ISSN 1930-1448

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Florida Fish and Wildlife Conservation Commission
Fish and Wildlife Research Institute
Technical Report No. 23 • 2018
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We suggest that this document be cited as follows:
Hostetler, Jeffrey A., Edwards, Holly H., Martin, Julien, and Schueller, Paul. 2018. Updated Statewide Abundance Estimates for the Florida Manatee. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute Technical Report No. 23.

Cover and text papers used in this publication meet the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48–1992(R2009).

Cover photograph: Aerial survey photograph of manatees by the shore in Palm Beach County.
Photograph by Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute (Amber Howell).

Abstract

Knowing how many manatees live in Florida is critical for conservation and management of this threatened species. Martin et al. (2015) flew aerial surveys in 2011–2012 and estimated abundance in those years using advanced techniques that incorporated multiple data sources. We flew additional aerial surveys in 2015–2016 to count manatees and again applied advanced statistical techniques to estimate their abundance. We also made several methodological advances over the earlier work, including accounting for how sea state (water surface conditions) and synchronous surfacing behavior affect the availability of manatees to be detected and incorporating all parts of Florida in the area of inference. We estimate that the number of manatees in Florida in 2015–2016 was 8,810 (95% Bayesian credible interval 7,520–10,280), of which 4,810 (3,820–6,010) were on the west coast of Florida and 4,000 (3,240–4,910) were on the east coast. These estimates and associated uncertainty, in addition to being of immediate value to wildlife managers, are essential new data for incorporation into integrated population models and population viability analyses.

Introduction

Abundance, or the number of organisms of a species in a region at a given time, is a fundamental quantity in population and conservation biology (Williams et al. 2002, Sutherland and Royle 2016). Therefore, obtaining robust and accurate estimates of abundance is essential in the study and management of threatened and endangered populations. For many animals it can be challenging for biologists to obtain these estimates. Challenges include widespread and changing distribution of animals and, during surveys, animals that are missed because they are either in the study area but not available to be detected by observers or are available to be detected but are still missed by observers.

These issues make estimating abundance of the threatened Florida manatee (*Trichechus manatus latirostris*) difficult. Manatees exhibit complex partial migration patterns (Deutsch et al. 2003). During warmer months, some manatees travel great distances from wintertime warm-water aggregation sites to feeding and breeding locations, some of which are outside of Florida. Coastal and freshwater habitats in Florida alone cover more than 11,500 km^2 (FWC, unpublished GIS data), making any effort for a comprehensive census (complete enumeration of a population) impractical. In addition, as aquatic mammals, manatees are often too far below the surface to be visible from aircraft, depending on water clarity and other factors. Even when they are near the surface, manatees can be missed by observers during aerial surveys. Failing to account for these sources of error can lead to substantial underestimation of abundance. This is problematic, as abundance is a key source of information used by natural-resource managers for the assessment of the conservation status of the Florida manatee (Runge et al. 2017, U.S. Fish and Wildlife Service 2017).

From 1991 through 2014, the only statewide manatee counts came from aerial synoptic surveys, which are flown almost every year, during the coldest part of winter (Ackerman 1995, Martin et al. 2015, Fish and Wildlife Research Institute 2018). These surveys are intended to be comprehensive, but they do not account for the number of manatees that are missed because they are absent from surveyed sites, present at surveyed sites but not available to be detected, or available yet not detected. The high level of variability in the counts from synoptic surveys suggest large degrees of year-to-year variation in these factors. As such, synoptic surveys provide minimum counts that can be used as lower bounds of abundance, but they should not be considered an estimate of abundance or used to infer population trends.

In 2015 the Fish and Wildlife Research Institute (FWRI), a division of the Florida Fish and Wildlife Conservation Commission (FWC), accomplished one of its primary conservation goals by conducting and publishing the first statewide Florida manatee abundance estimate (Martin et al. 2015), for 2011 (when the west coast was surveyed) and 2012 (when the east coast was). Researchers used a stratified random sampling design and developed models for reducing errors associated with imperfect detection and spatial variation in density and availability. Martin et al. (2015) estimated a statewide manatee population of 6,350 (95% Bayesian credible interval: 5,310–7,390) manatees statewide, with 2,790 (2,160–3,540) on the west coast and 3,560 (2,850–4,410) on the east coast. These surveys provided a single estimate of abundance for a given year on a given coast (or over a pair of years for a statewide estimate). Repeating surveys not only updates estimates, it adds information that better characterizes the population, improving the reliability of the results.

Martin et al. (2015) also identified several limitations to their approach, including the inability to include parts of the state in which no manatees were counted or to account for the effects of sea state (water surface conditions, as measured by the Beaufort scale) on the probability of manatee availability. Therefore, the goals of this study were: 1) to fly new surveys of both coasts, ideally at a time of year with better weather conditions; 2) to extend the availability study to include more conditions, including sea state; 3) to provide Florida manatee abundance estimates from

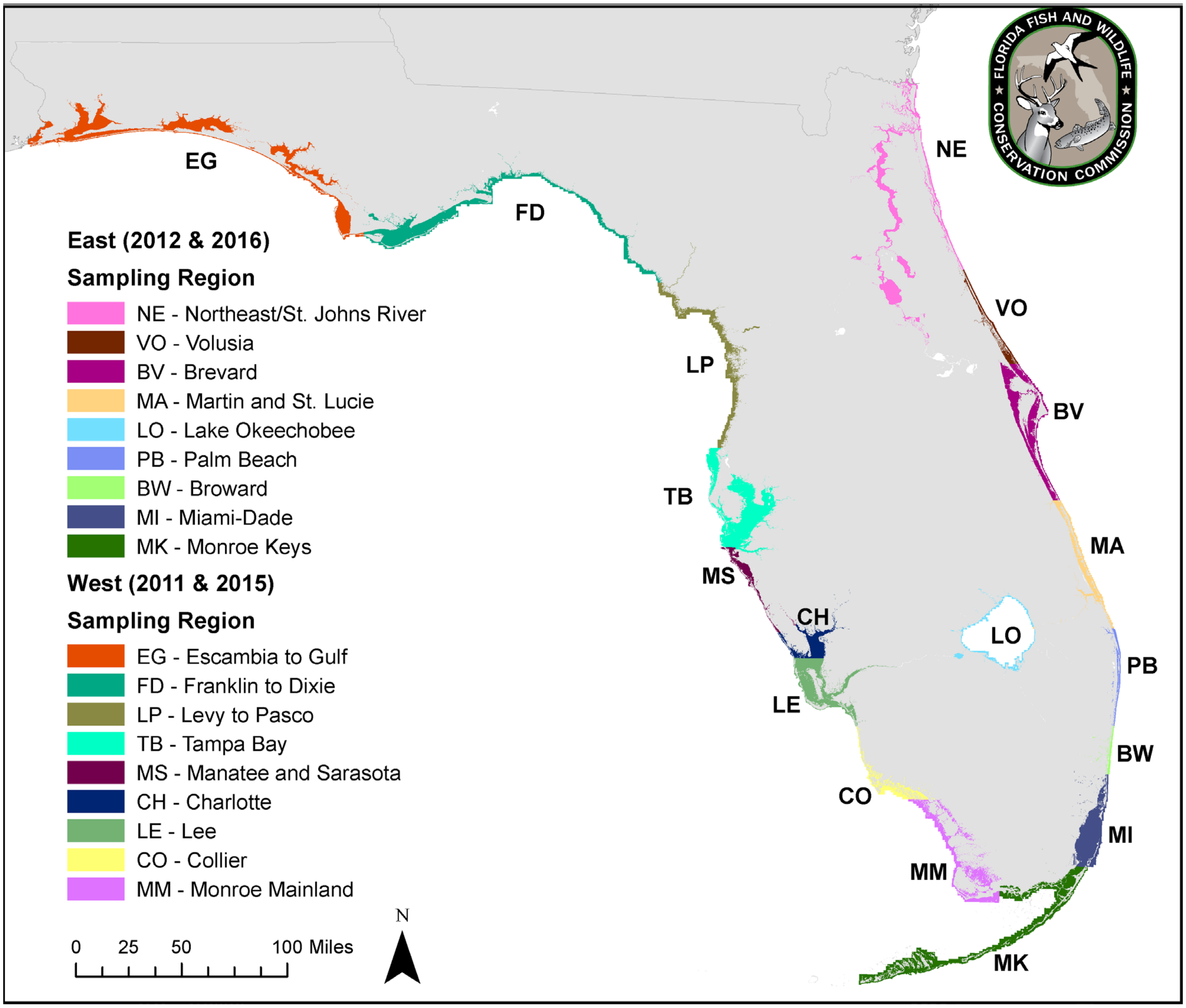

Figure 1. Sampling regions of abundance surveys.

the new surveys; and 4) to provide updated abundance estimates from the original (2011 and 2012) surveys that account for the effects of both sea state and synchronous surfacing behavior on manatee availability and include all parts of Florida in the area of inference. We also discuss limitations to the inferences that might be drawn from these estimates, and we recommend enhancements to survey and estimation methods for this threatened mammal.

Methods

Field surveys

Abundance surveys

We conducted aerial surveys from Cessna 172 fixed-wing aircrafts between February 28 and March 22, 2011, and during December 1–9, 2015, on the west coast and during March 5–13, 2012, and December 5–12, 2016, on the east coast (Martin et al. 2015; see Appendix I, Tables S1–S4 for exact dates by location). Estuaries, rivers, creeks, and coastlines from all or part of 26 counties on the west coast and 21 counties on the east coast were surveyed. Each coast was divided into nine sampling regions (Figure 1).

