turbid water conditions, and would be an effective monitoring tool to detect changes in seagrass beds.

KEY WORDS: Zero-inflated negative binomial · ZINB · Kernel density filter · Geographic information system · GIS · ARGOS satellite · Foraging ecology · Spatial pattern

INTRODUCTION

Determining resource use by mobile faunal populations is one of the primary goals of animal telemetry and tracking (Alldredge & Ratti 1986, Aebischer et al. 1993). If the resource that a species uses is known, but the distribution and abundance of that resource is unknown, then tracking the animals can help identify the locations of that critical resource (e.g. Weimerskirch et al. 1993, Brooks et al. 2003, Repasky et al. 2006). The use of remote tracking data is especially valuable in areas where both the animals and their resources are difficult to detect.

Capitalizing on an animal's specialized senses, foraging needs, and familiarity with the landscape can greatly increase the efficiency of designing sampling plans to locate and characterize resources which the animals use, but are difficult to detect with conventional methods. One example of an important and difficult to detect resource is underwater seagrass

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beds growing in turbid conditions where remote survey techniques such as satellite sensors, aerial photography, or boat-based imaging are neither practical nor sensitive enough to identify them (McKenzie et al. 2001). The location, species composition, and density of seagrasses and other submerged aquatic vegetation is of great interest to scientists, resource managers, and the general public due to the many ecological and economic services they provide, including their value as a food resource (Costanza et al. 1997, Lefebvre et al. 2000, Orth et al. 2006). For remote areas and locations where environmental conditions make seagrasses difficult to detect and monitor, alternative methods are needed to characterize their distribution and abundance.

In the Ten Thousand Islands (TTI) of southwest Florida, transparency of coastal waters is poor due to high concentrations of suspended sediments and the discharge of colored dissolved organic matter (CDOM) from the extensive network of rivers and mangrove wetlands. Despite less than ideal optical water clarity, ample tidal flushing, an abundance of soft bottom sediments, and a semi-tropical climate provide an environment suitable for the growth of 6 species of seagrass in shallow water (Zieman & Zieman 1989). This mangrove coastal region has long been recognized as critically important fish and wildlife habitat (Schomer & Drew 1982), but the seagrass resources have never been adequately characterized (FWRI 2011).

The southwest Florida mangrove coast is threatened by anthropogenic changes of upstream urban development, widespread agriculture practices, and water diversion along its northern and eastern boundaries. This region is currently the focus of long-term plans for water management modifications associated with the Picayune Strand Restoration Project (PSRP) and the Comprehensive Everglades Restoration Plan (CERP), which may affect coastal environmental conditions and water quality (Swain & Decker 2009). Over the longer term, effects of sea level rise and expected global climate change will influence the distribution and abundance of seagrasses in this region.

Florida manatees *Trichechus manatus latirostris* benefit from the ecological functions of the TTI region by utilizing the extensive network of creeks, rivers, and canals draining freshwater from the northwestern Everglades. Data from ground and aerial surveys, satellite telemetry, and the analysis of movements derived from GPS-tagged animals indicate that some manatees remain in the TTI region year-round (Stith et al. 2006). The availability of freshwater, isolated refuges, and accessibility to seagrasses in shallow waters of the TTI are characteristics shared by other areas that manatees frequent (Lefebvre et al. 2000, Alves-Stanley et al. 2010). Despite the recognized importance of this region for manatees and the role of seagrasses as their primary food source, knowledge of the spatial distribution and characterization of seagrass is incomplete (FWRI 2011).

The objectives of this study are to capitalize on the specialized senses of the Florida manatee by analyzing telemetry records from GPS-tagged manatees tracked in the TTI. Our primary hypothesis was that areas of high manatee use near the outer islands of the TTI, where seagrass beds were known or suspected to occur, would be indicative of seagrass beds. This hypothesis was based on multiple instances in which manatees on these outer banks were observed by personnel from a boat, and found to be feeding on seagrass (J. P. Reid pers. obs.). Another possible behavior that could occur in the use areas is surface or bottom resting, but these behaviors are not likely to be common in these exposed, tidally influenced locations. From these data, we develop a stratified sampling protocol, methodology for sampling seagrass and macroalgae, and a Bayesian modeling framework for detecting and characterizing seagrass foraging areas.

MATERIALS AND METHODS

Study site

The Ten Thousand Islands region of southwest Florida is part of an extensive coastal system of mangrove forests, shallow bays, tidal channels, and intertidal and subtidal soft and hard bottom habitats. The TTI borders the open waters of the Gulf of Mexico (GOM) from approximately Cape Romano (25.86° N, 81.68° W) to Pavillion Key (25.70° N, 81.35° W), where it merges with the northwestern Everglades (Fig. 1). Ecologically, the TTI has many of the same biological characteristics found along the seaward margin of the northwestern Everglades north of Cape Sable (25.23° N, 81.16° W) (Schomer & Drew 1982). The islands are dominated by red mangroves *Rhizophora mangle*, and subtidal and intertidal soft bottom benthic habitats adjacent to the islands have diverse communities of macroalgae, seagrasses, bryozoans, and sponges. A distinctive feature of the region is the hard bottom habitats formed by exposed worm reefs and oyster beds, which are colonized by diverse invertebrate and macroalgal communities.

The climate is sub-tropical with easterly trade winds prevailing and alternating wet (May–Oct) and dry seasons (Nov–Apr). Average annual rainfall is 132 cm (www.intellicast.com), average low and high air temperatures range from 12 to 23°C in winter and 22 to 33°C in summer, and water temperatures range from 15 to 30°C. Tides are semi-diurnal with an average range of 1.4 m (www.noaa.gov). Salinity along the outer islands ranges from 20 in the wet season to 38 psu in the dry season (Soderqvist & Patino 2010).

Manatee tracking

From October 2002 through October 2005, researchers from the USGS Sirenia Project tracked the movements of 14 manatees in the TTI area (Stith et al. 2006). All manatees were captured at Port of the Islands, Collier County, Florida (25.957° N, 81.511° W) between October 2002 and November 2004, except one animal that was captured in Coot Bay, Monroe County, Florida (25.192° N, 80.916° W) in June 2005, and which subsequently travelled to the TTI area.

The animals were each fitted with a floating, satellite-linked (www.argos-system.org) GPS-equipped tag (www.telonics.com) attached to a peduncle belt by a nylon tether (Reid et al. 1995). Both belt and tether were engineered with specific tensile strengths that would allow the animal to break free should it become entangled. Five of the manatees were retagged during the study (2 were retagged twice), so a total of 21 tagging periods, or 'bouts', were recorded from the 14 animals. Each GPS receiver was programmed to record location points with an accuracy of <5 m, every 20 or 30 min while the tag was at the surface. From the top of the tag to the attachment point at the top surface of the peduncle was 178 cm, and depending on the size and behavior of the manatee, the tag was at the surface at all times in water <2 m deep at slow travel speeds. In deeper water, the tags were able to record locations when the manatee surfaced to breathe every few minutes (Hartman 1979).

