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Original Article

Abundance of Manatees in Panama Estimated from Side-scan Sonar

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ABSTRACT The Antillean manatee (*Trichechus manatus manatus*) is found in tropical and subtropical riverine and coastal waters across the Caribbean region. Little is known of its population status, particularly in Central America. We counted and mapped manatees using side-scan sonar in the San San Pond Sak wetland, a protected estuary in western Panama, for 12 months, and converted the sightings into density and abundance estimates. A total of 214 sonar transects, covering 1,731 km and detecting 1,004 manatees, were completed. The greatest density of animals was found in the narrow and relatively deep upstream tributaries and also in a shallow lagoon near the river mouth. The estimated mean number of manatees in the 18-km San San River system over the year was 18.3, but abundance was highly seasonal, with 33 animals present in May and just 2 animals in December. These figures are within the range reported for similar rivers in Central America and Florida, USA. Uncertainty of the population size was estimated with a Bayesian model, using daily variance in counts, and 95% credible intervals were 22–71 animals at peak season but just 1–6 animals in December. The active sonar survey used in this study located manatees, mapped their positions, and converted sightings into quantitative data for rigorous analysis. The method is cost-effective for repeated counts across seasons and years, needed to evaluate population trends.

KEY WORDS Antillean manatee, Bayesian model, Panama, population, San San Pond Sak, side-scan sonar, *Trichechus manatus manatus*.

The manatee genus *Trichechus* is found on 3 continents, but all 3 of its species are considered threatened and protected under international agreements, including the Convention on International Trade in Endangered Species and the Specially Protected Areas and Wildlife Protocol (Freestone 1991, UNEP-WCMC 2014). The most widely distributed of the species, the West Indian manatee, encompasses 2 subspecies, one in the southern United States (*T. manatus latirostris*) and the other throughout Caribbean coasts and islands (*T. m. manatus*). The former, the Florida manatee, is the better studied of the two, and many population surveys were recently reviewed (Martin et al. 2015, Littles et al. 2016). In contrast, the rare Antillean subspecies is poorly understood and vulnerable to extinction (Deutsch et al. 2008, Aragones et al. 2012, Self-Sullivan and Mignucci-Giannoni 2012). It feeds and calves in riverine and coastal wetlands from the western Gulf of Mexico to Brazil, and its largest breeding population is thought to be in Belize. Historical and archaeological evidence suggest its population has been greatly reduced by hunting (Dampier 1968, Rathbun et al. 1983, Olivera-Gómez et al. 2000, Self-Sullivan and Mignucci-Giannoni 2012, Wake et al. 2013). In Panama, manatees were hunted by Native Americans then by Spanish buccaneers (Exquemelin 1678, Dampier 1697), and after 1880, as food for banana workers. Legal protection was finally decreed in 1967 (Wake et al. 2013).

Despite interest in its conservation in Central America, there are few studies of the population status of Antillean manatees (Lefebvre et al. 2001). Existing survey methods, including interviews, historical records, and sightings from motorboat and aircraft have defined the manatee distribution but seldom led to estimates of abundance (Smethurst and Nietschmann 1999, Morales-Vela et al. 2000, Montoya-Ospina et al. 2001, Jiménez 2005, Olivera-Gómez and Mellink 2005). The few estimates of population size include 30–60 individuals in Costa Rica and 30–70 in Panama (Mou Sue et al. 1990, Reynolds et al. 1995, Lefebvre et al. 2001). Scarcity of such estimates can be largely attributed to turbid water in much of its habitat in Central America. Considering the conservation imperative of knowing the abundance of rare species, alternative estimation methods are needed, and sonar provides a novel technique for observing manatees through murky water (Rodas-Trejo et al. 2008, Gonzalez-Socoloske et al. 2009, Gonzalez-Socoloske and Olivera-Gómez 2012, Brice 2014, Castelblanco-Martínez et al. 2017). We therefore tested high-resolution dual-channel side-scan sonar to survey

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manatees in a protected Panamanian wetland over 12 months and developed Bayesian tools to create rigorous statistical estimators of abundance.

STUDY AREA

The Humedal San San Pond Sak (HSSPS) was a wetland along the Caribbean coast of western Panama, lying between the Rio Sixaola and the Boca del Drago Peninsula in the province of Bocas del Toro, at 9°31.679′N, 82°30.889′W (Fig. 1). Protected since 1993 and designated internationally important by the Ramsar Convention (Ramsar 2008), it was thought to harbor Panama's largest manatee population (Mou Sue et al. 1990, Lefebvre et al. 2001).

The HSSPS encompassed an area of 164 km^2 of poorly drained coastal flood plains <10 m above sea level. The climate was humid tropical, with 200–300 cm of annual rainfall feeding the 3 main rivers—the Negro, San San, and Changuinola—that form the wetland (Valdespino and Santamaría 1997). The vegetation was mostly flooded forest and shrubland, plus smaller areas of peat, grassland, pasture, mangrove, and cropland. In contrast to the surrounding agriculture, heavily impacted by plantations and artificial drainage for more than a century (Mou Sue and Chen 1990), there was no large-scale alteration of vegetation or streams inside the HSSPS protected area, and 90% of the surface area had native vegetation or natural drainage (Valdespino and Santamaría 1997, Guzman and Rivera 2014).