We used a stratified random sampling protocol in which all potential cool-season manatee habitat was included in the sampling frame, and allocated survey effort to three strata (Dorazio et al. 2013, Martin et al. 2015). Potential habitat was stratified using a geographical information system (GIS). Areas that were known to be suitable manatee habitat and likely to have manatees present during the survey (e.g., primary or secondary warm-water aggregation sites) were included in stratum 1. Any area that was considered probable manatee habitat, as determined by the presence of manatees either through aerial sightings, telemetry locations, or carcass recoveries, were

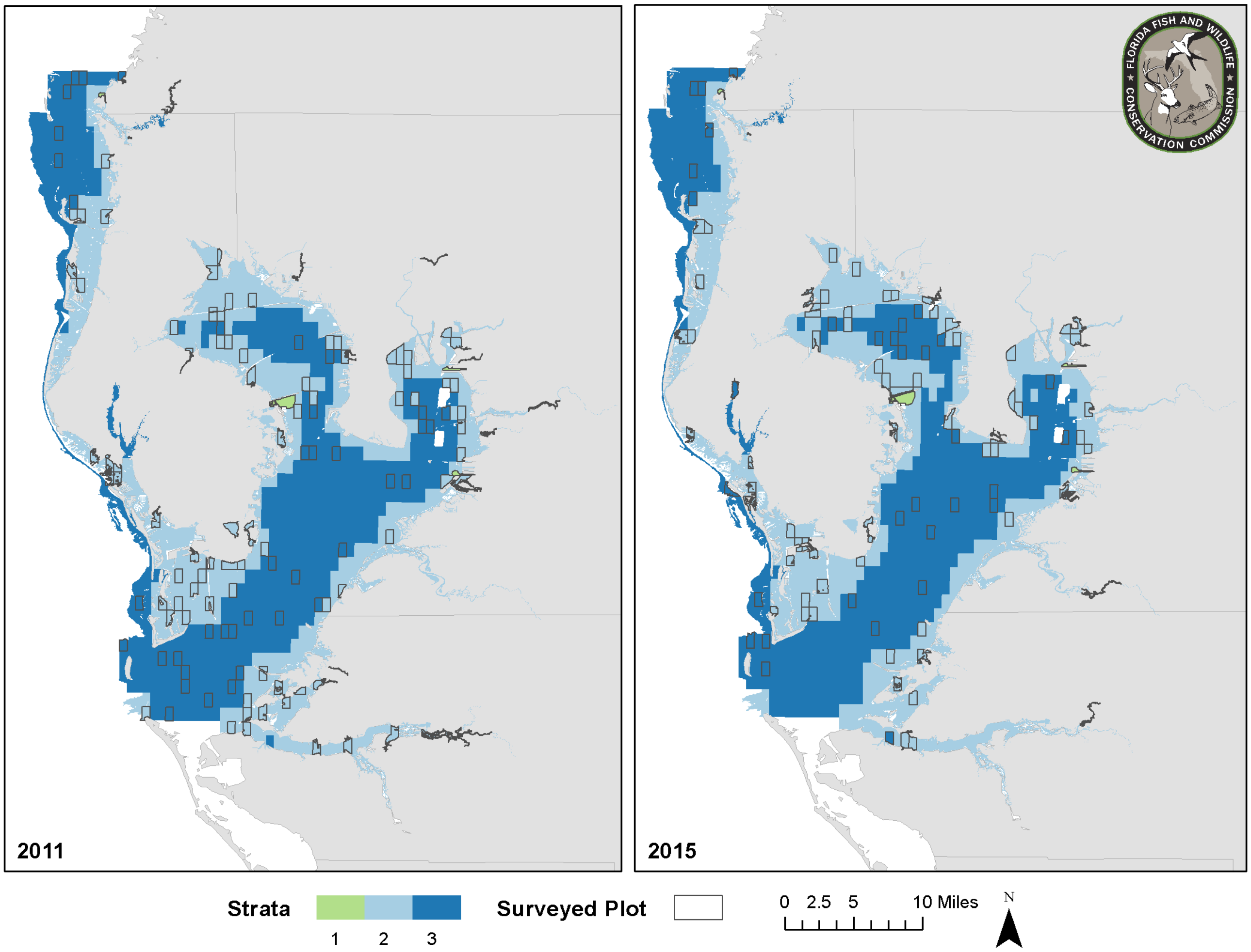

Figure 2. Example map of a sampling region (Tampa Bay). All plots are shown; colors indicate strata. In the panel on the left, plots flown in 2011 have a black outline; in the panel on the right, plots flown in 2015 have a black outline.

included in stratum 2. In areas where information about manatee presence was either not known or was sparse but that had water depths <3.7 m or that had seagrass beds present were likewise included in stratum 2. Areas without seagrass or water >3.7 m (habitat areas less likely to have manatees) or with cold ambient temperatures and no warm-water sites (e.g., parts of the panhandle region) were included in stratum 3.

The study area was subdivided into 11,149 plots (each ~1.3 km^2 in area) using a GIS. For each coast and sampling region, plots were randomly selected within each habitat stratum to be included in the survey (except that all stratum 1 plots were included). See Figure 2 for an example, and Appendix II, Tables S5 and S6 for data on plots selected. Selected plots were overflown by two observers at an altitude of 750 ft and a speed of about 80 kts. Manatees were counted during two consecutive passes (each taking about 2 min) at each plot; if a group of manatees was observed, a third pass was used to reconcile group locations between observers.

Availability study with manatee replica

To estimate the probability of manatees being available for detection by observers, we used the method described by Martin et al. (2015), which was inspired by Pollock et al. (2006). We constructed a replica of a manatee (see Fig. S3 in Martin et al. 2015) and lowered it at 0.5-m increments into the water from the surface to a depth of up to 3 m. Observers in the plane recorded the depth at which the replica could no longer be seen. We flew around the replica at three surface distance categories (200 m, 300 m and 400 m) at 15 sites that varied in water clarity and sea state. Each site was assigned to one of four visibility categories, v_k. A v_k of 1 meant that the water was clear and the bottom was visible; a v_k of 2 meant that the bottom was visible, but details were not clearly visible; a v_k of 3 meant that it was difficult to evaluate water clarity because the water was too deep for the bottom to be seen; and a v_k of 4 meant that the water was turbid. We used observations from the more experienced observer to determine the maximum water depth at which the replica could be seen under each combination of distances (d), visibility (v_k), and sea state (Beaufort scale <3 vs. ≥3). There was at least one site and as many as four for all combinations except $v_k = 1$, high sea state and $v_k = 4$, high sea state.

Statistical models

Model structure and general modifications

As the basis of our analyses, we used the model structure described in detail in Martin et al. (2015). As in that study, the number of manatees in strata 2 and 3 plots is assumed to follow a zero-inflated Poisson (ZIP) distribution, and the number of manatees in stratum 1 plots is assumed to follow a Poisson distribution. Detection probability (p) is broken down into two components: the probability that a manatee present in a plot is available to be detected (near enough to the surface, for the current sea state and visibility conditions; ${}^{A}p$) and probability that an observer perceives a manatee, given that it is available to be detected (${}^{D}p$). This is a modified N-mixture model (Royle 2004):

$$\begin{aligned} y_{it} &\sim \mathrm{bin}(N_i, p_{it}) \\ p_{it} &= {}^{A}p_{it} \cdot {}^{D}p_{it} \end{aligned} \tag{1}$$

where y_{it} is the count for pass t of plot i, N_i is the number of manatees in that plot, and bin is the binomial distribution. However, ${}^{A}p$ and ${}^{D}p$ come not from the N-mixture model itself but from the availability study and a double-observer analysis, respectively. This modeling framework is flexible, and, as additional information becomes available, we can update model parameters or model structure to improve estimates of abundance over time. Below we describe some of the changes to the original model implemented in this study.

1. We accounted for sea state effects on manatee availability. In addition to having more observations in the study with which to estimate mean availability probabilities, we used the updated availability study results (see above) to update the abundance estimation. First, we were able to include the effects of high sea state (Beaufort scale ≥3) on manatee availability directly, instead of excluding it or using ratios from a dugong study (Pollock et al. 2006, Martin et al. 2015). We only obtained two results for sea state 3: one at visibility 2 and one at visibility 3. Therefore, we continued to assume no sea state effect for visibilities 1 and 4. In some conditions (combination of visibility and distance), availability was higher in the high sea state in the new results. It is possible that weather conditions (such as cloud cover or glare) may make a single flight of the availability study not as reliable as multiple flights. Because we expect high sea state to only make availability worse or the same, for those conditions in which availability was higher in the high sea state, we substituted the low sea state probability for the high sea state one.
2. We relaxed the assumption that the probability of availability is 1 at visibility 1: The original study assumed that probability of availability was 1 at $v_k = 1$, based in part on availability study results in which the replica could always be seen at that visibility (Martin et al. 2015). The updated availability study allowed the manatee replica to be lowered to greater depths (to 3 m instead of to 2 m). The new results for visibility 1 showed that manatees were not always available to be seen at greater depths. Therefore, we discarded the assumption that probability of availability is 1 at visibility 1 and estimated mean probability of availability for visibility 1 using identical methods as for the other visibility levels. This generated mean probabilities for visibility 1 plots of average distance proportions of 0.96. See Appendix III, Figure S1 for all mean probabilities of availability.
3. We allowed plots to have multiple values for covariates: Abundance survey observers sometimes indicated that a plot had a range of covariate values (visibility or sea state conditions) or divided a plot into sections with different covariate values, instead of using a single covariate value for a plot. For plots with sections of different sizes, the old approach (Martin et al. 2015) was to use the covariate values of the largest part; when there was a range of covariate values or the sections were of equal size, they picked a value randomly. They did this because visibility and sea state are treated categorically in the abundance model, making it difficult to use an average covariate value. We developed an approach in which we applied covariate values using a weighting modification of the categorical approach already used (Martin et al. 2015) for coding the covariates. For example, if an observer indicated that a plot was roughly 75% visibility 3 and 25% visibility 4, under the old approach this plot would have been coded as visibility 3. Under the new approach, it is coded as 75% visibility 3 and 25% visibility 4. Under this weighted average approach, the plot's (mean) probability of availability is calculated by multiplying the estimated probability of availability under each condition by the proportion of visibility conditions observed.
4. We changed uniform priors: In the earlier approach, the coefficients for the zero-inflated Poisson generalized linear equations (Martin et al. 2015, equations

2–4) had uniform priors between −10 and 10 for both the zero-inflation and Poisson parameters. In the new approach, the coefficient priors were between −5 and 5 in most cases (for exceptions, see *Model variations, Include zero-count regions*). This did not prevent the priors from being reasonably noninformative, as intended (Gelman et al. 2008); for example, these priors would allow the proportion of stratum 2 plots of average size without manatees (taking into account both sources of zeros from the ZIP distribution) within a region to vary between 0.00669 and 0.99998. However, restricting these ranges improved convergence.

Model variations

Martin et al. (2015) presented model variations with and without an outlier group seen in the third pass in the west coast 2011 survey. Because 1) we believe that the model with the outlier is more accurate, 2) no outlier data points were detected in the 2012, 2015, and 2016 surveys, and 3) this model variation has already been presented, we present only results with the outlier. The other source of model variation presented in Martin et al. (2015) pertained to manatee availability at high sea state conditions. Our new availability study results make this model variation moot (see *Model structure and general modifications*). The models we ran in this study include four new model variations: include zero-count regions; beta–binomial probability of availability; survey-level probability of perception; and model-averaged probability of perception.

Include zero-count regions.—The original abundance estimation excluded 1) sampling regions in which no manatees were seen during abundance surveys (LO and EG; Figure 1) and 2) strata 2 and 3 in sampling regions when no manatees had been seen in those strata (CH; Martin et al. 2015; no manatees were seen in LO and EG again during the new surveys, but no manatees were seen in strata 2 and 3 of FD instead of CH). These were excluded because their inclusion would have caused convergence and parameter identifiability problems for the zero-inflated abundance model. While excluding regions with zero observed manatees prevented inflated variances of abundance estimates, it is still likely that at least one manatee existed in those regions but were not detected, and including all regions is ideal for a statewide abundance estimate. Still, two problems could result from including these regions in the model. First, having zero observed manatees in a region does not provide the model with sufficient information to estimate what proportion of these zeros arises from the Poisson (zeros likely arising from chance variation from low overall density) versus the zero-inflation portion of the model (abundance is zero in that plot, but not necessarily low in other plots of the region). This makes abundance estimates unstable because only a small fraction of plots was sampled. The other problem is the lack of sensible lower bounds on density.