Telemetry analysis

The study area was subdivided into $10^{-4} \times 10^{-4}$ degree grid cells (cell size 10 × 11 m) in ArcMap 9.2 (Environmental Systems Research Institute, 1992–2006). The size of the grid was 4622 × 3324 cells (46.28 × 36.82 km) resulting in 15.36×10^6 cells covering from 81.6912° W to 81.2290° W and from 25.9714° N to 25.6390° N. The water area in this grid, or a subset thereof, was used for all analyses and sampling plans. We eliminated all GPS points from the tracked manatees that occurred more than 1 km from the outermost islands (for example, in inner bays or rivers), because habitat use inshore has been observed by the authors to be far less deterministic of foraging as compared to offshore use. For example, manatees use inner bays for resting, thermoregulation, and freshwater access, as well as foraging. The offshore location data were classified by travel speed and distance. Sequential pairs of points that were >300 m apart, with a speed faster than 0.6 km h^{-1}, were flagged, and the second point of each pair was eliminated from the database, because these rapid, long-distance moves indicated travelling rather than feeding or other habitat use. A basic straight-line path, rather than a least-cost or other computed path, was used because less than 1% of the short straight line paths in the dataset intersected land. See Slone et al.

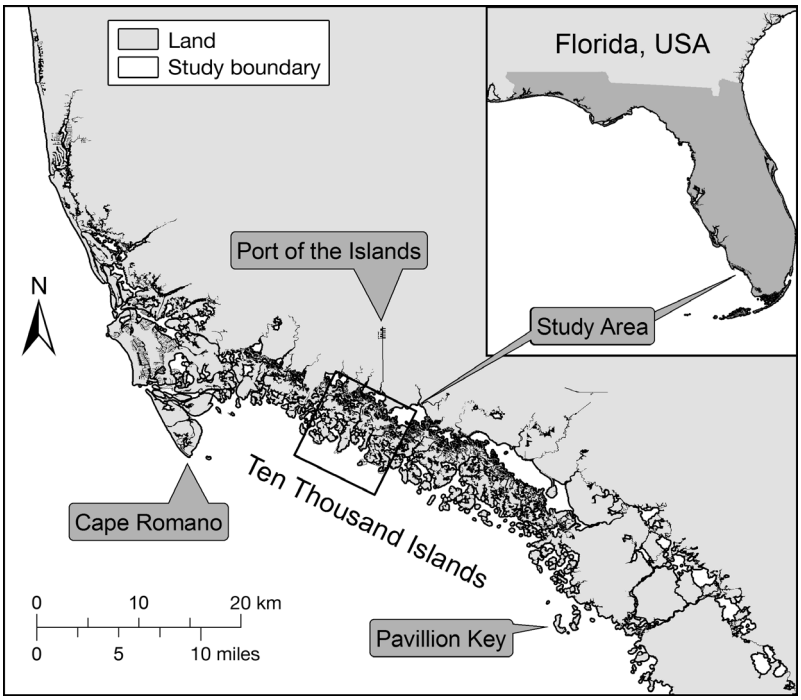

Fig. 1. Location of the study site in southwest Florida

Table 1. Rates and measurements for the 5 manatee use strata developed for seagrass sampling in the Ten Thousand Islands (TTI), Florida study area. The 5 sampling strata (3 densities of manatee use plus 100 and 1000 m buffers around manatee use areas) were measured by kernel density spatial analysis. NA: not applicable

Sampling strata	Kernel size (search radius)	Manatee GPS points m^{-2}	Sampling area (km^2)	Intended sampling intensity	No. sample points completed	Percent of stratum sampled
High	3 cells	0.320–∞	1.26	Very high	145	1.27
Medium	3 cells	0.106–0.320	1.00	High	80	0.88
Low	10 cells	0.020–0.106	2.02	Medium	121	0.66
100 m	NA	0–0.020	2.52	Low	33	0.14
1000 m	NA	0–0.020	9.61	Very low	24	0.03

(2012, 2013) for a complete description of the data filtering. The filtered points were then aggregated into manatee use levels of High, Medium, and Low, with kernel density analyses based on the quadratic kernel function described by Silverman (1986, p. 76, Eq. 4.5). For the 3 levels of kernel density aggregation, we used search parameters as seen in Table 1. For the Low use class, we used a 10 cell radius for liberally aggregating rarely-used locations, and chose the point density cutoff to exclude only single telemetry locations. This cutoff was found at the 97.5% density contour level. For the Medium and High use classes, we used a 3 cell radius for greater precision, and chose density contour levels that were proportionately less than the low density contour, at the 95 and 80% levels.

Field sampling

Field sampling took place between Whitehorse Key and Camp Lulu Key in the TTI (Fig. 2), during spring and fall 2008 (May 4–8, 2008 and October 14–18, 2008) and 2009 (March 31–April 6, 2009 and October 14–20, 2009). To test the hypothesis that the manatee use areas corresponded to areas of high seagrass occurrence, we developed a spatially stratified field sampling plan to randomly sample the benthic communities in each strata to determine the benthic habitat type and the abundance and species composition of seagrass (if any) in the sampling area. Three of the strata corresponded to the kernel density results for the High, Medium, and Low use classes. Two 'buffers' were then added around the areas selected by the kernel density analyses. The first was a zone within 100 m of the Low use stratum. This relatively narrow buffer was added to test whether the borders of any seagrass beds fell within or outside the Low-density stratum. The second buffer included all areas within 1000 m (1 km) of the Low use stratum that were not otherwise classified. This outer buffer was added to complete the sampling universe where inference could be made about seagrass occurrence. Fig. 2 shows the spatial extent of the High, Medium, and Low density manatee use strata, and the 2 buffer strata drawn around them. The 5 strata encompassed a strip approximately 3 km wide from Cape Romano Island to Pavilion Key in the TTI. Areas to the north and south of this study area and outside this strip are ecologically different from the TTI, and may show a different interpretation of manatee locations.

Once the strata were identified using GIS, field sampling stations were chosen in each stratum in a stratified random sampling design (Table 1; Quenouille 1949, Cochran 1977) Grid cells within each strata were aggregated into larger squares, the number of cells in each square being inversely proportional to the desired sampling rate for the stratum. Next, a random grid cell within each square was chosen as a proposed sample point, and accepted as a sampling point if it fell within the appropriate stratum. This spatial stratification avoided clumping of sampling points, and assured that the entire sampling area was covered. The manatee use areas were sampled at a higher rate than the buffers because they had smaller spatial extent, were expected to have higher seagrass density, and the higher sampling rates would allow for more precise estimates of abundance and species composition of any seagrass communities found there (Cochran 1977).

A marine GPS (Garmin 178s or Garmin 545s; Garmin International) — with the Wide Area Augmentation System (WAAS) enabled to increase accuracy — was used to locate the center point of each sampling station in the field, and then an anchored buoy marker was dropped to mark the location. The boat was then anchored or maintained on-station with the outboard motor.