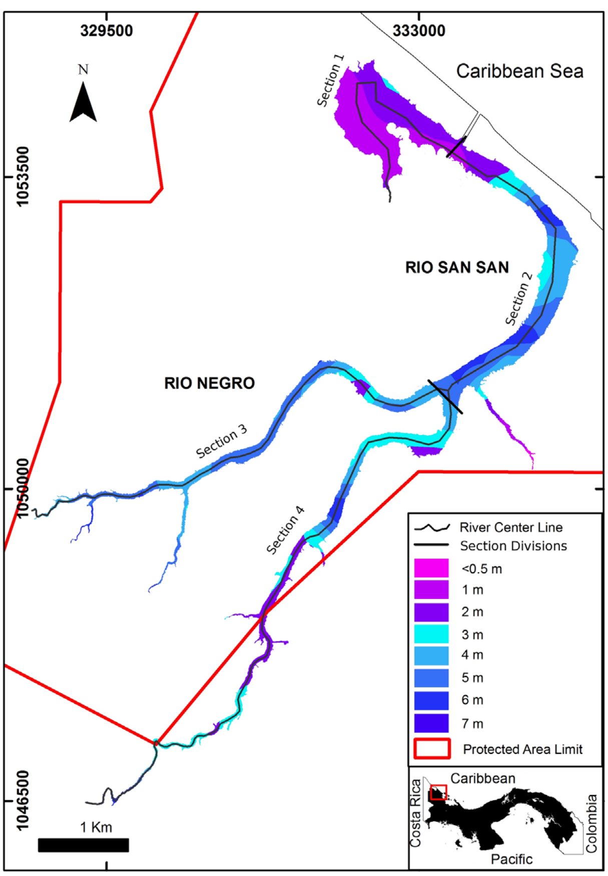

Figure 1. Map of the Rio San San and Rio Negro, Panama, showing depth contours and 4 river habitat sections used to analyze variation in manatee density during 2013–2014. Axes are labeled with UTM coordinates (zone 17). The centerline of the river is indicated in black, the reserve boundary in red. The small inset shows the location within far northwest Panama. Bathymetry is indicated by color.

The water was murky, stained by tannins, and brackish, influenced by both river and ocean, but the semidiurnal tide at the mouth of the wetland had a range of only 30 cm. From an acoustical perspective, the wetland comprises 4 different environments (Fig. 1): a marine-influenced lagoon dominated by snapping shrimp (*Alpheidae* spp.) impulses; brackish water of the lower river system, where a deep channel with flowing water produced low frequency sound; and 2 freshwater environments upstream also dominated by the sounds of current (Rivera et al. 2015).

The geomorphology of the wetland was affected in recent decades by dredging in the surrounding banana plantations, deforestation of nearby plains, and a tsunami triggered by the 1991 earthquake (7.6 on the Mercalli scale) that caused the coast near the river mouth to subside 0.50–1.0 m (Camacho 1994, Camacho and Víquez 1994). Other morphological changes happen regularly in the lower riverine system during seasonal floods and heavy runoff. Continuing threats to the wetland include logging, hunting, pollution, farming, tourism, sand mining, and overfishing (Valdespino and Santamaría 1997).

METHODS

Acoustic Survey and Data Acquisition

We designed an acoustical survey in the highly turbid but navigable Rio San San and its tributary, the Rio Negro (Fig. 1). The nearby Rio Changuinola and its artificial channels were covered with dense aquatic vegetation and thus could not be surveyed with sonar (Brice 2014). We used high-resolution, dual-channel, side-scan sonar (Imagenex Technology, Port Coquitlam, BC, Canada; YellowFin Model 872) fixed 60 cm below the waterline near the starboard bow of a 5-m inflatable boat (Avon, Dafen, South Wales, UK). The boat was powered by a 4-stroke outboard motor and navigated along the river's centerline (i.e., equidistant by visual reckoning to the two banks), at speeds of 5.5 to 9.3 km/hr, slightly faster than other surveys in the region using smaller sonar equipment (Gonzalez-Socoloske and Olivera-Gómez 2012, Brice 2014). The sonar was operated at 330 kHz and 770 kHz, following the suggestion of Jaffe et al. (2007) that a frequency higher than 171 kHz reliably detects manatees. Animals were observed in real time, when they were on the side-scan beam, perpendicular to the boat's route. The boat's coordinates were recorded at the moment of each manatee sighting using a GPS with 3-m accuracy (Global Positioning System, model 62stc; Garmin International Inc., Olathe, KS, USA). Data were stored immediately in a portable computer using the YellowFin software on a Windows operating system (Microsoft, Redmond, WA, USA). Images were checked later in the laboratory to confirm animals and reject false-positives made *in situ*. All surveys were made by the same personnel, experienced at differentiating rocks, tree roots, branches, and logs from the unique peanut-shaped shadow of manatees (Gonzalez-Socoloske and Olivera-Gómez 2012, Brice 2014). The Animal Care and Use Committee of the Smithsonian Tropical Research Institute approved all procedures used in the work.