To overcome the convergence and parameter identifiability issues arising from the inclusion of regions with zero observed manatees, we changed the distributional assumptions of the model and included external information on minimum abundance. To include the zero-count sampling regions in the analyses and address the problem with two sources of zeros, we changed the distribution for these regions from zero-inflated Poisson to Poisson. This greatly reduces the possibility of large groups in unsampled plots, because under the Poisson distribution the zeros observed suggest low overall density. To address the lower bound problem, we used incidental observations from the abundance surveys and data from other surveys and telemetry. In 2012, one manatee was spotted on the abundance survey in LO, although not in one of the sampled plots. In December 2015, telemetry data indicated there was at least one manatee in EG. Therefore, we adjusted density priors in those years so that the expected number of manatees in those sampling regions was at least one. There was no direct evidence of manatees in EG in 2011 or in LO in 2016, but manatees have been seen in those regions at those times of year in other years, so we adjusted priors so that the expected number was at least 0.5.

Beta–binomial probability of availability.—Martin et al. (2011) developed a version of the N-mixture model that addresses nonindependence in detections of individual animals, as well as heterogeneity in detection probability over space. Generally, such nonindependence can arise from multiple sources. For example, the correlated singing patterns of birds and amphibians could lead to most of the animals being detected in some survey sites, with very few of the animals present being detected in other sites. With respect to aerial surveys of Florida manatees, nonindependence might arise from synchronous surfacing behavior among individuals. Under a traditional binomial N-mixture model, nonindependent detections can lead to biased estimates of abundance (Martin et al. 2011). Martin et al. (2011) addressed nonindependence of detections using a beta–binomial model:

$$\begin{aligned} y_{it} &\sim \mathrm{bin}(N_i, p_{it}) \\ p_{it} &\sim \mathrm{beta}(\alpha, \beta) \end{aligned} \tag{2}$$

where y_{it} is the manatee count at site i and pass or survey t, N_i is the abundance at site i, p_{it} is the detection probability at site i and survey t, bin corresponds to the binomial distribution, and beta to the beta distribution with shape parameters α and β. This model can also be written as:

$$y_{it} \sim \text{beta–bin}(N_i, \overline{p}, \rho) \tag{3}$$

where $\overline{p}$ is the mean detection probability and ρ is its correlation, given by

$$\begin{aligned} \overline{p} &= \frac{\alpha}{\alpha+\beta} \\ \rho &= \frac{1}{\alpha+\beta+1} \end{aligned} \tag{4}$$

Martin et al. (2011) estimated ρ between 0.33 and 0.35 for their manatee example data set, depending on the model used for N. They emphasized that this was an example data set that was not intended to reflect the true abundance or detection of Florida manatees. However, a preliminary independent analysis of a different set of aerial survey data for the Florida manatee estimated very similar ρ values (between 0.27 and 0.3; Edwards et al. pers. comm.).

Martin et al. (2011) did not separate detection components, but the beta–binomial model can be applied to either probability of availability or probability of perception, as appropriate. Because we believe the primary reason for nonindependent detections of manatees is synchronous surfacing behavior, we applied the beta–binomial model to probability of availability. However, the previous procedure for estimating availability brings in multiple sources of information, including probabilities of manatees being at different depths, visibility (water clarity), and sea state (surface conditions) at each plot, proportions of each plot in different distance categories from the plot's edge, and average results from the manatee availability study (Martin et al. 2015). We wanted an approach that would allow for synchronous surfacing behavior without omitting that information. To do this, we calculated the expected probability of availability for each plot (${}^{A}\overline{p}_i$) from the multiple sources of information, assuming $\rho = 0.33$, and reversed equation 4 to compute α_i and β_i at the plot level as:

$$\begin{aligned} \alpha_i &= {}^{A}\overline{p}_i\left(\frac{1-\rho}{\rho}\right) \\ \beta_i &= \left(1-{}^{A}\overline{p}_i\right)\left(\frac{1-\rho}{\rho}\right) \end{aligned} \tag{5}$$

We modeled probability of availability as varying on the plot and pass level using the beta–binomial distribution, similar to Martin et al. (2011).

Survey-level probability of perception.—The original method modeled probability of perception (${}^{D}p_{it}$) as beta–binomial-distributed at the plot level (${}^{D}p_{it} \equiv {}^{D}p_i$), informed by a double observer (backseat observer and front-seat observer) perception analysis (Martin et al. 2015). This had the effect of treating the uncertainty in front-seat perception probability as variability between plots. Probability of perception may vary within a survey, but there is little reason to believe that it varies at the plot level. Therefore, we developed a model variation in which the probability of perception is beta–binomial-distributed at the survey level (${}^{D}p_{it} \equiv {}^{D}p$), which treats the uncertainty in perception probability as uncertainty in survey-level perception probability.

Table 1. Estimates of probability of perception from the double-observer analysis for each abundance survey, and the model-averaged probability of perception for the two west coast surveys. The parameter ${}^{D}p$ is the estimated probability of perception, SE(${}^{D}p$) is its standard error, and ${}^{D}\alpha$ and ${}^{D}\beta$ are the shape parameters for a beta distribution with that estimate and standard error.

Survey	Coast	${}^{D}p$	SE(${}^{D}p$)	${}^{D}\alpha$	${}^{D}\beta$
2011	west	0.730	0.039	93.5	34.5
2012	east	0.763	0.029	166.1	51.6
2015	west	0.617	0.032	142.7	88.6
2016	east	0.731	0.039	97.5	35.9
2011/2015	west	0.674	0.067	32.5	15.8

Model-averaged probability of perception.—The probability-of-perception estimate for the 2015 survey (west coast) was considerably lower than those for the other three surveys (Table 1). Some variation in perception rates may be expected between years and coasts, e.g., due to changes in weather and habitat. But there are several reasons that we found it inconsistent that the 2015 estimate was lower than the 2011 estimate on the same coast. Conditions were better overall in 2015 (compare Tables S1 and S3), and the observers were mostly the same people, but more experienced. Our double-observer perception model may be too simple to fully encompass the uncertainty in perception probabilities.

Therefore, we developed a model variation that takes into account more uncertainty in west coast perception probability. We did this by borrowing from methods used for averaging estimates from more than one model (Burnham and Anderson 2002):

$$\begin{aligned} {}^{D}\overline{p} &= \sum_{s=1}^{2}\left(w_s \cdot {}^{D}p_s\right) \\ \mathrm{SE}\left({}^{D}\overline{p}\right) &= \sum_{s=1}^{2} w_s \sqrt{\mathrm{SE}\left({}^{D}p_s\right)^2 + \left({}^{D}p_s - {}^{D}\overline{p}\right)^2} \end{aligned} \tag{6}$$

Table 2. Abundance models run.

Model	Surveys	Description
a	All	Exclude zero count regions, informed binomial availability, plot-level perception from specific survey
b	All	Include zero count regions, informed binomial availability, plot-level perception from specific survey
c	All	Include zero count regions, informed beta–binomial availability, plot-level perception from specific survey
d	All	Include zero count regions, informed beta–binomial availability, survey-level perception from specific survey
e	2011 and 2015	Include zero count regions, informed beta–binomial availability, model averaged survey-level perception

where ${}^{D}\overline{p}$ is the model averaged estimate of perception probability, s is an index variable for the two surveys, w_s is the weight for survey s, ${}^{D}p_s$ is the estimate of perception probability from survey s, SE(${}^{D}p_s$) is the estimate of standard error for perception probability from survey s, and SE(${}^{D}\overline{p}$) is the unconditional standard error estimate across surveys. We used the same weight (0.5) for both surveys. The model-averaged estimate was used as the prior for probability of perception for both west coast surveys in this model variation.

We ran four or five models per survey, building on the previous model to change one model variation at a time (Table 2). Model e, which included the model averaged probability of perception, was run only for the west coast surveys. We consider model e to be the most reasonable and useful for 2011 and 2015 and model d to be so for 2012 and 2016, and we refer to these as the baseline models. So, model variation e is the baseline model for the west coast and d is the baseline for the east coast.

Model implementation and goodness-of-fit testing

We developed all models in JAGS version 4.2.0 (Plummer 2003), an implementation of the BUGS language (Lunn et al. 2000), adapting code developed for earlier abundance estimates (Martin et al. 2015). Models were run using the jagsUI package (Kellner 2016) in program R, version 3.4.2 (R Development Core Team 2017). Except where otherwise indicated, we used noninformative priors for estimation. Posterior summaries were based on three Markov chain Monte Carlo (MCMC) chains run for 80,000–100,000 iterations after an initial burn-in of 20,000, with no thinning. We confirmed model convergence using the Gelman–Rubin statistic (Gelman and Rubin 1992) and visual examination of the chains. At least 1,000 samples were drawn from the posterior distribution of each model with minimal autocorrelation.

We used the means of the posterior distributions as the point estimates, which is the most common standard in Bayesian analysis and minimizes mean-squared error of the estimate relative to the posterior (Link and Barker 2009). We used the 0.025 and 0.975 quantiles of the posteriors as the 95% Bayesian credible intervals, one measure of uncertainty. Another measure of uncertainty, coefficient of variation (CV), is the standard deviation divided by the mean and is unitless and therefore useful for comparing the uncertainties of estimates of different magnitudes. We made abundance estimates at the statewide, coastal (west and east), and management unit (northwest or NW and southwest or SW on the west coast and Upper St. Johns or USJ and Atlantic Coast or ATL on the east coast) scales.

Goodness-of-fit testing, also known as model checking, is the process of comparing observed data with model outputs to look for systematic discrepancies that may indicate the model assumptions and distributions chosen do not conform to the data (Williams et al. 2002, Conn et al. 2018). These tests may be less often applied for Bayesian models, but not for any lack of importance. The main method used for Bayesian goodness-of-fit testing is posterior predictive tests, which can be used to generate Bayesian p-values and $\hat{c}$ values, or overdispersion parameters (Kéry and Royle 2015, Conn et al. 2018). The idea is that, for each MCMC iteration used in the posterior, a discrepancy function, such as χ^2, is used to compare the observed count data to their expected values, given the parameter values in that iteration:

$$\chi^2(y,\boldsymbol{\theta}) = \sum_i \frac{\left(y_i - E\left(y_i \mid \boldsymbol{\theta}\right)\right)^2}{E\left(y_i \mid \boldsymbol{\theta}\right) + e} \tag{7}$$

where $\chi^2(y,\boldsymbol{\theta})$ is the discrepancy function for count data y and parameter vector $\boldsymbol{\theta}$, E($y_i \mid \boldsymbol{\theta}$) is the expected value for a given count (in this case, the estimated abundance times the availability and perception probabilities), and e is a small value added to the denominator to prevent division by zero. For each iteration, simulated count data are generated from the distributional assumptions and current parameter values of the model, and equation 7 is applied to the simulated count data as well. Inference about goodness-of-fit or lack thereof comes from comparisons of the two discrepancy function results. Bayesian p-values are estimated as the proportion of iterations in which the χ^2 value is greater for simulated than for observed count data, with values near 0 or (less often) 1 indicating lack of fit. The comes from the mean ratio of the χ^2 value from the observed data to the χ^2 value from the simulated data, and how far it is from 1 indicates the magnitude of the lack of fit. Generally, the goal is to have *p*-values above 0.05 and $\hat{c}$ close to 1.