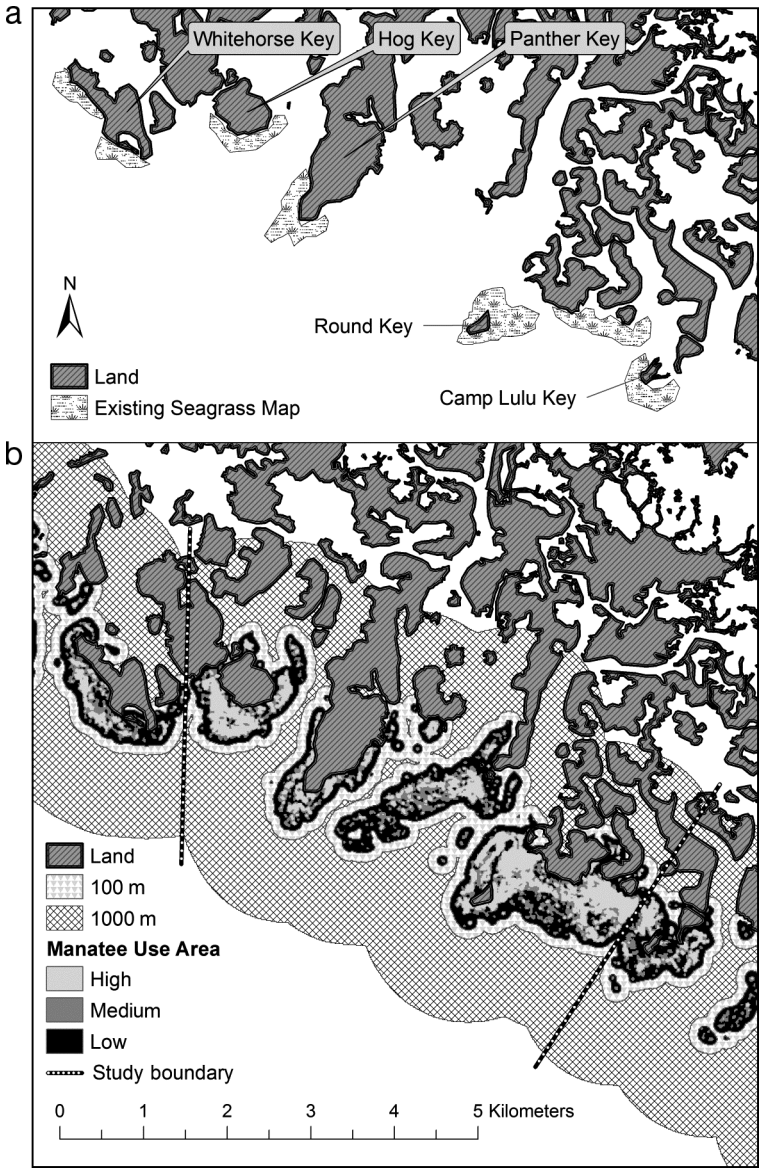

Fig. 2. Sampling area between Whitehorse Key and Camp Lulu Key, showing (a) extent of previously mapped seagrass beds (FWRI 2011), and (b) the spatial arrangement of the 5 sampling strata, including the High, Medium, and Low manatee use areas, and the 2 buffers (100 m and 1000 m) surrounding the manatee use strata. The straight lines in (b) are the eastern and western boundaries of the seagrass sampling area

At each sampling station, water depth was recorded with an Onset water level logger Model U20-001-04 (Onset Computer) that was attached to the buoy anchor and set to record every 30 s. The logger was deployed at each station for the duration of the sampling, retrieved and then re-deployed at the next station. To view the bottom and characterize the seagrass species composition and abundance, we developed a video-based benthic sampling device called the 'Quad-Cam'. It consisted of a low-light, high resolution video camera (Sartek Industries SDC-CAL with 2.9 mm lens) mounted on a swiveling PVC frame, with the camera aligned straight down at a distance of 13 cm from the substrate. The camera frame was attached to a PVC pole with a flexible U-joint, which kept the frame upright on the seafloor and allowed the operator to rotate the camera head assembly within the frame to capture 4 quadrats on video (see Slone et al. 2012, 2013 and Figs. S1 & S2 in Supplement 1 at www.int-res.com/articles/suppl/m476p285_supp.pdf). The camera output was recorded on a Sony Mini-DV 900 recorder with a resolution of 720 × 480 pixels. With this camera and lens combination, the view of the seafloor was 22.5 × 16 cm, so the pixel size on the substrate was approximately 0.3 × 0.3 mm. The distance of 13 cm was chosen after on-site testing to give the best compromise of view size and clarity to identify seagrass species, considering the poor visibility in the area. Each drop consisted of submerging the camera frame down to the substrate, and while focused on the bottom, the camera was rotated a quarter-turn 3 times to capture 4 separate views. Total sampling area within each view was 0.036 m^2, and for each drop, 0.144 m^2. The camera could record in color down to 0.3 lx, and black and white down to 0.0003 lx, and contained white LED lights to provide extra illumination if needed.

At each sampling station, the camera was dropped 8 times in haphazard locations within the selected 10 × 11 m cell. The camera was viewed live on the DV-900 monitor, which was shrouded against sunlight for a clear view. Presence/absence of each species of seagrass and the presence/absence of macroalgae within each view frame was recorded for each camera drop. We also noted the predominant bottom type (hard, coarse, shell, sand, mud) and the presence of any other conspicuous items in each view, such as sponges or tunicates. All data recording was done live on-site by a pair of dedicated recording personnel, one to view and interpret the camera output and one to record the data. Any questionable frames were marked and later reviewed using the digital tape recordings. Representative samples of seagrass were collected to verify species identification if necessary.

Data analysis

Depth readings collected at each sampling station were adjusted to mean tide level (MTL). A second water level logger (Onset U20-001-04) was attached below the low tide level at a fixed, centrally located position, such as a channel marker for the duration of the sampling trip. Data from this fixed logger were calibrated to the NOAA Round Key tide table (Station TEC4185, Location 25.833° N, 81.533° W) retrieved from the software package Tides & Currents (Version 2.5, Nautical Software). Calibration to local tide conditions was accomplished by adding the mean error between the fixed logger and the tide table to the fixed logger reading. Next, the MTL at Round Key of 0.701 m (www.tidesandcurrents.noaa.gov) was subtracted from the corrected fixed logger data. This was then subtracted from the data taken from the logger deployed at each sample station:

$$D_{MTL} = D_t - D_{Ft} + \frac{\Sigma_t (D_t + D_{Ft})}{T} - MTL \quad (1)$$

where D is depth in meters, F indicates the fixed station, S is the predicted tide stage in meters, and T is the domain of all the time steps t (30 s intervals) during the sampling trip. An averaged reading from these data during the time spent at each station provided the depth of the stations at MTL (Fig. S3 in Supplement 1).

Field sampling data were analyzed in the statistical computing package R (Version 2.11.1, The R Foundation for Statistical Computing). To visualize the data, a boxplot of station depths in each manatee use class was calculated. Next, the station depths were binned into 0.5 m classes from 0 to 5 m. Boxplots of seagrass and macroalgae occurrence by depth class were then calculated. Seagrass occurrence by species was classified as the number of camera drops at each station where the species was recorded.