Surveys were conducted from February 2013 to January 2014, for 3–9 consecutive days in each month except when bad weather intervened (permitting just 2 d in Feb and 1 d in Aug). On each day, transits were repeated up and down the entire river system for an average of 7 hr (but weather-dependent, ranging from 1 to 13 hr). We defined individual transects as intervals of time during which both boat and sonar were operated continuously; 1–9 such transects were completed per day over 45 days, each transect 1–13 km in length, yielding a total of 214 transects spanning 1,731 km (Table 1). Unpredictable weather coupled with the 3 radiating river branches rendered it impossible to repeat every section of the river exactly the same number of times, and on any one day some sections were passed as many as 5 times while others only once (or with bad weather, not at all).

Water depth was measured from a kayak on separate trips, using a Humminbird® 385ci DI 200/455 kHz Dual-Beam sonar with built-in precision GPS and 500 Watts RMS power output, along with a 455/800 kHz Down-Imaging sonar (both from Marine Electronics, Johnson Outdoors, Eufaula, AL, USA), using a chart-plotting routine recording every 10 m. Results were processed into a bathymetry map of the area at 0.5-m depth intervals using ArcGIS 10.2 (ESRI, Redlands, CA, USA).

River and Manatee Mapping

We could not locate published digital maps of the San San River, so we created our own by digitizing onto a Google satellite image using GPSVisualizer (A. Schneider, 2014, http://www.gpsvisualizer.com, accessed Sep 2015). Precise coordinates of both banks were recorded, and a line down the center of the river was added by eye, the latter matching our efforts at navigating down the centerline during manatee surveys. The 2 banks and centerlines were stored as a series of connected line segments defined by UTM (Universal Transverse Mercator, zone 17) coordinates of their vertices: 1,567 coordinate pairs for the banks and 208 for the centerline. Maps were created by connecting those line segments. Distance upstream was calculated as the length along the centerline from the river mouth.

The start and end coordinates of each of the 214 transects were estimated with GPS as the position of the boat when one set of observations began and ended. Define S_i as the starting coordinates of transect i (UTM x and UTM y) and E_i as the ending coordinates. In all cases, both pairs were close to, but not precisely on, the mapped centerline, so for S_i we located $\hat{S}_i$, the nearest point on the centerline, and likewise $\hat{E}_i$. Then transect i was defined as the centerline between $\hat{S}_i$ and $\hat{E}_i$. The coordinates of the boat at the moment a manatee was detected were designated M_{ij}, indicating the jth manatee sighted during transect i; again, we found a corresponding $\hat{M}_{ij}$, the closest point on the centerline. The perpendicular distance D_{ij} from boat to manatee was also recorded from the sonar, but we did not know on which side of the boat manatees were located.

All manipulation of map data was done in statistical software R 3.30 (R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/, accessed Sep 2015) using geometry of point-to-line distances and perpendicular bisectors. Many such calculations are available in geographic information software (GIS), but our own algorithms better matched the details we needed.

Transects and Plots

Our survey method was a line transect, a standard tool for quantifying abundance of marine mammals, including manatees, from either boats or airplanes (Smith 1981, Miller et al. 1998, Edwards et al. 2007). Each transect defined a precise area inside which animals were counted. To examine manatee density at different depths, distances, and river sections, we divided each transect into 25-m units along its entire length, from $\hat{S}_i$ to $\hat{E}_i$ (Fig. 2), and assigned each

Table 1. Size and sampling statistics for 4 sections of the Rio San San and Rio Negro, Panama, surveyed in 2013–2014. Exact geographic coordinates (Fig. 1) were used to estimate surface area, length, and width. The start position refers to the distance from the ocean to the closest point in each section, and the end position is where the section ends (as far as we surveyed, or for Section 2 where it meets Sections 3 and 4). Transect length is the sum of all transects within a section, and total area sampled is the transect area (length × full river width); the sampling area <40 m from the boat is length × full river width where narrower than 80 m, otherwise the rectangular area, length × 80 m. The total number of manatees, and those <40 m from the boat, are given for each section. Nineteen other manatees were observed at the end of transects, beyond the last plot.

	River section				
	1	2	3	4	Total
River area (ha)	77.1	91.8	57.7	63.6	290.3
Start (km)	0.13	0.13	3.91	3.91	
End (km)	2.86	3.91	9.68	10.56	
Length (km)	2.72	3.77	5.77	6.65	18.91
Mean width (m)	280.5	241.6	99.5	94.9	152.4
Mean depth (m)	2.1	6.0	7.2	5.8	5.8
Sampling days	31	40	39	44	45
Transect length (km)	167.6	357.9	507.0	698.4	1,731.0
Total area (ha)	5,041.9	8,774.2	5,423.1	7,032.3	26,271.6
Area <40 m (ha)	1,359.5	2,885.0	3,719.1	4,802.4	12,766.0
Total manatees	141	154	331	359	985
Manatees within 40 m	106	84	296	314	800