Unfortunately, posterior predictive tests are conservative, with *p*-values biased toward 0.5 and $\hat{c}$'s toward 1. Even when that conservatism is taken into account, small violations of the assumptions of N-mixture models often fail to trigger lack of fit in posterior predictive tests, even when they cause large biases in estimates of abundance (Link et al. 2018). In the case of our models, however, it is unclear whether this issue applies or whether N-mixture-model-specific alternative approaches (Duarte et al. 2018) can be used, because estimated detection probabilities come from other sources than the N-mixture model itself. Even a test result demonstrating lack of fit may not be conclusive, because the count data being compared to model outputs do not represent the full relevant data set (which also includes backseat-observer-group counts and external data on availability). We calculated Bayesian *p*-values and $\hat{c}$ values for each model, but primarily for exploratory purposes, and warn readers to interpret both passing and failing results with skepticism in this case.

Results

Observer assessments of general weather conditions were mixed during the March surveys but were good to excellent during the December surveys (Appendix I, Tables S1–S4). At least 253 manatees were seen by front-seat observers during the first two passes in March 2011 and 455 in December 2015 (west coast); the totals were 494 and 467 in surveys conducted in March 2012 and December 2016 (east coast), respectively. The number and percentage of plots surveyed, broken down by region and strata, are given in Appendix II.

Baseline models

The updated baseline estimated abundance of manatees in Florida was 6,810 (95% Bayesian credible interval: 5,680–8,110; estimates rounded to the nearest ten) in 2011–2012 and 8,810 (7,520–10,280) in 2015–2016 (Figure 3, Table 3). On the west coast, the estimate from 2011 was considerably lower than the estimate from 2015, although the broad credible intervals allow for a range of population trajectories (albeit mostly those of growth; Figure 4, Table 3). The east coast estimate from 2012 was similar to the estimate from 2016, although, again, the broad credible intervals would permit a range of population trajectories (Figure 4, Table 3).

Uncertainty was even higher when coastwide abundance estimates were split into management units (Figure 5, Table 3; CVs ranged from 0.108 to 0.252). Both east coast management units had similar abundance estimates in March 2012 and December 2016, although with somewhat lower uncertainty in the later survey. West coast management unit abundance estimates showed unusual patterns (see Discussion).

Model variations

Incorporating the general changes had minor effects on estimates of abundance for 2011 and 2012 (–3% and –2% changes, respectively; Figure 6, compare models "pub" and a). Including zero-count regions had little effect on estimated abundance for any of the surveys (Figure 6, compare models a and b). Incorporating a beta–binomial availability probability increased estimated abundance estimates for all surveys (4–14%; Figure 6, compare models

Table 3. Baseline abundance estimates (with 95% credible intervals and coefficient of variation) by region and survey. Estimates and 95% CRI are rounded to the nearest 10.

Region	2011/2012 survey			2015/2016 survey		
	Estimate	95% CRI	CV	Estimate	95% CRI	CV
Statewide	6,810	5,680–8,110	0.092	8,810	7,520–10,280	0.080
West coast	2,940	2,190–3,880	0.147	4,810	3,820–6,010	0.116
East coast	3,870	3,060–4,820	0.116	4,000	3,240–4,910	0.107
NW	660	390–1,030	0.252	270	160–470	0.299
SW	2,270	1,620–3,090	0.166	4,460	3,500–5,610	0.121
USJ	90	50–180	0.350	70	60–110	0.182
ATL	3,790	3,000–4,740	0.117	3,920	3,160–4,830	0.108

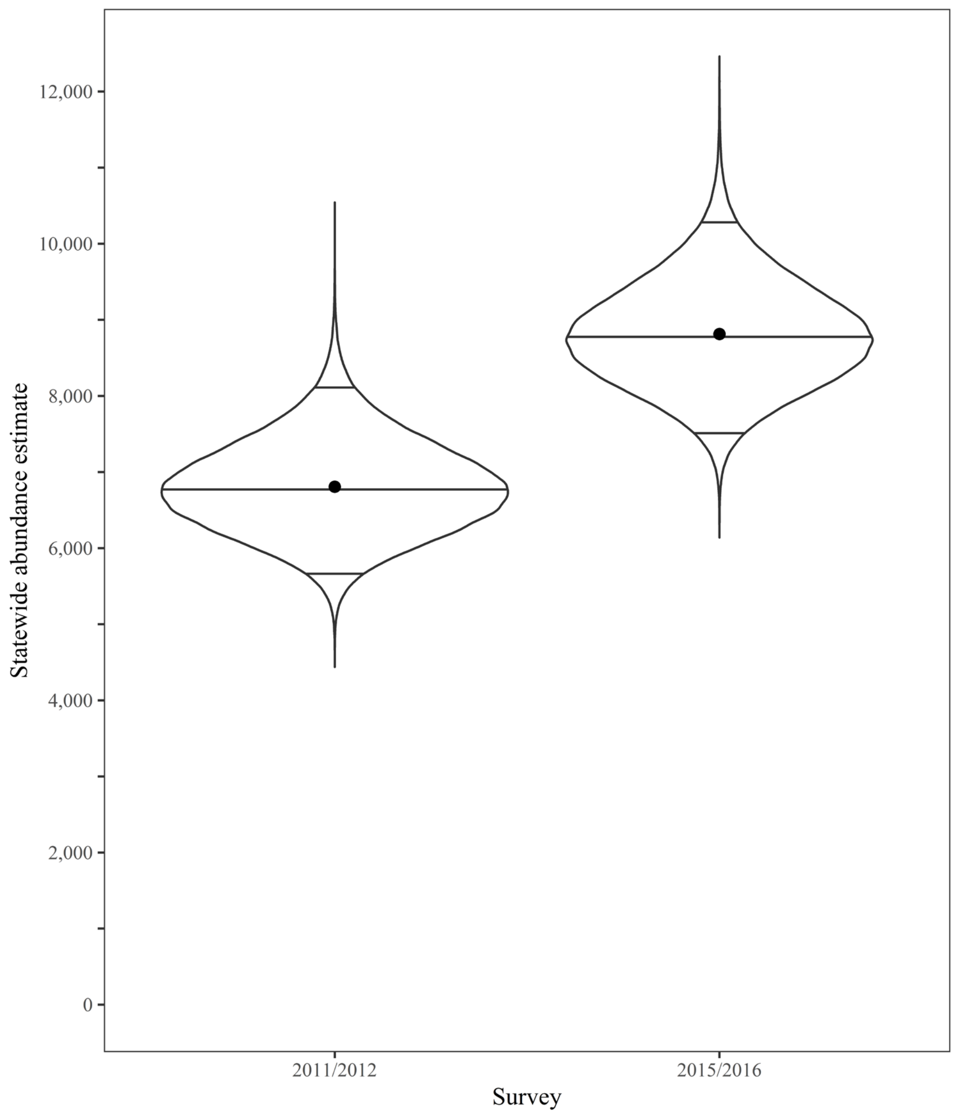

Figure 3. Violin plots of baseline estimates and posterior probability distribution densities of statewide manatee abundance. Violin plots show rotated and mirror-imaged densities of all values of the posterior, with the width indicating how common a value is. The dots indicate the means and the horizontal lines the median and 95% Bayesian credible intervals.

b and c). Switching to survey-level perception probability slightly reduced estimated abundance for all surveys (0 to –3%) but increased uncertainty (CV change 4–9%; Figure 6, compare models c and d). Incorporating model-averaged perception probabilities on west coast surveys increased estimated abundance by 5% in 2011 and reduced it by 9% in 2015 (Figure 6, compare models d and e). In both years, however, uncertainty increased with this change (9% and 8%, respectively).

We provide two example goodness-of-fit plots for the 2015 survey in Figure 7. The top panel (model b) shows evidence of lack of fit: all actual-data χ^2 values are greater than simulated-data χ^2 values, so the points are all below the $x = y$ line and $p = 0$. The average degree of overdispersion, however, is only moderate ($\hat{c} = 1.53$). The bottom panel (model e) shows much less evidence of lack of fit, with between one-seventh and one-eighth of the points above the line ($p = 0.133$, $\hat{c} = 1.18$). For all surveys, models a and b showed clear evidence of lack of fit ($p = 0$, $\hat{c} = 1.81$–2.68; Figure 8). Models c, d, and e, in contrast, showed more evidence for model fit ($p = 0.10$–0.19, $\hat{c} = 1.16$–1.23; Figure 8). The baseline models' Bayesian p-values were 0.10, 0.16, 0.13, and 0.18 for 2011, 2012, 2015, and 2016, respectively; the baseline models' $\hat{c}$ values were 1.23, 1.20, 1.18, and 1.17, respectively.

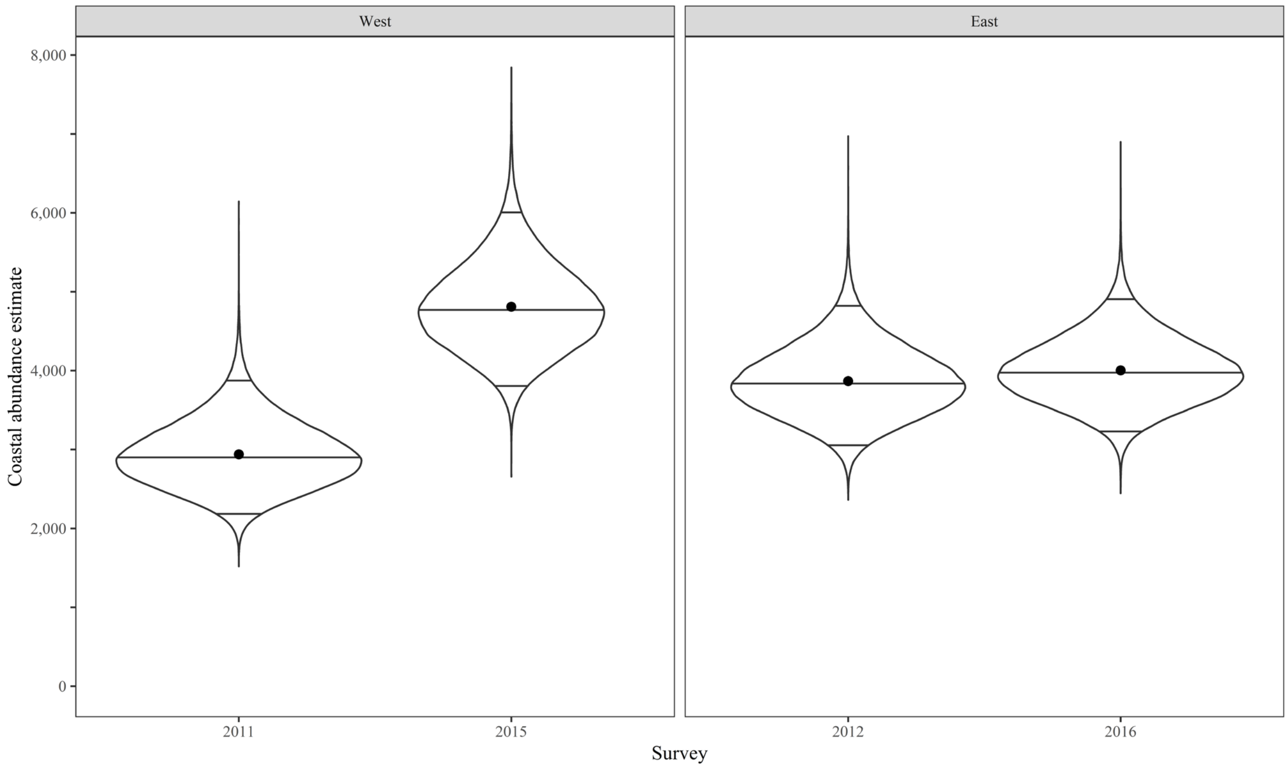

Figure 4. Baseline coastwide abundance estimates and probability densities.