To calculate statistical distributions of abundance and patchiness for hypothesis testing, a Bayesian model was developed to choose and parameterize a spatial process function (Bolker 2008) that could reproduce the observed patterns for each species of seagrass and macroalgae in each manatee use strata (see Supplement 2 at www.int-res.com/articles/suppl/m476p285_supp/). These spatial process functions are probability density functions that capture the spatial variability in a data set. The model was implemented in R using the packages R2WinBUGS (Version 2.1-16) and BRugs (Version 0.5-3), which link R to the software package OpenBUGS (Version 3.1.0, OpenBUGS Foundation). Preliminary summaries of the field data led us to incorporate zero-inflation, or a greater than expected number of zero samples, and censored data, because many statistical distributions include an infinite upper tail, and our field data truncated at 8 subsamples. We explored several spatial process functions, including zero-inflated Poisson, exponential, zero-inflated exponential, beta binomial, zero-inflated beta binomial, and zero-inflated negative binomial. Due to the wide range of tested process function shapes, and the 'large data set' nature of the problem, flat uninformative priors were chosen for all parameters (Kass & Wasserman 1996, Lunn et al. 2009). The Gibbs sampling algorithm in OpenBUGS was used to estimate the joint posterior distribution. To counter slow mixing, 140 000 steps were run and discarded as a burn-in, followed by an additional 140 000 steps that were recorded. After testing indicated that the minimum thinning value to eliminate significant serial correlation was 7, we thinned all chains by that value. We generated 5 independent chains and only accepted solutions where all burn-in chains visually converged, all recorded chains had visually equivalent distributions, and the Monte Carlo error divided by standard deviation was <5% for all parameters (Roberts 1996 as implemented in BRugs samplesStats). The tracked variables for each seagrass species included the proportional zero-inflation and distributional parameters of the spatial process function and the expected value of the number of camera drops where the seagrass species or macroalgae would be recorded. The suite of statistics output by BRugs samplesStats was recorded for each parameter, including the mean, standard deviation, Monte Carlo error, 0.025 quantile, median, and 0.975 quantile. Presence or absence of mapped seagrass beds was also considered as a variable. To ascertain the proper fit of the final model, the mean error in prediction for each number of camera drops between the model and field data for each species was recorded.

RESULTS

Manatee tracking and analysis

The 21 manatee tracking bouts resulted in 68 849 GPS locations within the overall study area (average 3279 points per bout, maximum 9981, minimum 122). Manatees were tracked year-round, with a minimum of 3 and a maximum of 10 tracks recorded each month, all years combined (Fig. 3). Preliminary ana-

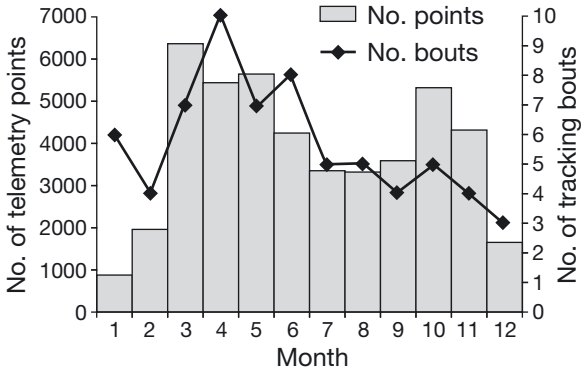

Fig. 3. Monthly distribution of tracking points and bouts that were used for this study. The reduced number of points relative to tracking bouts seen in the winter months was due to manatees' propensity to stay inland during cold periods in the Ten Thousand Islands (TTI) region (Stith et al. 2010)

lysis of the GPS data table indicated that the fix rate of the GPS tags was >90%. Periods where the fixes were missed were associated with rapid, long-range movements among habitat patches. This is a known issue with floating GPS tags as they are drawn under the surface of the water during directed travel movements. Slow-speed movements, such as those typically associated with feeding, showed an almost 100% rate of GPS fixes.

We were concerned that manatees may have used deeper water areas (>2 m), thereby introducing the possibility of the GPS transmitter being temporarily unavailable at those locations. If this behavior had happened while the animals were feeding in seagrass beds there might have been a bias in those locations resulting in a lower probability of inclusion in the manatee use areas (D'Eon 2003, Nielson et al. 2009). We did not find any part of the GPS data when the animals were in the study area that showed unexplained gaps. Furthermore, the benthic habitat sampling plan included areas just offshore from the manatee use areas to reveal any seagrass that might occur in these deeper waters, so any potential for depth bias would appear to be unrealized in this study.

After filtering high-speed movements from the data set (Slone et al. 2012, 2013), the kernel density analysis of the remaining data points revealed manatee use areas off each island facing the open, nearshore waters of the GOM (Fig. 2). The total area of manatee use delineated in the TTI region with tracking data was 33.7 km^2, and the use area in the smaller sampling area from Whitehorse Key to Camp Lulu Key was 4.28 km^2 (Table 1), compared to previously mapped seagrass beds of 4.72 km^2 in the TTI region and 0.96 km^2 in the smaller study area (FWRI 2011). If the manatee use areas correspond to seagrass beds, then these data represent a 4 to 7 fold increase in our ability to detect seagrass in this area.

Field sampling

During our 4 sampling trips, we acquired data for seagrass, macroalgae, and water depth at 403 stations; 256 of these were sampled in spring and 147 in fall. The spatial sampling density was distributed as shown in Table 1. We obtained and analyzed 12 896 camera sampling frames. There were more proposed sampling stations, but some were found to be within mangroves, or were too deep to sample. During 2008, our maximum sampling depth was 4.5 m at mean tide, which was the maximum depth we could reach with the pole camera. We reduced our maximum sampling depth to 3 m in 2009 after encountering logistical difficulties at the deeper sample points and confirming with SCUBA divers that the maximum depth at which we found seagrass was just over 2 m. Secchi disk values at the sampling stations ranged from 40 to 150 cm and were generally <1.0 m

Higher manatee use areas were generally shallower, but the Low use class spanned the widest range of depths of any class (Fig. 4). The Low use class included shallow shoals, as well as channels that were found on the edges of seagrass beds. There was a tidal signature in the manatee GPS data, with manatees moving into shallower areas at high tide, and staying in deeper areas at low tide (see Fig. S4 in Supplement 1). At low tide (–0.1 to 0.1 m tide stage), they were recorded at an actual depth of 1.2 ± 0.4 m

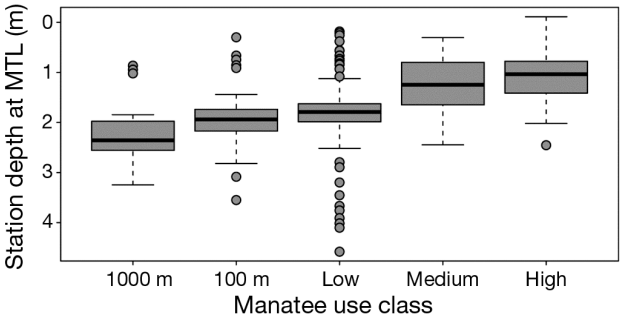

Fig. 4. Boxplots of depth for each of the manatee use and buffer strata at mean tide level (MTL). Higher manatee use classes were concentrated in shallow water, but the Low use class spanned a wide range of depths. Boxes show interquartile range and median; whiskers are 1.5× interquartile range; circles are all other outlying data points