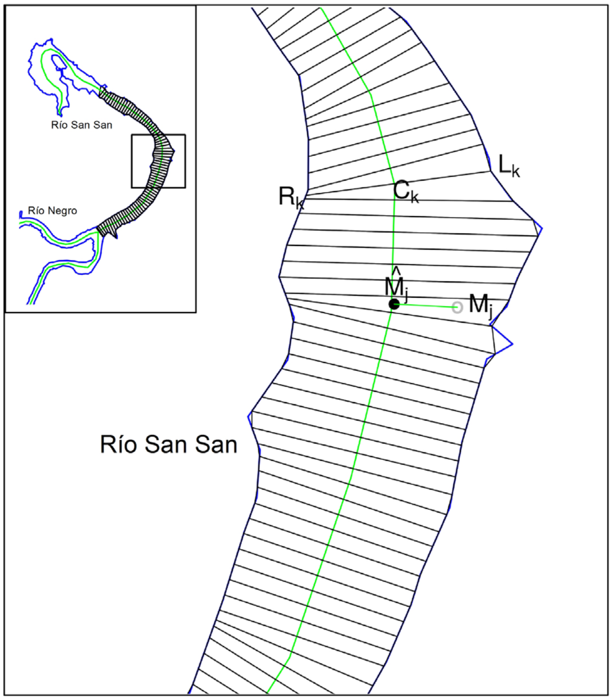

Figure 2. Manatee transects in one portion of the Rio San San, Panama, surveyed in 2013, illustrating the division of transects into plots (inset at top locates it). The green line is the river centerline, divided into segments with points every 25 m. The lines crossing the river are perpendicular to the centerline, and intersect one bank at point L_k, the other at R_k. A hypothetical manatee is indicated at position M_j, and the nearest point on the centerline by $\hat{M}_{ij}$. The manatee would be assigned a plot based on the position of $\hat{M}_{ij}$ (not M_j).

manatee sighting to a unit. Define the dividing points as C_{ik} for the kth point of transect i, with the initial point $C_{i0} = \hat{S}_i$ and the final point $= C_{in}$, where n was the number of units. The latter was not the end point $\hat{E}_i$, because transects were arbitrary in length and a portion <25 m long remained. Those short remainders were eliminated from analyses, reducing slightly the number of manatees used in calculations. River width W was estimated using segments perpendicular to the centerline from every point C_{ik} to the banks at L_{ik} and R_{ik} (Fig. 2). We refer to each 25 m unit along a line transect, outlined by perpendiculars to the banks, as a single plot with area of $25W\,\mathrm{m}^2$ (Fig. 2). Length, area, mean width, and mean depth of each of the 4 river habitats is given in Table 1, and details of the calculations are provided in Guzman and Condit (2017).

Manatee Abundance and Detectability

Each manatee sighting j was assigned to a plot based on its position $\hat{M}_{ij}$ on the centerline. The number of manatees in a single plot was an integer from 0 to 8, and we tested for overdispersion of counts per plot using Poisson expectations. Mean density was found by dividing the total manatee count in plots by the number of plots.

To assess detectability of manatees as a function of distance from the boat, we used a standard distance-sampling method (Emlen 1971; Buckland et al. 2001, 2005). Each plot was divided into a series of bands 5-m wide and parallel to the centerline, and each manatee sighting was assigned a band using its distance recorded by sonar. Manatee count and river surface area in each 5-m distance interval were then summed across all plots, leading to an estimate of manatee density as a function of distance from the boat. The same procedure was repeated in reverse to estimate density of sightings relative to distance from the river bank. Details are provided in Guzman and Condit (2017).

Overview of the Abundance Model

Direct counts of manatees in each month of the year provided a crude indicator of relative abundance and seasonal fluctuation. These counts, however, were biased by variation in sampling effort across months, caused chiefly by uncertain weather. We overcame this bias using the density of sightings per plot area, then added one additional step to bring the estimate of sighting density closer to the true density of manatees, based on the simplest distance-sampling method described by Emlen (1971). The distance beyond which sighting density declined appreciably was determined to be 40 m, and our estimate of manatee density was then based only on sightings and river surface area within that cutoff.

Dividing transects into small plots allowed quantitative modeling of abundance as a function of characteristics of the river defined in each plot (as in Auil 2004, Edwards et al. 2007, Fonnesbeck et al. 2009). The response variable in all models was $\mu = \log(\pi)$, where π is the density of manatees ha^{-1} of river surface in the plots. We were interested in seasonal variation, differences between segments of the river, depth, and distance from the river mouth. Our method was a general linear model (GLM), with a negative-binomial link function between the overdispersed integer counts and log density. The negative binomial is a common tool for describing the variance of count data in ecology, which are often overdispersed (Bliss and Fisher 1953, Ver Hoef and Boveng 2007).

A mixed-level regression coupled with a Bayesian likelihood method served to fit the parameters of the GLM, estimating manatee density by month, by river section, and as a function of river distance or depth. Bayesian methods are common in ecology since Gelman and Hill (2007). They have the advantage of producing estimates of confidence in all parameters of the model in the form of their posterior distributions (Mech and Fieberg 2015), and thus fully propagate errors at each step through to the final estimate of manatee abundance. The mixed-level method was important because of the irregular sampling, including varying number of repetitions on different parts of the river on one day. Multiple plots within a day were repeated measures, and treating them as independent would greatly inflate sample size (i.e., pseudo-replication). In each model, date was a random effect, thus defining the unit of replication as days, not plots nor transects.

Model Details

We treated month as a factor because we had no *a priori* notion of how density would vary across seasons. Because little sampling was done in February and August, January and February were pooled into one "month," and likewise August and September. The model thus involved fitting 10 different "monthly" parameters. With day of the year as a random effect, the basic model was

$$\mu \sim m + (m|j) \qquad \text{(Model1)}$$

where m is month (a factor, not numeric) and j is date (again a factor, not numeric). The parentheses indicate that m is a fixed effect while j is a random effect, following the terminology of Gelman and Hill (2007) and Bates et al. (2015). Model 1 was run in the 4 sections of the river system separately (Fig. 1).