Discussion

We estimated statewide manatee abundance at 6,810 (95% credible interval: 5,680–8,110) in 2011–2012 and 8,810 (7,520–10,280) in 2015–2016. Several considerations should be taken into account in putting these results into context. The estimates of abundance have relatively broad credible intervals and CV of 0.080 and 0.092 for the statewide estimates (more for regional estimates; see Table 3), indicating a reasonably high degree of uncertainty. We emphasize that it is important to consider the 95% credible intervals and not only the measures of central tendencies (i.e. mean and median) when interpreting our results. Assuming that the model is correct and that it is a good reflection of reality, we are 95% confident that the true abundance is within the 95% credible interval. Thus, given the large uncertainty associated with the models, we encourage the reader to be more focused on the credible interval than on the mean.

As stated below, the survey methods and models have limitations. The ambiguous goodness-of-fit results from even the best-fitting models suggest that the estimated parameters might not adequately describe variation in the observed data, although they may also represent merely the inadequacy of current goodness-of-fit tests for these models. We have developed these methods to be as accurate as possible and to account for conditions encountered during aerial surveys, but factors not included in our models likely also contributed to lack of fit. With only two abundance estimates, each with some degree of uncertainty, we recommend against inferring population trends or population growth rates for the state or for any region within it by comparing the two point estimates (see below for a better approach that we are planning). Instead, we emphasize the role of sampling variability in generating the uncertainty around these estimates. Reducing sampling variability allows for more precise estimation of the parameters of interest (abundance), which leads to stronger ecological inference. We now have abundance estimates from two points in time, which improves the reliability of the information available compared to that from one abundance estimate. As more surveys are conducted and more information becomes available, reliability should improve and our confidence in the estimates increase.

We note that N-mixture models can be highly sensitive to nonindependence and heterogeneity of detections (Martin et al. 2011, 2015, Dorazio et al. 2013; also see section Beta–binomial probability of availability); therefore, we conducted the availability study to estimate the probability of availability independently from the N-mixture model. Nevertheless, we retained the basic structure of an N-mixture approach, so the estimated lack of fit is not surprising. Using a probability of availability based on the

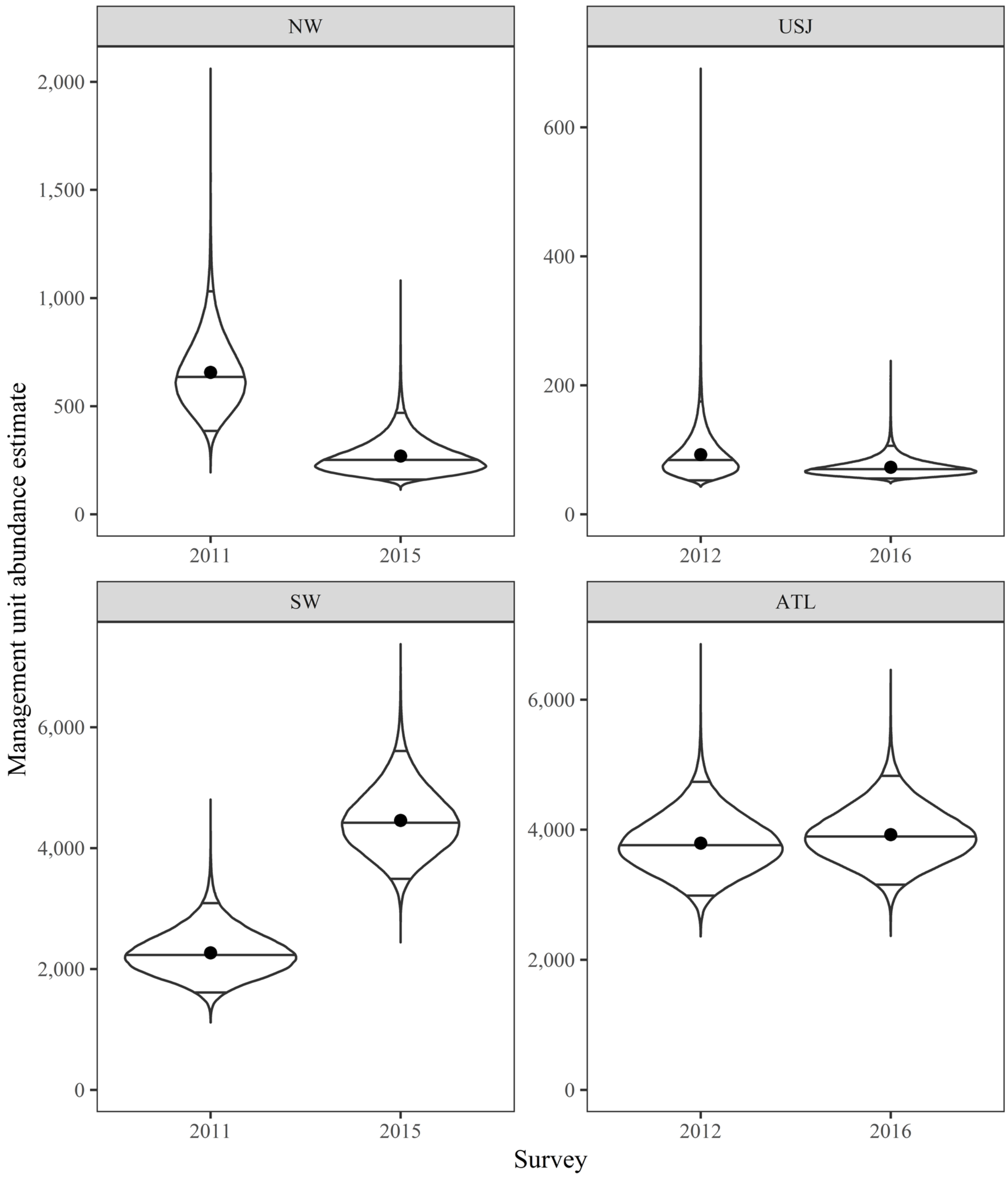

Figure 5. Baseline management unit abundance estimates and probability densities. Note that the panels have different y-axis ranges.

availability study should reduce any errors induced by fitting an N-mixture model in which detection is estimated directly from the repeated surveys.

We have at least partly addressed two possible sources of bias highlighted by Martin et al. (2015): we now include regions with zero counts, and we now can (partly) account for the effects of sea state on manatee availability. Some possible sources of bias remain, however. We still do not account for effects of group size on detectability of those groups or address detectability of individuals within groups. The model assumes that manatee diving depth distribution is the same throughout the manatee's range in Florida, but that may not be true. Edwards et al. (2016) found that the proportion of time that manatees spent within 1.25 m of the surface was strongly related to the depth of the water. In addition, we still do not fully account for the effects of conditions such as sea state, glare, and cloud cover on manatee availability. Because weather conditions were worse for the first set of surveys (Appendix I), this last source of

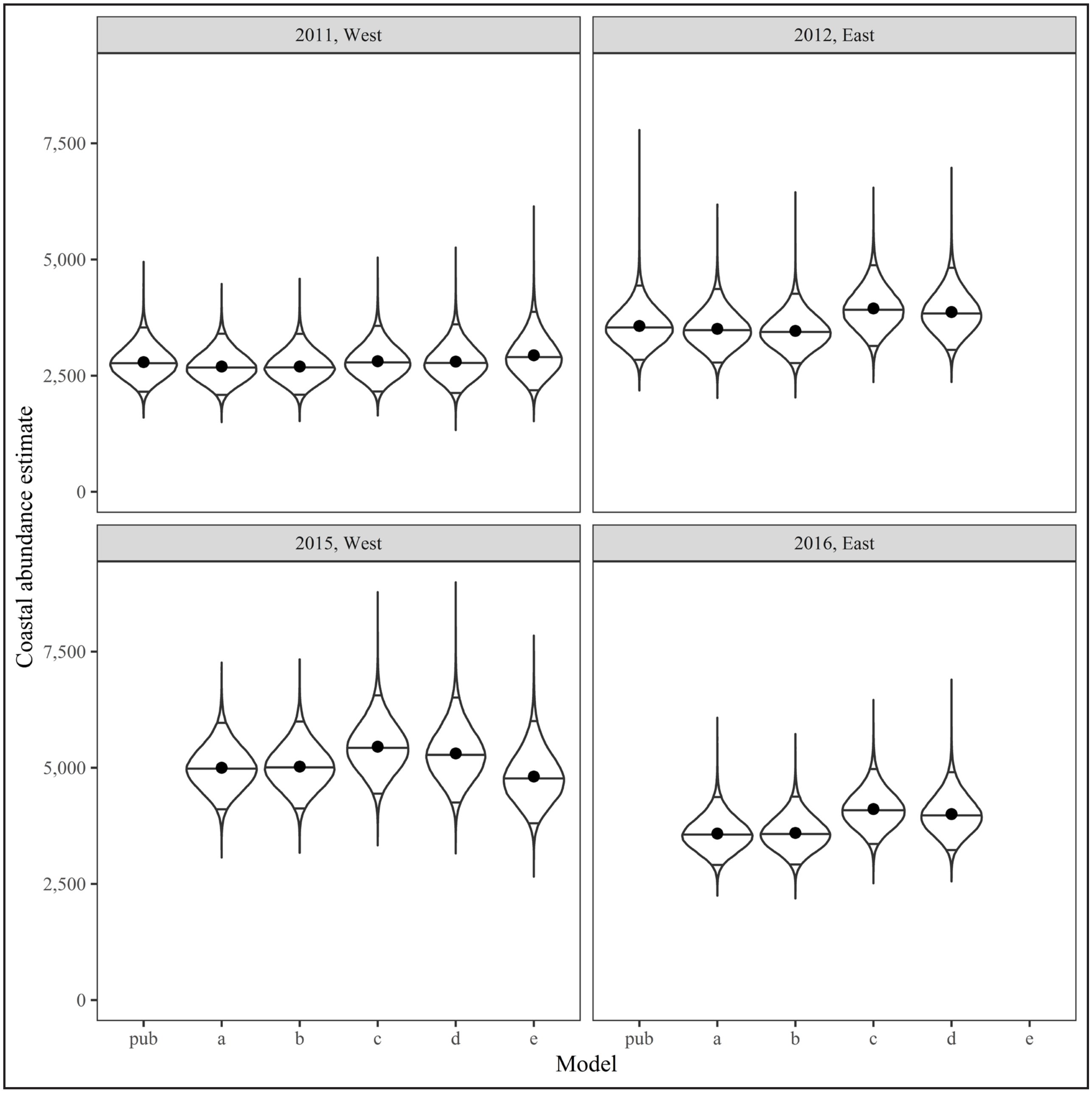

Figure 6. Model-specific estimates and probability densities of coastwide abundance. Model "pub" is the published baseline estimates (Martin et al. 2015, models 2 and 4) for 2011 and 2012. For other model definitions, see Table 2.

bias may affect the 2011–2012 estimates more than the 2015–2016 estimates.