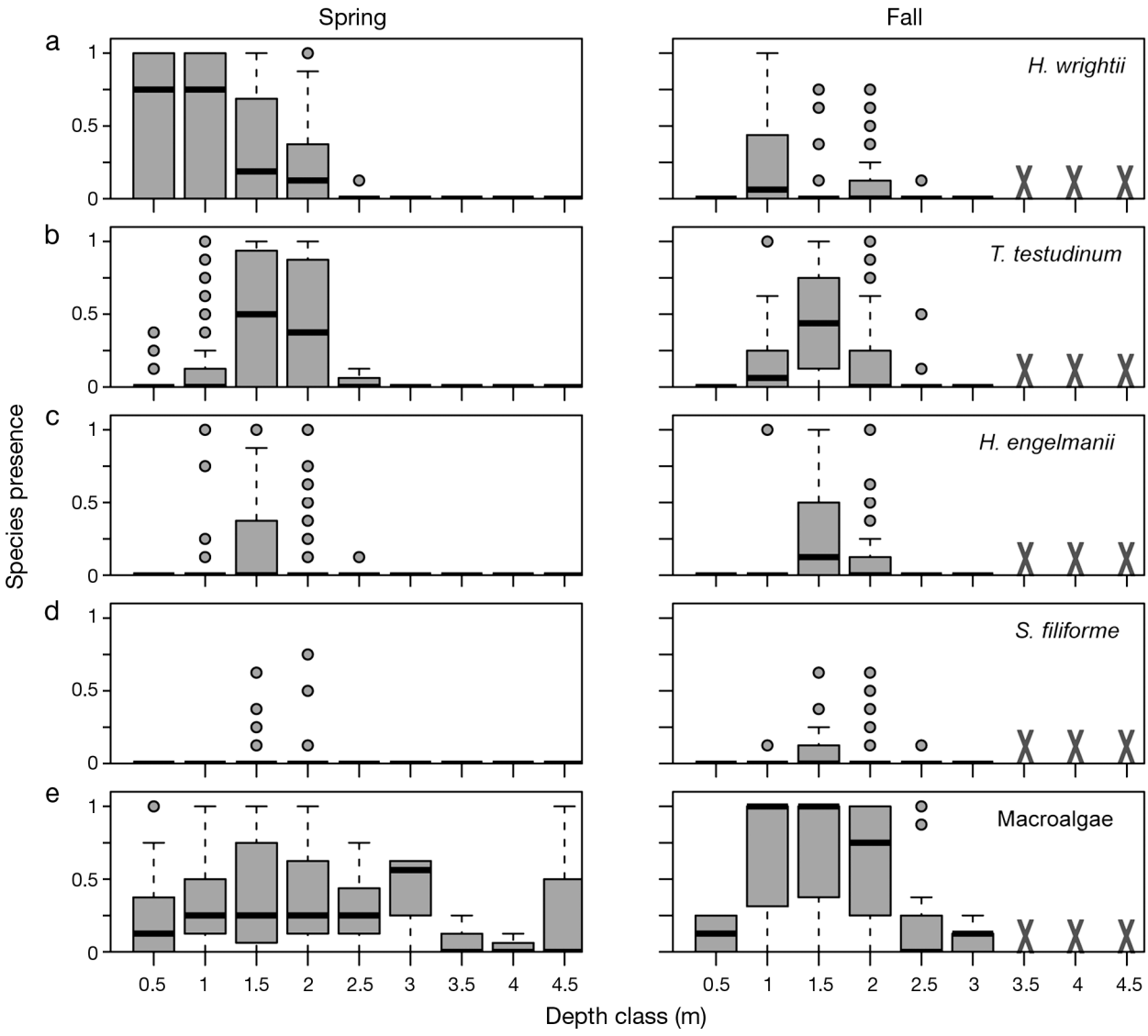

Fig. 5. Seagrass and macroalgae presence by depth class at mean tide level and season of field sampling (spring and fall). (a) *Halodule wrightii*; (b) *Thalassia testudinum*; (c) *Halophila engelmannii*; (d) *Syringodium filiforme*; (e) macroalgae; X = depth not sampled. Boxplots show interquartile range and median; whiskers are 1.5× interquartile range; circles are all other outlying data points

(mean ± SD), and at high tide (1.3 to 1.5 m tide stage), manatees were recorded at an actual depth of 1.8 ± 0.6 m. These high tide feeding locations would have had an actual depth of 0.4 m at low tide — too shallow for manatee use at the low tide stage. There was also a trend toward shallower habitat use at night (18:00 to 6:00 h) as compared to daytime (see Fig. S4 in Supplement 1).

We documented the presence of 5 species of seagrass in our study area (Figs. 5 to 8). *Halodule wrightii* and *Thalassia testudinum* were the most abundant, followed by *Halophila engelmannii* and *Syringodium filiforme*. *Halophila decipiens* was found twice in October 2009 at approximately 2 m depth, and was not included in the analyses. Seagrasses were found mostly in water shallower than 2 m (Fig. 5); the deepest sampling point with seagrass was 2.18 m at MTL. *H. wrightii* was associated mostly with very shallow water <1 m and was relatively more abundant in spring, while *T. testudinum, Halophila engelmannii* and *S. filiforme* were found more often between 1 m and 2 m depth.

Macroalgae were found in moderate densities at all sampled depths in spring and fall, with the highest densities being found between 0.5 m and 2.0 m in the fall. We did not attempt to separate species of macroalgae, but a large diversity was observed, including at least 3 species of *Caulerpa*; fleshy red and green

taxa; filamentous red, brown, and green algae; and turf forming species.

Data analysis and model results

The presence of mapped seagrass beds was a poor predictor of seagrass found in the field sampling because there were so few known beds; it was thus removed as a variable. Manatee use strata was a significant predictor, and so was incorporated. The zero-inflated negative binomial (ZINB) model was chosen because all other models clearly failed to capture the spatial pattern of at least one seagrass species or failed to converge on a stable, bounded solution. Program stability issues were encountered when the ZINB was modeled directly, so we instead modeled the negative binomial as a gamma-Poisson (Bolker