We employed a similar model using river distance (upstream from the ocean) as a predictor,

$$\mu \sim m + d + (m + d|j) \qquad \text{(Model2)}$$

where d is distance in km. This was also executed in the 4 river sections separately. An alternative model, with river depth substituted for distance, was tested as well, but because distance and depth were correlated within each river section, they were not used together. In most cases, neither distance nor depth was a significant predictor, and because Model 1 is a more robust estimate of manatee abundance, it formed the basis for our main population estimates. Maps were produced with Model 2 to illustrate variation along the river. Total monthly abundance was found by multiplying density π by river surface area.

In the simpler model, omitting depth and distance, the key parameters to be estimated were μ_j, the log of manatee density on each day j, and $\hat{\mu}_m$, the mean of μ_j for days in month m. There were 2 more parameters required to handle variance: ε for the standard deviation of daily μ_j around the monthly means $\hat{\mu}_m$, and κ, the clumping parameter of the negative binomial; ε and κ were assumed constant across days and months, a typical approach in multiple regression (Gelman and Hill 2007). In a single river section, Model 1 thus involved estimates of 57 parameters: 45 daily estimates μ_j, 10 monthly estimates $\hat{\mu}_m$, plus ε and κ.

Fitting those parameters required 2 separate log-likelihood functions. The first covers the probability of observations on one day given the daily parameters. On day j, with N plots sampled, defining x_i as the number of manatees observed in the ith plot, the log-likelihood of the observations is

$$L_j = \sum_{i=1}^{N} log\left[NegBinom\left(x_i, mean = \mu_j, clump = \kappa\right)\right] \qquad (1)$$

The *NegBinom* term indicates the negative binomial probability of observing x_i manatees given the mean density and clumping parameter. The summation covers all N plots on day j. The full log-likelihood of the observations over all days is $\Gamma_x = \sum L_j$, the sum of the daily log-likelihoods. The second likelihood function is the upper level in the mixed-level model, giving the probability of observing daily parameters given the monthly means. For one month with J observation days,

$$L_m = \sum_{j=1}^{J} log\left[Norm\left(\mu_j, mean = \hat{\mu}_m, sd = \varepsilon\right)\right] \qquad (2)$$

Norm means the Gaussian probability of observing a daily parameter μ_j given the monthly mean $\hat{\mu}_m$ and its standard deviation ε. The full upper-level log-likelihood is $\Gamma_u = \sum L_m$, the sum across monthly log-likelihoods. The total log-likelihood of observed manatee counts given a full set of parameters is $\Gamma = \Gamma_x + \Gamma_\mu$.

To add distance (or depth) to the model required a linear regression relating log density in plot i to distance upstream, $\mu_i = \mu_j + \rho d_i$, with slope ρ and intercept μ_j (distance d_i was centered by subtracting the mean distance per river section, so the intercept = the daily mean). The slope parameter ρ was assumed constant across months, as in a multiple regression with no interaction. The log-likelihood for the observed counts becomes

$$L_j = \sum_{i=1}^{N} log\left[NegBinom\left(x_i, mean = \mu_j + \rho d_i, clump = \kappa\right)\right] \qquad (3)$$

The upper-level likelihood (Eq. 2) must be expanded to 2 equations, one for slope and one for intercept, and there must be 2 different errors, ε_μ and ε_ρ, describing daily variation of each parameter.

The Bayesian approach meant sampling the posterior distributions of each parameter with repeated Metropolis updates based on the likelihood functions. Flat priors were used, meaning any valid parameter value was equally likely. The chain of each parameter was interpreted as its posterior distribution. The posterior distribution of total population size was calculated by transforming each element of the entire chain of $\hat{\mu}_m$, the estimate of monthly log-density, to abundance. Chains were run 12,000 steps for each model, and the initial 2,000 discarded as burn-in after visual inspection of graphs of parameter chains. We report the mean of chains as best estimates, and quantiles at 0.025 and 0.975 as 95% credible intervals. The models and parameter-fitting routine were all coded in the statistical language R. The entire dataset of manatee sightings and transects, sufficient for full reanalysis, is available at a permanent, online data archive (Guzman and Condit 2017).

RESULTS

River

Maximum depth in the river system was 8 m. There were 2 main shallow areas <2 m deep, one in the lagoon where manatees often aggregated, the other midway upstream and seldom utilized by manatees (Fig. 1). The rest of the system consisted of narrow channels in the tributaries, averaging 4 m in depth, including some pockets of shallow water where mothers and calves aggregated.

Manatee Counts and Density

Manatees were recorded in 83% of the 214 transects, including 1,004 individual animals. Nineteen of those animals were found in the short transect remainders outside 25-m-long plots, leaving 985 as the basis of modeling. A total of 69,760 plots were surveyed, so the mean density per plot was 0.014. Animals were in groups: 735 plots had a single animal, while 98 plots had 2–8 animals. Counts were thus highly overdispersed. With density = 0.014 per plot and a random (Poisson) distribution of counts, the expectation would be 7 plots with 2 animals and none with 3 animals or more. Tables listing every transect, every manatee sighting, plus raw counts per month and per river section, are provided in the online supplement (Guzman and Condit 2017).