In general, uncertainty in abundance estimates increased as the scale at which they were examined decreased. We especially recommend against inferring population growth rates from two population estimates at the management-unit or a finer scale. The point estimates showing large and, we think, unrealistic changes in the abundance of manatees in the NW and SW management units were surprising and difficult to explain. However, we considered several possible explanations for the decrease in the NW estimate between March 2011 and December 2015 and the large increase in the SW estimate from March 2011 to December 2015 (Appendix IV).

Improvements in estimating abundance

We have made several improvements in the survey and abundance methods. These include accounting for new availability study results and using weighted averages of survey conditions for plots with a range of values. In addition, models b–e allowed us to include the zero-count re-

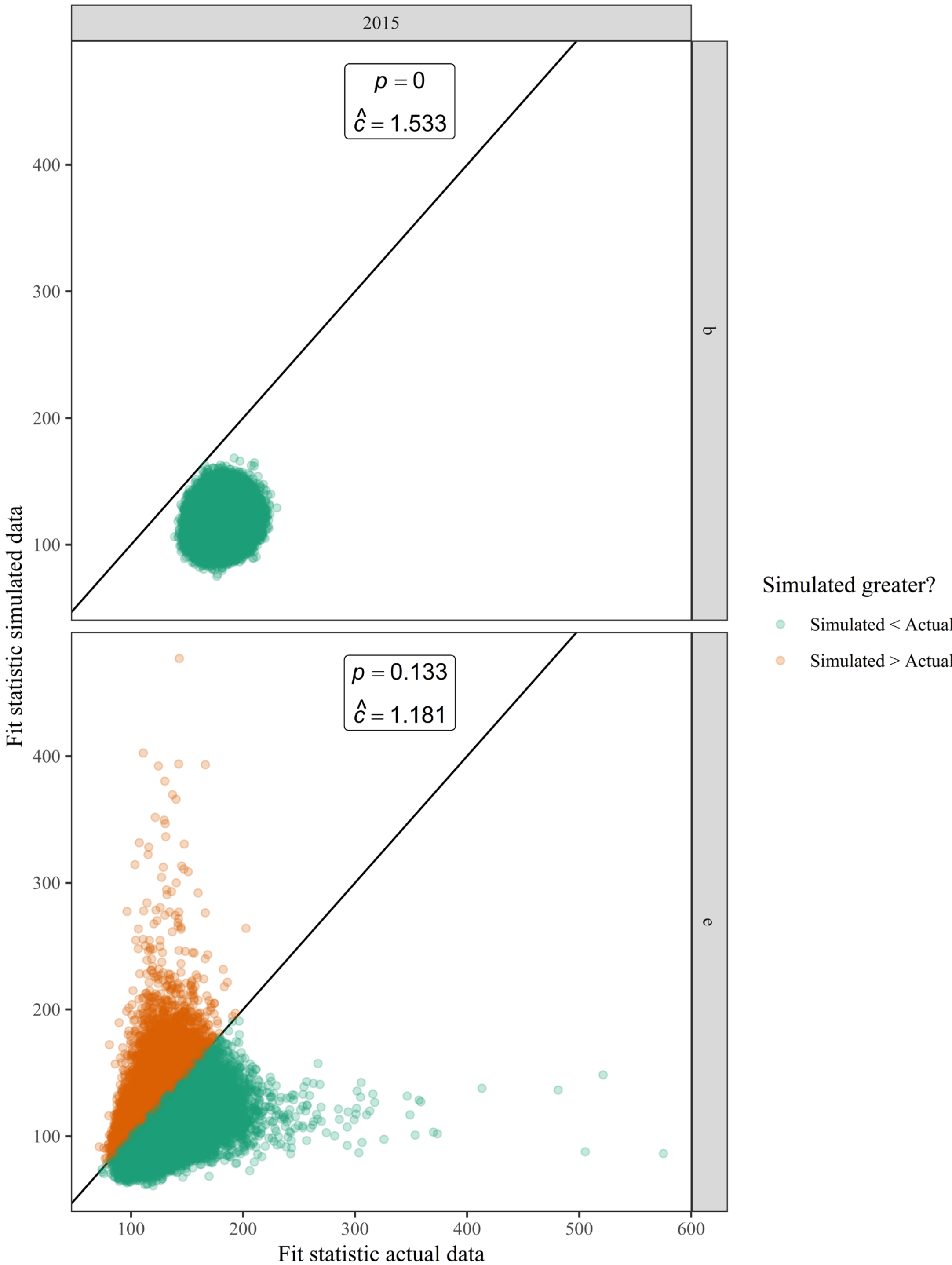

Figure 7. Example goodness-of-fit plots from the 2015 survey. For the full set of plots see Figure 8. The top panel represents model b (include zero count regions, binomial availability, plot-level perception from specific survey) and the bottom panel model e (include zero count regions, beta–binomial availability, model-averaged survey-level perception). Each point represents an iteration in the model posterior, with its x position being the χ^2 discrepancy of the actual data (equation 7) and the y position being the same discrepancy function calculated for simulated data. The point's color emphasizes on which side of the $x = y$ line it exists. In the box are two summaries of this comparison: the Bayesian *p*-value (p), the proportion of points above the line; and $\hat{c}$, the mean ratio of the actual data χ^2 value to the simulated data χ^2 value.

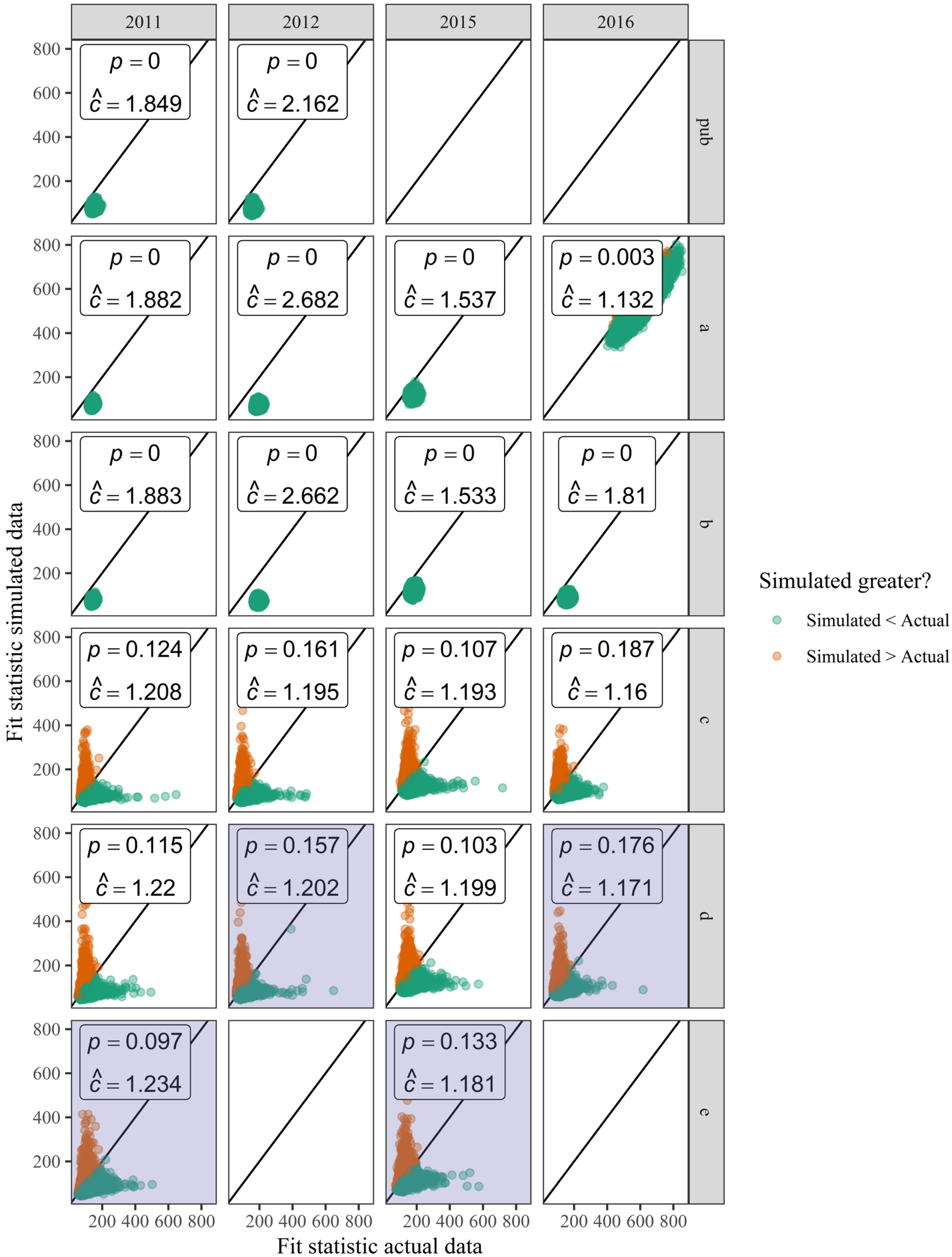

Figure 8. Full set of goodness-of-fit plots. For model definitions, see Table 2; for plot elements see Figure 7. Highlighted panels show the baseline models. Better fit is indicated when p is closer to 0.5 (above 0.05) and $\hat{c}$ is closer to 1.

gions and make this a truly statewide abundance estimate. Models c–e accounted for extra variation in manatee availability over space and time; models d and e allowed for uncertainty in survey-level perception probability; model e (west coast only) accounted for extra uncertainty in the perception probability estimates generated by our double observer model for those surveys.