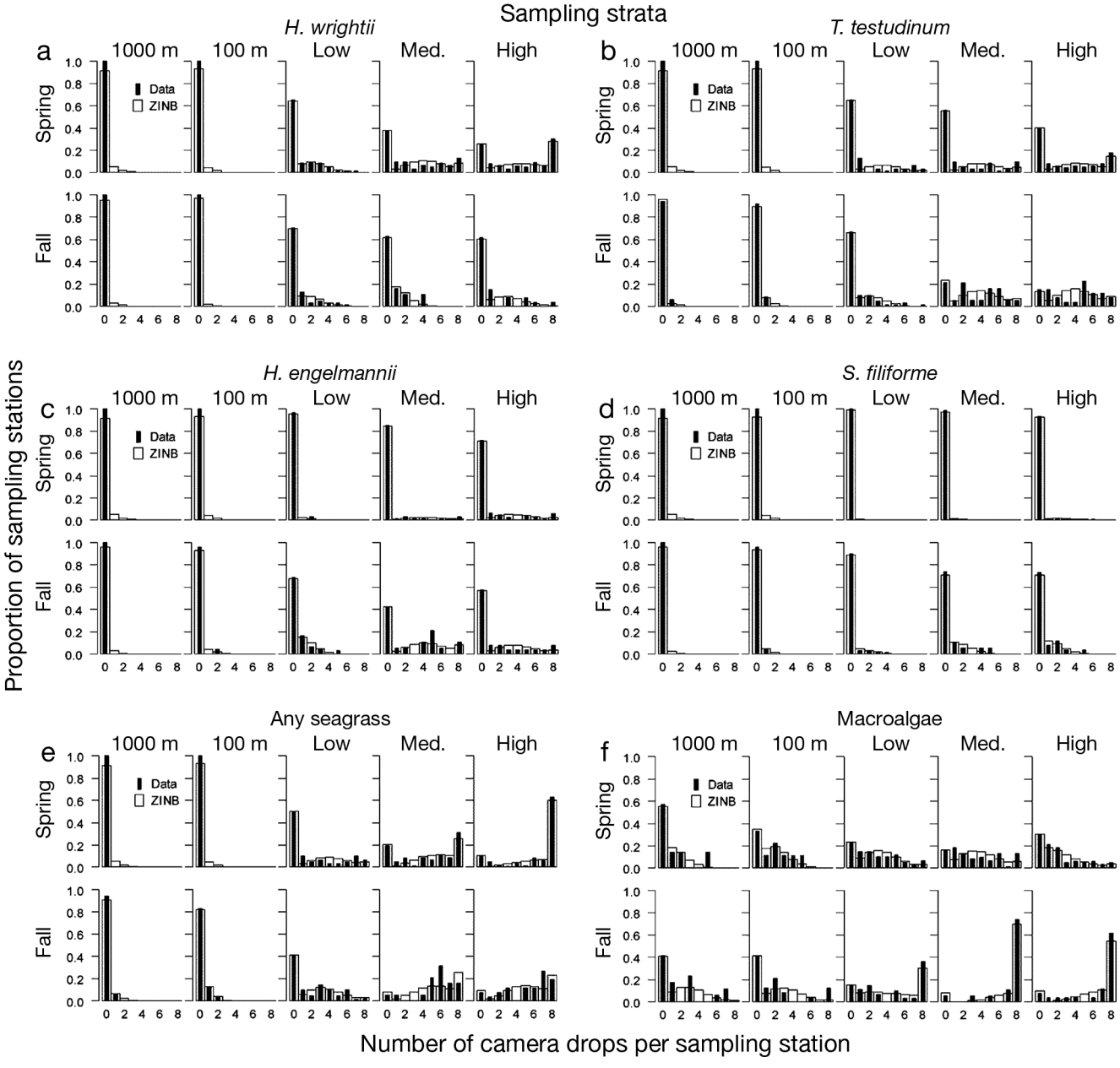

Fig. 6. Output from the Zero-Inflated Negative Binomial (ZINB) model (wide white bars), compared to field data from camera samples (narrow black bars within the white bars). (a) *Halodule wrightii*; (b) *Thalassia testudinum*; (c) *Halophila engelmannii*; (d) *Syringodium filiforme*; (e) any seagrass; and (f) macroalgae

2008). The ZINB model fit data from all of the seagrass species and macroalgae well, despite the wide range of spatial patterns and densities seen in the data set (Fig. 6): the mean error in predicting the proportion of sampling points with 0 to 8 camera drops was $<10^{-18}$ for each species, and the median error was $<10^{-3}$, indicating a lack of bias. The most striking patterns were the lack of seagrass in the 2 buffer strata (1000 m and 100 m) and the progressively higher seagrass densities recorded in the higher manatee use strata. Macroalgae was seen in all strata, though there was a trend towards relatively higher densities in the higher manatee use strata, especially in the fall.

The significant zero-inflation component indicated spatial heterogeneity, or grass bed patchiness, in the sampling area, representing the proportion of unsuitable habitat in each strata. This component was not significant for all seagrass species in the 100 m and 1000 m buffers, nor was it significant for *Syringodium filiforme* in all manatee use strata and *Halophila engelmannii* in the Low manatee use stratum. The zero-inflation component was estimated to be less than 0.10 for all the other seagrass species in the manatee use strata, except for *Halodule wrightii* in the Low strata (fall = 0.17, spring = 0.12) and in the Medium strata (fall = 0.27), and for *Thalassia testudinum* in the Low strata (fall = 0.12). The zero-inflation component for the macroalgae model was less than 0.1, except for the buffer strata in the spring (1000 m = 0.25, 100 m = 0.15).

One important model output was the expectation of finding any seagrass or macroalgae at a sample site (Fig. 7). This can be interpreted as spatial coverage. A second important model output was the number of camera drops where each seagrass species or macroalgae could be expected to be found at each sample site, in areas of suitable habitat (Fig. 8). There were strong patterns found in the seagrasses, with all species showing greater spatial coverage (Fig. 7a–e) and higher density (Fig. 8a–e) in the higher manatee use strata, except *Syringodium filiforme*, which showed

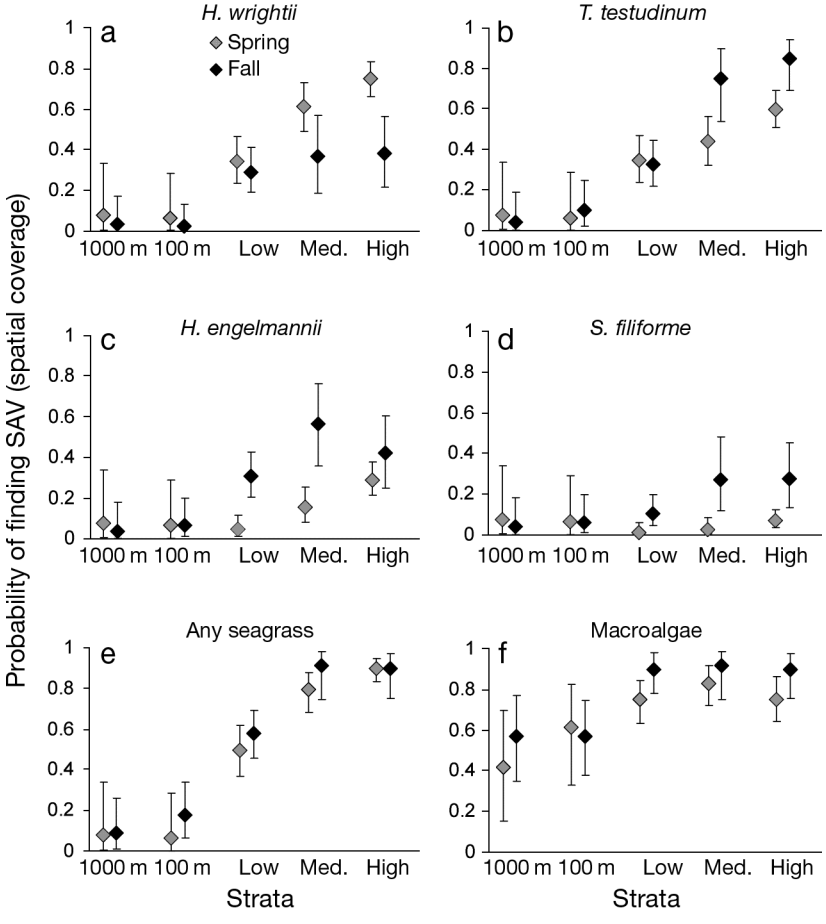

Fig. 7. Expectation of finding any seagrass at a sample location. This can be interpreted as landscape-level expectation or coverage. (a) *Halodule wrightii*; (b) *Thalassia testudinum*; (c) *Halophila engelmannii*; (d) *Syringodium filiforme*; (e) any seagrass; and (f) macroalgae. Error bars represent 95% credible intervals from the ZINB model. SAV: submerged aquatic vegetation