The density of manatee detections per river surface declined with distance from the boat, especially beyond 40 m; not a single animal was observed >100 m from the boat (Fig. 3). Indeed, >80% of all manatees observed were within 40 m of the boat (Table 1; Fig. 3), but only 49% of the transect area was <40 m. Manatee detection density was also low close to the boat (Fig. 3). These observations led us to estimate manatee density using only detections and survey area <40 m from the boat (as stated in Methods). We found little indication manatee density varied with distance from the bank, though there were fewer than expected detections within 5 m of shore (Fig. 3).

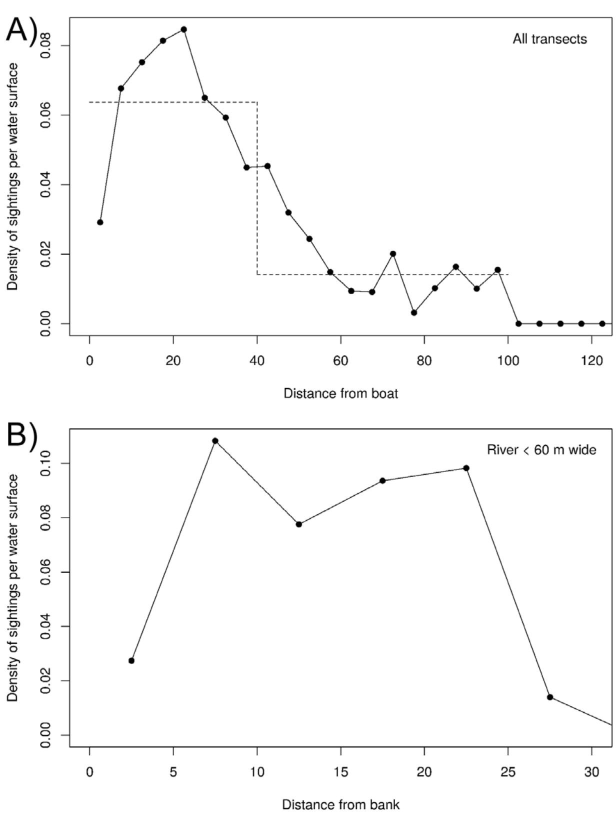

Figure 3. Density of manatee detections during 2013–2014 in the Rio San San and Rio Negro, Panama, as a function of distance from the transect (the boat) or distance from the river bank. If manatees were uniformly distributed at all distances, these curves would be flat. (A) Density versus distance from boat across the entire river system. The dashed line illustrates the step function we used to estimate population density, assuming detections <40 m from the boat produced an estimate of population density closest to the true density. (B) The same calculations used to estimate detection density versus distance from shore, including only those plots where the river was <60 m wide. In that area, the distance effect was not confounding, so this can be interpreted as an estimate of manatee density at varying distances from the bank. The low density at 25–30 m from the bank corresponds with the low density <5 m from the boat, but the low density <5 m from the bank cannot be attributed to poor detection at distance because manatees were often observed 25–30 m from the boat.

Manatee density in the core 80-m-wide transect was 0.063 ha^{-1} of river surface (800 manatees observed in 12,766 ha surveyed; Table 1). In the total river system of 290 ha, the estimated mean number of manatees across the entire year was thus $0.063 \times 290 = 18.3$.

Seasonal Variation

Manatee abundance was sharply seasonal (Fig. 4). In December–February, there were fewer than 3 animals estimated in the entire river system. Numbers rose sharply in March and remained fairly high through July, with a peak estimate of 33 manatees in May (Table 2). Credible intervals on abundance were substantially different in the low season (1–6 manatees) versus the high season (22–71 manatees).

Variation Among River Sections

The upper tributaries, Sections 3 and 4 of the river system, had the greatest number of manatees, peaking at 10 animals each in May or June (Table 2). Section 2 had the fewest, with a maximum of 6 animals (in May). All sections followed the same seasonal trend, with greatest numbers present in May–June; however, manatee numbers rose in March in Sections 3 and 4, but not until May in Sections 1 and 2 (Table 2).

In most of the river, neither depth nor distance upstream was correlated with manatee density. In Sections 2–4, the slope parameter ρ (increase of log density per km up river) varied in sign and had credible intervals overlapping zero. In Section 1, however, both distance and depth (tested separately) had strong effects, picking up the same trend: manatees were more abundant further upstream, where the water was shallowest, which is the wide marine lagoon (Fig. 5). The estimated effect of distance was $\rho = 0.81$ (95% credible intervals 0.32–1.32), indicating a 2.3-fold change every km, or a 9-fold increase in density over the 2.7-km section (Fig. 5).

DISCUSSION

We estimate a mean population of 18 manatees throughout the year in the 18-km stretch of the Rio San San and Rio Negro that we surveyed. Abundance was highly seasonal, though, and we found 2–4 manatees from November to February and >30 in May Uncertainty was carefully incorporated, and we determined 95% credible intervals of 22–71 animals at the peak.