We also hope to further improve our abundance survey and estimation methods. Additions and changes may include: obtaining more information about the effects of conditions (glare, cloud cover, sea state, and visibility) on availability; accounting for any effects of floating, emergent, or overhanging vegetation on perception; obtaining more diving data for manatees in areas with variable water depth; determining optimal allocations of survey effort across regions and strata based on current results; evaluating improvements in seasonal timing of surveys (<50 manatees in strata-1 plots, post–warm season migration); encouraging more calibration between observers for covariate levels; accounting for differences in mean water depth between plots and its possible effects on availability and perception (Edwards et al. 2016); accounting for perception probability at both the group and individual manatee levels (Clement et al. 2017); using models that account for variation in perception probability among observers; and modeling perception or availability separately for calves and adults.

We are working on more robust methods for inferring both abundance and annual population growth rates. These include an integrated population model (IPM), which is a single, unified analysis of population count data and demographic data (Schaub and Abadi 2011, Zipkin and Saunders 2018). By integrating survival, reproductive, and abundance estimates, carcass recovery data, and possibly other data streams, researchers should be able to increase accuracy of estimates of abundance, population growth rates, survival rates, reproductive rates, and the effects of unusual mortality events for Florida manatee populations. Although FWRI and U.S. Geological Survey (USGS) are starting IPM work in the SW management unit, the plan is to develop models for all Florida manatee populations.

Acknowledgments

We thank S. Hardy, D. Fagan, T. Rivenbark, L. Utley, A. Krzystan, and M. Nausbaum for setting up surveys, creating maps, and entering or processing data. We also thank S. Hardy, T. Reinert, K. Rigney, M. Barlas, J. Gorzelany, C. Borland, K. Scolardi, M. Garrett, D. Fagan, A. Perna, A. Honaker, J. Cassady, J. Koelsch, L. Utley, A. Howell, M. Land, L. Oberhofer, D. Semeyn, D. Levine, B. Greer, J. Ortega, S. Calleson, K. Klingenberge, K. Curtin, J. Kleen, A. DiMaggio, E. Quintana, R. Quarles, A. Rhoads, A. Rovira, A. Allen, K. Therriault, M. Melichercik, and P. Quinn for conducting aerial surveys. We thank D. Slone and J. Reid for sharing manatee telemetry information with us. We appreciate the assistance of K. Rood for photo-ID query and discussion. We also appreciate the goodness-of-fit advice that P. Conn and M. Kéry were able to give us. L. Ward and G. McRae provided leadership and support. C. Deutsch provided guidance and probing questions. L. Ward, C. Deutsch, G. McRae, M. Barlas, J. Reid, D. Slone, J. Kleen, M. Runge, K. Rood, M. Ross, A. Krzystan, R. Mezich, C. Knox, C. Langtimm, and M. Kosempa provided useful discussion in meetings about this analysis. Finally, we thank C. Deutsch, C. Shea, and L. Ward for reviewing versions of this report. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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Appendix I: Survey weather conditions

Table S1. Survey conditions during the 2011 abundance survey (west coast). The survey was delayed because of a cold front. Sea fog present in some areas. Cloudy, windy, warm, and some showers on day of some surveys. For survey region codes, see Figure 1.

Survey date	Survey location by aircraft	Survey region	Overall survey condition
28 February 2011	Sarasota/Charlotte	MS/CH	fair/poor
28 February 2011	W. Charlotte/N. Lee	CH/LE	fair
28 February 2011	Lee/Collier	LE/CO	fair/good
28 February 2011	Collier	CO	good
28 February 2011	Monroe (#1)	MM	very good
28 February 2011	Monroe (#2)	MM	fair/good
28 February 2011	Charlotte/Lee/Collier	CH/LE/CO	fair/good
01 March 2011	Citrus/Hernando/Pasco	LP	good
01 March 2011	S. Pasco/N. Tampa Bay	LP/TB	poor/good
01 March 2011	Tampa Bay (#1)	TB	fair/good
01 March 2011	Tampa Bay (#2)	TB	fair
01 March 2011	Tampa Bay (#3)	TB	not recorded
01 March 2011	Levy/Citrus	LP	very good
03 March 2011	Manatee/Sarasota	MS	very good
03 March 2011	S. Pasco/W. Pinellas	LP/TB	good
03 March 2011	Wakulla/Dixie	FD	fair/good
03 March 2011	Franklin/Dixie	FD	excellent
21 March 2011	St Joe's/Destin	EG	very good
22 March 2011	Destin to Stateline	EG	excellent/very good

Table S2. Survey conditions during the 2012 abundance survey (east coast). Survey was postponed by one day because of rainy and windy weather. There was mild weather during the survey. For survey region codes, see Figure 1.

Survey date	Survey location by aircraft	Survey region	Overall survey condition
5 March 2012	Florida Keys (#1)	MK	good
5 March 2012	Florida Keys (#2)	MK	fair
5 March 2012	Florida Keys (#3)	MK	very good
5 March 2012	Florida Keys (#4)	MK	poor/fair
5 March 2012	Florida Keys (#5)	MK	good
5 March 2012	Florida Keys (#6)	MK	very good
7 March 2012	Jacksonville	NE	fair
7 March 2012	St. Johns River (#1)	NE	poor
7 March 2012	St. Johns River (#2)	NE	poor
7 March 2012	St .Johns River (#3)	NE	fair/good
7 March 2012	Blue Spring	NE	poor

(continued)

Table S2 (continued).

Survey date	Survey location by aircraft	Survey region	Overall survey condition
8 March 2012	Brevard/Indian River	BV	not recorded
8 March 2012	Brevard (#1)	BV	very good
8 March 2012	Brevard (#2)	BV	good
8 March 2012	Brevard (#3)	BV	good
8 March 2012	Volusia	VO	good
9 March 2012	Miami-Dade (#1)	MI	very good
9 March 2012	Miami-Dade (#2)	MI	not recorded
9 March 2012	Broward	BW	very good
9 March 2012	Palm Beach	PB	fair
9 March 2012	Martin/St Lucie	MA	not recorded
12 March 2012	Jacksonville/St. Augustine	NE	very good
13 March 2012	Lake Okeechobee	LO	excellent/very good

Table S3. Survey conditions during the 2015 abundance survey (west coast). Survey followed a dip in temperatures. Weather during the survey was mild. Conditions were rated as good or better throughout the areas surveyed. For survey region codes, see Figure 1.

Survey date	Survey location by aircraft	Survey region	Overall survey condition
1 December 2015	Monroe (#1)	MM	very good
1 December 2015	Monroe (#2)	MM	very good
1 December 2015	Collier	CO	very good
1 December 2015	Charlotte/Lee (#1)	CH/LE	excellent
1 December 2015	Charlotte/Lee (#2)	CH/LE	very good
2 December 2015	Sarasota-Manatee	MS	very good
2 December 2015	Tampa Bay (#1)	TB	very good
2 December 2015	Tampa Bay (#2)	TB	good
2 December 2015	Citrus to Pinellas	LP	very good
2 December 2015	Citrus/Levy	LP	good
3 December 2015	Franklin/Dixie	FD	good
3 December 2015	Franklin/Levy	FD/LP	good
4 December 2015	Panhandle	EG	good/very good
7 December 2015	Pinellas	EG	very good
9 December 2015	Monroe	MM	excellent/very good

Table S4. Survey conditions during the 2016 abundance survey (east coast). Survey followed a dip in temperature. Windy during the early part of the survey, otherwise good conditions. For survey region codes, see Figure 1.

Survey date	Survey location by aircraft	Survey region	Overall survey condition
5 December 2016	Florida Keys (#1)	MK	good
5 December 2016	Florida Keys (#2)	MK	excellent
5 December 2016	Florida Keys (#3)	MK	very good
5 December 2016	Florida Keys (#4)	MK	good
5 December 2016	Florida Keys (#5)	MK	good
5 December 2016	Miami-Dade	MI	good
5 December 2016	Florida Keys (#6)	MK	excellent
6 December 2016	Miami-Dade (#1)	MI	very good
6 December 2016	Miami-Dade (#2)	MI	good
6 December 2016	Broward	BW	good
6 December 2016	Palm Beach	PB	good
6 December 2016	Martin/St Lucie	MA	poor
7 December 2016	Brevard (#1)	BV	very good
7 December 2016	Brevard (#2)	BV	excellent/very good
7 December 2016	Brevard/Indian River	BV/MA	excellent
7 December 2016	Brevard (#3)	BV	good
7 December 2016	Volusia	VO	very good
8 December 2016	St Johns (#1)	NE	excellent
8 December 2016	St Johns (#2)	NE	very good
8 December 2016	St Johns (#3)	NE	very good
8 December 2016	Jacksonville	NE	excellent
8 December 2016	St Johns (#4)	NE	excellent
12 December 2016	Lake Okeechobee	LO	excellent

Appendix II: Plots surveyed

Table S5. Number (and %) of plots surveyed in first set of abundance surveys (2011–2012), by region (management unit or coast) and stratum with totals.

Region	Stratum 1	Stratum 2	Stratum 3	Total
NW	9 (100)	102 (7)	36 (2)	147 (5)
SW	17 (100)	222 (10)	63 (5)	302 (9)
USJ	1 (100)	44 (12)	7 (9)	52 (12)
ATL	16 (94*)	370 (14)	133 (8)	519 (12)
West coast	26 (100)	324 (9)	99 (4)	449 (7)
East coast	17 (94*)	414 (14)	140 (8)	571 (12)
State-wide	43 (98*)	738 (11)	239 (5)	1,020 (9)

* One plot not flown in 2012 due to air-space conflict.

Table S6. Number (and %) of plots surveyed in the second set of abundance surveys (2015–2016), by region (management unit or coast) and stratum, with totals.