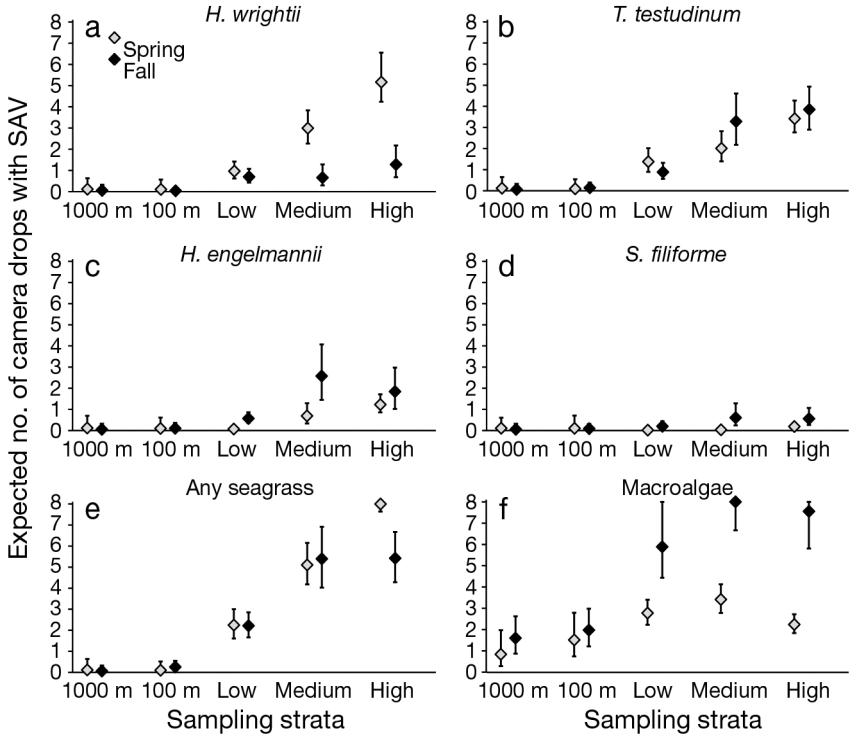

Fig. 8. Expected number of camera drops (out of 8) with visible seagrass, given acceptable habitat (zero-inflation component removed). This can be interpreted as a measure of local density. (a) *Halodule wrightii*; (b) *Thalassia testudinum*; (c) *Halophila engelmannii*; (d) *Syringodium filiforme*; (e) any seagrass; and (f) macroalgae. Error bars represent 95% credible intervals from the ZINB model

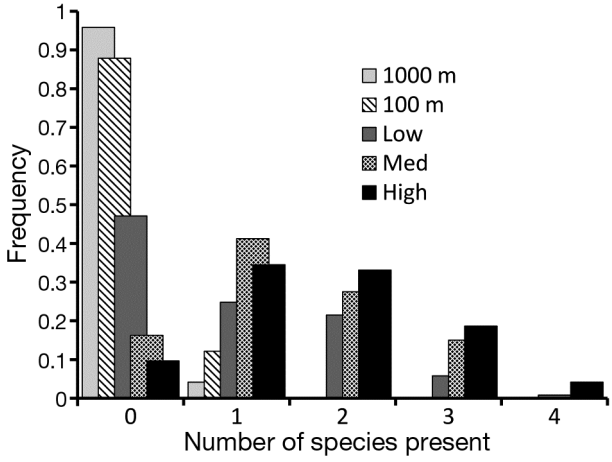

Fig. 9. Number of seagrass species present in a sample plot. This was greater on average in the higher manatee use strata than in the buffers

the same pattern, but was found in too few numbers to show significant differences. *Halodule wrightii* also showed a strong seasonal component, with spatial coverage (Fig. 7a) and local density (Fig. 8a) being higher in the spring. *Thalassia testudinum* and *Halophila engelmannii* showed more spatial coverage in the fall (Fig. 7b,c), but approximately the same density between seasons (Fig. 8b,c). Combining all seagrasses, there was close to a 100% expectation of finding some species in the Medium and High manatee use strata, regardless of season (Fig. 7e), but overall more density in the spring (Fig. 8e). Macroalgae showed higher coverage (Fig. 7f) and density (Fig. 8f) in the fall, and somewhat greater coverage and density overall in the higher strata, but less so than the seagrasses. The pattern of high seagrass abundance in the manatee use zones relative to the buffers was not confounded by the overall shallower depths in the manatee use zones. When depth was binned into 0.5 m depth classes, the pattern remained significant for all depth classes (see Fig. S5 in Supplement 1).

The number of species found in the samples was greater in the higher manatee use areas. While the few samples from the 2 buffer zones that had any seagrass showed only one species, the manatee use areas often showed 2, 3, or — in the Medium and High use strata — sometimes even 4 species together in the same location (Fig. 9). Finally, the sampling and modeling procedures presented here were surprisingly efficient, with 95% credible intervals of the

expected value of seagrass coverage measuring less than ±20% for 20 field sampling locations, ±15% for 40 samples, and ±10% for 100 samples.

DISCUSSION

Our field sampling revealed the occurrence of 5 species of seagrass, all known to grow in the coastal and offshore waters of the eastern GOM (Iverson & Bittaker 1986, Zieman & Zieman 1989, Fourqurean et al. 2002, Hale et al. 2004, Hammerstrom et al. 2006, Fonseca et al. 2008). Two species, *Halodule wrightii* and *Thalassia testudinum*, were the most commonly encountered in this study, followed by *Halophila engelmannii*. Two additional species frequently observed offshore in deeper waters of the west Florida Shelf, *Syringodium filiforme* and *Halophila decipiens*, were rarely observed during our sampling. Prior studies that have surveyed the potential seagrass habitat along the west coast of Florida did not include the nearshore region of the TTI (Iverson & Bittaker 1986, Fourqurean et al. 2002, Hale et al. 2004); however, our data suggest that the shallow turbid waters in the TTI have diverse seagrass and macroalgal communities contributing to the primary production of the region, as well as providing important fish and invertebrate habitat and manatee foraging grounds. Given the similar biophysical conditions present throughout the northwestern Everglades, it is highly probable that the entire 80 km nearshore region between Cape Romano and Cape Sable have similar communities of seagrass and macroalgae, which have not yet been adequately characterized or mapped. This coastal region is the focus of large-scale water management programs, including the Comprehensive Everglades Restoration Program and the Picayune Strand Restoration Program, and the potential impact to seagrasses from changes in salinity and water quality indicate that there is a critical need to quantitatively characterize the benthic primary producers.