Manatees were numerous in the narrow and relatively deep upstream segments and in the shallow lagoon near the river mouth. There were smaller numbers in the middle section of the river. Neither distance from the river mouth nor river depth was a consistent predictor, as was evident from high manatee density in both the deepest and shallowest parts of the river. Manatee abundance in the study area is probably driven by a combination of factors, with plant density likely most important, in turn affected by salinity, water temperature, or depth. Moreover, because vegetation is not abundant in the San San and Negro river system and manatees are commonly observed feeding on grass along the riverbanks,

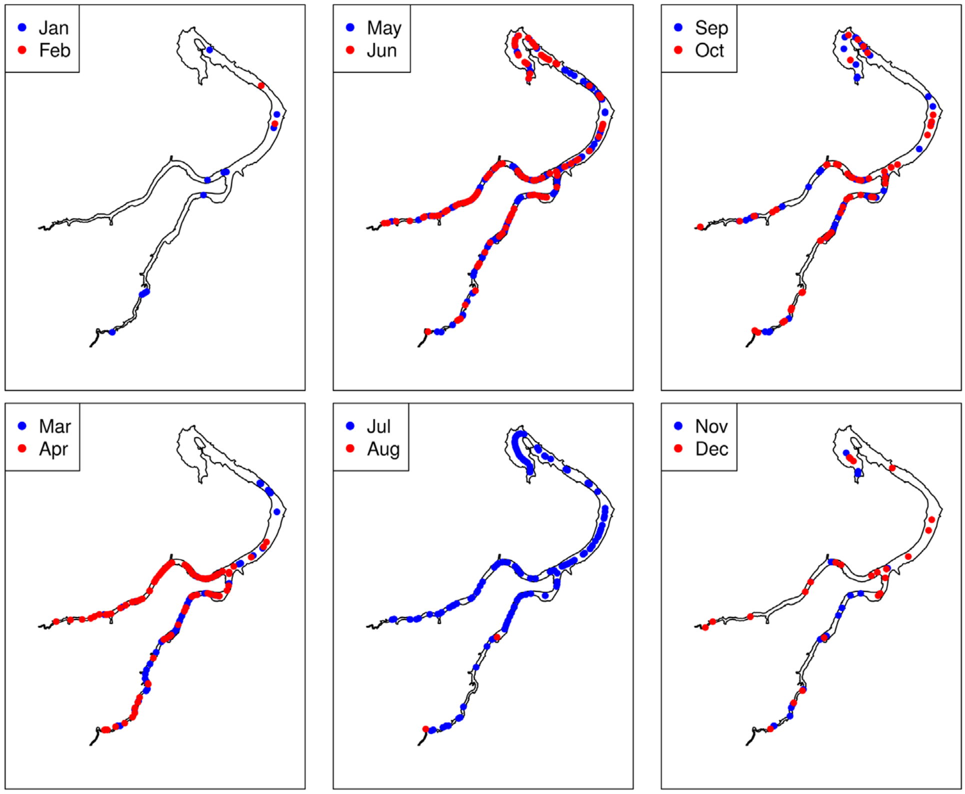

Figure 4. All individual manatee sightings by month during 2013–2014 in the Rio San San and Rio Negro, Panama. Each is indicated by its projected position $\hat{M}_{ij}$ on the river centerline. These are raw sightings, not corrected for the sampling effort (e.g., the absence of manatees in Section 1 in March was simply because we did not visit Section 1 in March). Our modeling approach assessed density by counting manatees within subdivisions of the transects we refer to as plots, and thus corrected for sampling differences.

aquatic factors alone may be insufficient to predict abundance patterns.

Deutsch et al. (2003) reviewed seasonal movements in tropical streams of Central America and Africa, where water temperature is never limiting to manatees, and concluded that the most frequent pattern is upstream movement during the wet season, perhaps when new plant growth peaks. This hypothesis, however, does not provide a clear explanation for seasonal patterns we observed. Though the abundance peak

Table 2. Estimated monthly number of detectable manatees in each river section and the total across all sections in the Rio San San and Rio Negro, Panama, in 2013–2014. Credible intervals of 95% (CI) are given for the total; intervals were calculated in every section and every month, but were omitted for brevity.

	Abundance					
Month	**Sect. 1**	**Sect. 2**	**Sect. 3**	**Sect. 4**	**Total**	**95% CI**
Jan–Feb	0.1	1.1	0.7	0.8	2.7	1.6–6.4
Mar		2.4	7.0	6.7	16.1	10.4–32.3
Apr	0.1	0.5	8.4	6.8	15.7	11.0–24.9
May	9.0	6.3	7.6	9.9	32.8	22.2–70.9
Jun	9.4	3.6	9.9	5.1	28.0	18.2–63.3
Jul	9.7	2.7	4.5	4.3	21.2	13.6–45.2
Aug–Sep	1.9	0.2	1.4	2.2	5.7	3.5–13.8
Oct	0.9	0.2	1.1	2.3	4.6	3.2–8.8
Nov	1.6	0.0	0.4	1.9	4.0	2.2–11.8
Dec	0.2	0.4	1.1	0.4	2.2	1.3–5.7