Region	Stratum 1	Stratum 2	Stratum 3	Total
NW	9 (100)	103 (7)	36 (2)	148 (5)
SW	17 (100)	224 (10)	56 (5)	297 (9)
USJ	1 (100)	33 (9)	7 (9)	41 (10)
ATL	17 (100)	372 (14)	135 (8)	524 (12)
West coast	**26 (100)**	327 (9)	92 (4)	445 (7)
East coast	**18 (100)**	405 (13)	142 (8)	565 (12)
State-wide	44 (100)	732 (11)	234 (5)	1,010 (9)

Appendix III: Mean probability of availability, by visibility and sea state

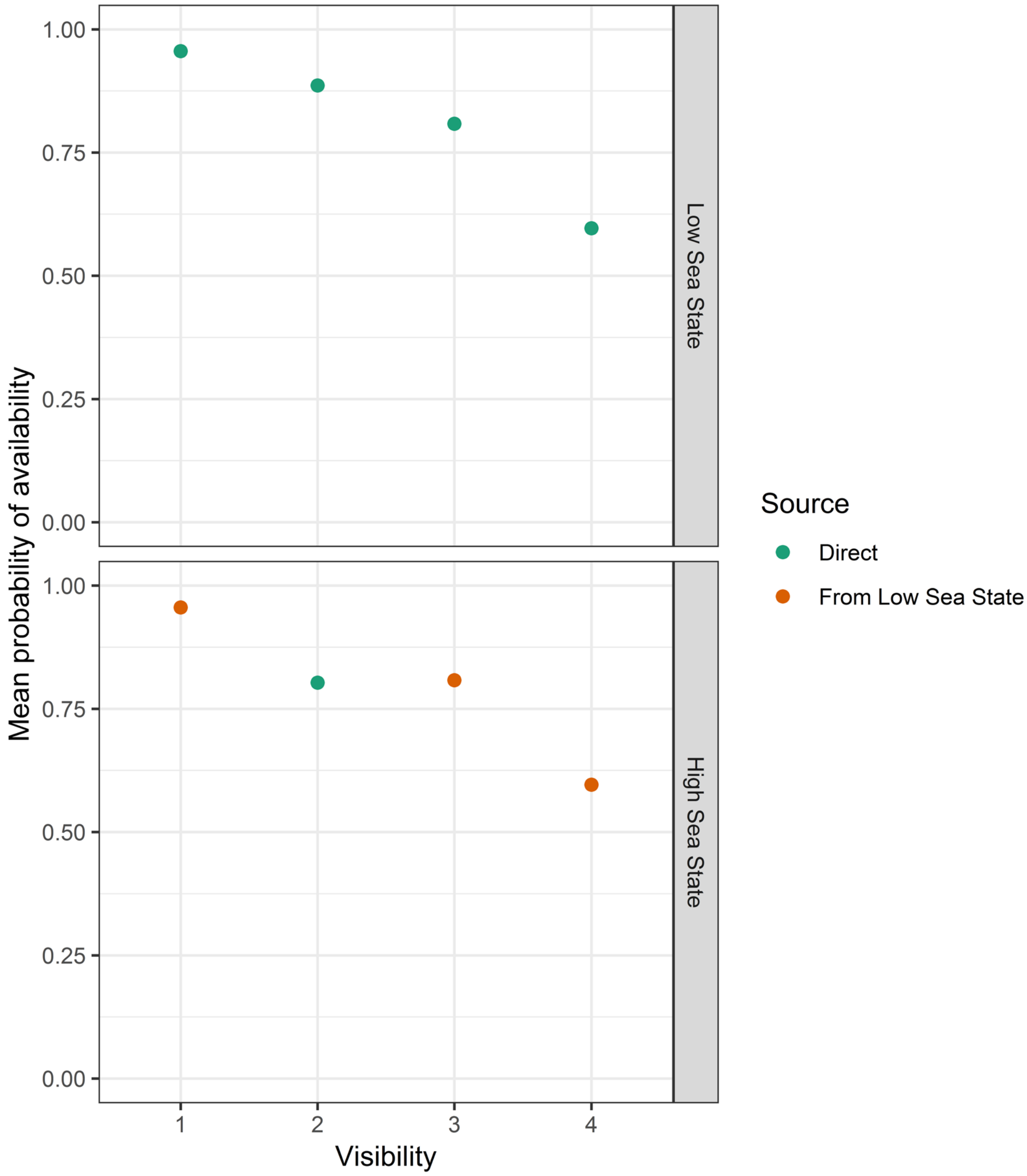

Figure S1. Mean probabilities of availability estimated from manatee replica study (uncertainty is not shown, as it varies with abundance model) by visibility and sea state category. Visibility categories are: 1) clear water, bottom is visible; 2) bottom visible but details are unclear; 3) difficult to tell water clarity because the bottom is not visible due to depth; and 4) water is turbid. Sea state categories are: Low, Beaufort scale <3 and High, Beaufort scale ≥3. Many of the probabilities of availability were estimated directly from one or more sites with that combination of sea state and visibility. Some high-sea-state combinations were either not available (visibilities 1 and 4) or were available only from a single site with anomalously high estimated availability, so were taken from the low-sea-state results with the same visibility.

Appendix IV: Possible explanations for anomalous changes in regional abundances on Florida's west coast

The observed changes in population estimates for NW and SW were unexpected and not concordant with other information available to us. For instance, the NW estimate for 2015 was 270 (95% credible interval 160–470), which is less than that for the 2011 survey (Table 3, Figure 5). Traditional aerial survey counts in the Crystal River area in December are quite variable both between and within years, ranging from <50 to more than 600, but are usually >300, including that for the survey later in 2015–2016 winter (J. Kleen, USFWS, pers. comm.). The difference suggests either that manatees were missed during our December abundance survey because they were out of the survey area (out of state, in the SW region, offshore, or up rivers and creeks beyond the survey boundaries) or the NW abundance estimate was biased low.

Manatees in the SW management unit experienced a major unusual mortality event in 2013 due to an intense red tide. The estimated additional mortality rate due to this event (and a similar one in 1996) was 15.6% (95% Bayesian credible interval 10.0–23.0) for calves and 6.7% (5.2–8.4) for subadults and adults (Runge et al. 2017). Thus, it is counterintuitive or unexpected that the abundance estimates point to a large increase in population in the SW over the period that covers the 2013 event. Furthermore, the annual rate of growth necessary to account for such changes is beyond what is biologically feasible via internal regional recruitment.

We considered several possible explanations for the decrease in the estimate in the NW from March 2011 to December 2015 and the large increase in the estimate in the SW from March 2011 to December 2015. These explanations fall into two categories: sampling-related and shifts in distribution.

Possible sampling-related explanations include: poor weather conditions during surveys in 2011, especially in the SW; some manatees being outside state waters during one of the surveys; movement of animals between strata in the NW; nonrepresentative sampling of strata 2 and 3; and chance events. Observer-reported flight conditions were considerably worse in March 2011 than in December 2015 (Appendix Tables S1 and S3), especially for the earlier flights, which were largely in the SW. These conditions were, in fact, a major impetus for shifting the surveys' timing from March to December. Although, in theory, the conditions that affect manatee availability or detectability are accounted for in the models, we strongly suspect that the estimates from the surveys in March 2011 are underestimates, especially in the SW. It is also possible that some manatees were outside state waters during one or more surveys, although surveys were timed to avoid this possibility. In any case, we doubt that there were enough manatees outside of Florida waters during any of the surveys to make much of an impact on abundance estimates.

Although the point estimate of abundance in the NW was higher for March 2011 than for December 2015, the raw counts from observers in 2015 were slightly higher. When counts are broken down by both region and stratum, one sees that the increase in the counts were all in stratum 1 (counts in strata 2 and 3 decreased). This provides a proximate explanation for the discrepancy: the models extrapolate abundance estimates from surveyed stratum-2 and -3 plots to unsurveyed plots of the same strata, but in stratum 1, all plots are usually surveyed, so no extrapolation is done. If the sampling of strata 2 and 3 was done representatively (and it appears to be so on maps), then on an average survey the extrapolation should lead to an unbiased estimate of abundance. However, it is possible that by chance the sampling of strata 2 and 3 was not representative with regards to manatee abundance in at least one of the surveys.

Another possible explanation is a shift in manatee distribution across management units between surveys. Shifts can be characterized as annual (changing between years), seasonal (changing between seasons), and seasonal by annual (changing between seasons, but in different ways different years). An annual shift (not a seasonal migration, but large numbers of manatees moving their winter or year-round habitation from NW to SW) seems highly unlikely. Such a shift would likely also show up on synoptic counts, but the proportion of manatees seen in the SW during synoptic surveys has been relatively stable (Figure S2). When temperatures rise manatee often disperse from winter aggregation areas. While some remain near their winter refuges during warmer weather, others travel extensive distances along the coast and far up rivers and canals (Weigle et al. 2001). Manatees exhibit a range of migration patterns on both coasts (Weigle et al. 2001, Deutsch et al. 2003), so a seasonal (some manatees migrating from the SW to the NW at some point each year between early December and March) or seasonal by annual (seasonal movements between management units that are variable by year or weather) shift seems more plausible. Based on a review of long-term photo-identification data, we do not believe that these putative shifts result from manatees changing their preferred overwintering site (management units). It is possible that before tem-

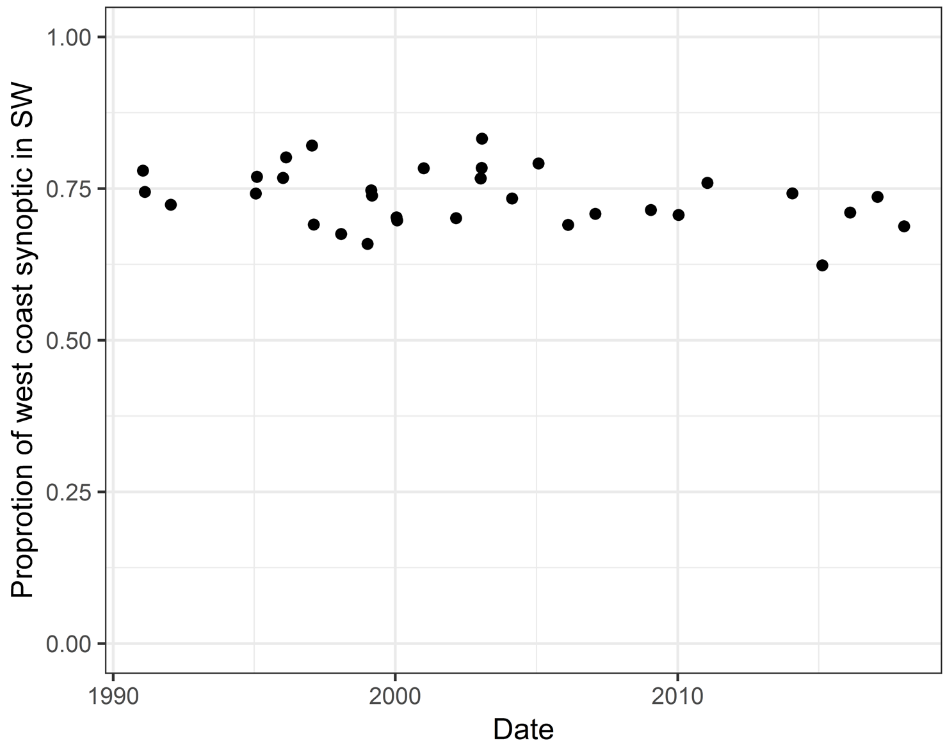

Figure S2. Proportions of each west coast synoptic count within the SW management unit.

peratures drop below 18°C, for example in early December, some manatees may still be in regions other than their overwintering location. Therefore, it is possible that some NW manatees were still in the SW region during the early December survey before moving northward for winter.

It may not be plausible to postulate that NW-wintering manatees move to the SW each summer (or fall) in numbers large enough to 1) offset any movement the opposite direction, 2) explain the apparent decrease in the NW, and 3) explain the apparent high increase in the SW. But such movement does occur, and the variability of movement patterns (Weigle et al. 2001) and counts (Kleen and Breland 2014; J. Kleen, USFWS, pers. comm.) in these regions means we can't rule it out as having happened in 2015, and in numbers large enough to at least partly explain the anomalous changes in abundance estimates. Variability in counts in both traditional surveys and abundance surveys could have other explanations, however, such as small-scale movements to plots not sampled. Any of those scenarios might be possible, but more years of data are needed to determine the magnitude of these influences on estimates at the smaller scales.