Our data for the TTI showed zonation in the depth distribution of the seagrasses, with *Halodule wrightii* tending to be relatively more abundant in the shallowest water, especially in the spring sampling (Fig. 5). *Thalassia testudinum* was more abundant at depths >1 m MTL, similar to the distribution of *Halophila engelmannii*. The most striking result of our survey was the limited maximum depth to which seagrasses in the TTI were found. While macroalgae was observed down to our deepest samples at 4.57 m, the deepest observations of seagrass were 2.18 m for *H. wrightii* and 2.14 m for *T. testudinum*, and most observations were from depths <2.0 m MTL. This restricted depth distribution is much shallower than reported for seagrasses further offshore on the shelf north and south of the TTI and in the offshore waters (Fonseca et al. 2008). For example, both *H. wrightii* and *Halophila engelmannii* grow to depths of 7 to 10 m while *T. testudinum* and *Syringodium filiforme* grow to 6.7 to 8.5 m (Hale et al. 2004). Both of these species grow even deeper in the waters south of the TTI (Fourqurean et al. 2002). The offshore regions of the west Florida shelf have optically clearer water (Iverson & Bittaker 1986, Hammerstrom et al. 2006), while the nearshore waters have very poor water transparency due to high concentrations of suspended sediments and CDOM. During our study, Secchi disk values were generally <1.0 m. The moderately robust correspondence between Secchi depth and the maximum depth of seagrass growth suggests that water transparency is a very important factor in controlling the depth distribution of seagrasses in the TTI to a relatively shallow band <2.0 m deep (Dennison 1987, Kenworthy & Fonseca 1996). The marginal water clarity conditions limit the development of continuously distributed high biomass climax communities, as reported further south in Florida Bay and the Florida Keys (Fourqurean et al. 2002) or north in the big bend region of the west Florida shelf (Zieman & Zieman 1989). The limited depth distribution of seagrasses in the TTI suggests that sea level rise would have an impact on seagrass distribution and abundance. In the turbid water of the TTI, raising the elevation of the water column will cause a retreat of the lower depth distribution. The area of potential seagrass habitat could also shrink with rising water levels if the outer fringe of mangroves did not move landward and provide suitable substrate for seagrasses to colonize.

Tides, in combination with water clarity, play important roles in understanding the complex relationship between the distribution of the seagrasses and the foraging process of the manatees at the local scale of the TTI. Tides affect seagrass distribution at the deep edges by elevating the water column and accentuating light limitation during periods of high water levels. Tidal energy also contributes to the resuspension of sediments and delivery of CDOM-laden water, which are both responsible for attenuating light. Tides also affect the shallow upper edges of the seagrass distribution where, during low tide, the intertidal and shallow subtidal flats are exposed to natural disturbances from high (summer) and low (winter) temperatures, dessication, and in some locations higher wave energy.

At longer time scales, extreme weather events (e.g. tropical cyclones) have relatively more physical impacts in shallow water. More frequent and potentially more intense disturbances in the shallowest depths favor the fast-growing opportunistic species like *Halodule wrightii* that are better adapted for responding to both chronic and acute disturbances than the larger, slower-growing *Thalassia testudinum* (den Hartog 1971, Williams 1990, Kenworthy et al. 2002, Whitfield et al. 2002). Seagrass beds can shift in response to storm events and movement of sediments and seagrass patches (Marba & Duarte 1995, Fonseca & Bell 1998, Fonseca et al. 2000). Though the manatee telemetry data were from 2002 to 2005, there was no indication that significant shifting of the seagrass beds had occurred on the scale that we were sampling, which is somewhat surprising, considering that several storms influenced the TTI between 2004 and 2008 (Ivan 2004, Katrina 2005, Rita 2005, Ernesto 2006 and Fay 2008; www.csc.noaa.gov/hurricanes), including a direct hit from a category 2 hurricane (Wilma) in 2005. One possible explanation for the robustness of seagrass bed locations in the area is that several of the beds were framed by rocky reef margins on the seaward side.

The spatial analysis of the manatee telemetry data combined with field sampling enabled us to develop a close correspondence between relative manatee use and the presence/absence of seagrass using a ZINB model (Fig. 6). The field data showed a distinct increasing seagrass density with increasing manatee use areas, and a lack of seagrass in the buffer strata (Figs. 7 & 8). Significant zero inflation was seen especially in the Low use strata. The ecological significance of zero inflation is that habitat patchiness is a significant component in the landscape. It indicates that either the manatee use areas were not homogeneous in their ability to support seagrasses or that there were dynamic forces at work such as storm damage or intense herbivory. It is not surprising that we observed patchiness in the distribution of seagrasses in the Low use stratum. This was the stratum with the greatest depth range, and in the field studies we observed that the Low use strata was often found along channel edges and mangrove fringes, which are marginal habitats for seagrasses.

The methodology that we pursued, specifically the use of animal telemetry to develop a stratified field sampling plan, resulted in a great increase in efficiency compared to a completely random sampling plan. Considering the large size of the buffers compared to the manatee use areas (Table 1) and the lack of seagrass found in those buffers, a fully randomized study would have led to finding far fewer stations with any seagrass. Reports from researchers in the area suggest that most have had difficulty locating extensive seagrass resources in the TTI (P. Carlson pers. comm.). Additionally, a compilation of previously mapped seagrass beds (FWRI 2011) showed less than a quarter of the seagrass spatial extent that we found, suggesting that the manatee tracking data made a significant improvement in our ability to detect where seagrasses occur.

One immediate use for efficient, camera-based field sampling, such as presented herein, would be to detect the response in density or spatial coverage of known seagrass beds to factors such as water management practices, changes in water quality, grazing, severe storms, or climate change. We found our camera sampling methodology to be quite efficient at determining the expectation of finding seagrass. As reported above, the largest 95% credible intervals for the expectation of finding seagrass was ±20% or less with only 20 sampling stations, each with 8 camera drops. This precision is sufficient to quickly determine gross changes in abundance. Our team regularly surveyed this number of locations with a single boat in less than a day.

A possible bias in the tracking data that was addressed in the field sampling was the possibility of seagrass occurring in areas that the tracked manatees were not using, either because they were inaccessible, there were not enough tracking data, or the population was not large enough to exploit the entire resource. If this bias existed in the tracking data, it would have been observed in the field samples from the buffer strata. The distinct lack of seagrass found in the buffers indicates that in the study area, manatees are using all of the available seagrass beds for foraging. While our field sampling area was well covered by manatee tracking bouts, it is certain that at some distance from the manatee capture site of Port of the Islands, the number of tracking bouts in our data set would diminish to the point where it cannot adequately represent the spatial extent of seagrass present. Likewise, manatee telemetry data are not available everywhere. For these situations, we are currently developing a physical model based on the findings from this study that will predict the extent of seagrass beds in the region without the need for manatee telemetry. We are also gathering representative samples of seagrass for biomass measurements. In the end, we will have a documented estimate of seagrass extent and caloric value in the TTI that will be valuable baseline information for ecosystem management and detection of change.

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