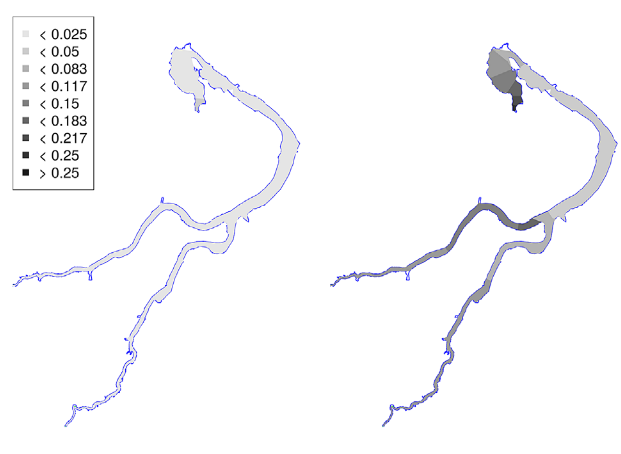

Figure 5. Density map of manatees in 2 seasons in the Rio San San and Rio Negro, Panama, during 2013–2014. These are based on results of the distance model, which produced an estimated density at every position in each river section; monthly estimates were averaged across 4 months as indicated. Density is in manatees ha^{-1} of river surface. The significant increase in density with distance in Section 1 is evident from the rapid change moving away from the river mouth and around into the wide lagoon. The depth model in Section 1 picked up the same trend because the lagoon was the shallowest section. The distance effect was not significant in the other 3 sections, as indicated by weak variation throughout each.

coincided with the rainy season from April to August, even the driest months (Sep–Oct) get >15 cm of precipitation in Bocas del Toro, and November–December, when there were few manatees, are the wettest months (Kaufmann and Thompson 2005).

The region around the San San drainage includes considerable additional manatee habitat from the Rio Sixaola (6 km north) to the Rio Changuinola (6 km south), with many agricultural drainage channels between, plus nearshore marine habitat, including extensive seagrass beds near the Bocas del Toro archipelago (20 km east). These habitats are sufficiently connected that we view this as a regional manatee population of which we surveyed one portion thoroughly. The average density we estimated in that portion was based on counts that fluctuated as manatees moved in and out of the transects. The range of confidence we present, 22–71 manatees at a peak, is based on those fluctuations and refers to detectable manatees in the San San drainage at any one time. Agricultural channels and the 2 other rivers are often covered with plants, making boat surveys impossible, but we have observed numerous signs of manatees feeding in those plants, and we hypothesize that the regional population could be considerably greater than our estimate for the San San and Negro rivers.

Our study represents the first use of sonar to estimate manatee abundance. Like any counting estimate, it depends on detectability, but we found the large, slow-moving animals easily visible in the sonar image. By calculating density only in the 80-m-wide core of the line-transects, we corrected for reduced detectability beyond 40 m. Still, we have not made independent counts to assess detection rate, so we cannot be precise about how many were missed within 40 m. Prior work compared sonar detections of manatees with visual observations (Rodas-Trejo et al. 2008, Brice 2014, Castelblanco-Martínez et al. 2017), and Gonzalez-Socoloske and Olivera-Gómez (2012) found that sonar identified >80% of animals that were seen. None of those observations, however, led to abundance estimates. The best way to estimate detection in the future will be by attaching telemetry tags on manatees, as has been done with aerial counts (Flamm et al. 2005, Edwards et al. 2007, Castelblanco-Martínez et al. 2013, Gonzalez-Socoloske et al. 2015), or by individual acoustic tonal recognition (Castro et al. 2016).

Previous manatee surveys in Panama were done by air. Mou Sue et al. (1990) and Riquelme et al. (2004) both reported animals in the Olla lagoon, the same lagoon near the mouth of the San San River that we surveyed. The latter noted 9 adults and 4 calves in February 2005, and 9 adults and 2 calves in April 2005. Those counts exceed what we encountered in February and April, months of low to medium abundance in our surveys. But they are similar to the 9–10 animals we counted in the lagoon area in May–July. Because our surveys spanned just a single year, it remains possible that there is year-to-year variation in abundance and seasonal patterns.

Outside Panama, we located other estimates of manatee populations in which a quantitative population density could be derived. In 3 rivers in Florida and Belize, the greatest aerial counts of manatees included 1–3 animals km^{-1} of river (Morales-Vela et al. 2000, Scolardi et al. 2009), similar to the 33 we estimated to inhabit 18 km of the San San River at peak season. In one aerial survey of a shallow bay, Olivera-Gómez and Mellink (2002) counted 20 manatees in a 100×0.8 km transect, or 0.25 manatees km^{-2}, but in contrast, winter aggregations in warm spots in Florida bays reach densities of 100 manatees km^{-2} (Kochman et al. 1985). In the San San River system, we estimated a manatee density of 10 km^{-2} of river surface, well within this range.

MANAGEMENT IMPLICATIONS

The use of active sonar seems promising. We were able to find manatees, map their locations precisely, and convert the sightings into quantitative occurrence data that could be subjected to rigorous analysis. The peak of 33 animals present in 18 km of river is well within the range of densities for similar rivers in Central America and Florida. The sonar device is costly—in the range of US$20,000—but once purchased, surveys can be finished for the cost of gasoline and thus repeated across seasons and years, allowing tests of population trends and seasonality. On the other hand, the unknown detection rate and difficulty with floating vegetation must be recognized as limitations to sonar (Gonzalez-Socoloske et al. 2009, Brice 2014, Castelblanco-Martínez et al. 2017), and aerial surveys are more efficient at covering large areas. Long-term conservation planning would thus benefit by wider counts from the air to establish manatee distribution across Panamanian wetlands, combined with more detailed local studies with active sonar, satellite tags, and perhaps new methods based on individual recognition of vocalizations (Castro et al. 2016), a method we are currently testing in the Changuinola River.

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