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Author(s) :Catherine A. Langtimm, Robert M. Dorazio, Bradley M. Stith and Terry J. Doyle
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Research Article

New Aerial Survey and Hierarchical Model to Estimate Manatee Abundance

CATHERINE A. LANGTIMM,[1] *U.S. Geological Survey, Southeast Ecological Science Center, 2201 N.W. 40th Terrace, Gainesville, FL 32605, USA*

ROBERT M. DORAZIO, *U.S. Geological Survey, Southeast Ecological Science Center, Department of Statistics, University of Florida, Gainesville, FL 32611-0339, USA*

BRADLEY M. STITH, *Jacobs Technology contracted to U.S. Geological Survey, 2201 N.W. 40th Terrace, Gainesville, FL 32605, USA*

TERRY J. DOYLE,[2] *U.S. Fish and Wildlife Service, Ten Thousand Islands National Wildlife Refuge, 3860 Tollgate Boulevard, Suite 300, Naples, FL 34114, USA*

ABSTRACT Monitoring the response of endangered and protected species to hydrological restoration is a major component of the adaptive management framework of the Comprehensive Everglades Restoration Plan. The endangered Florida manatee (*Trichechus manatus latirostris*) lives at the marine-freshwater interface in southwest Florida and is likely to be affected by hydrologic restoration. To provide managers with prerestoration information on distribution and abundance for postrestoration comparison, we developed and implemented a new aerial survey design and hierarchical statistical model to estimate and map abundance of manatees as a function of patch-specific habitat characteristics, indicative of manatee requirements for offshore forage (seagrass), inland fresh drinking water, and warm-water winter refuge. We estimated the number of groups of manatees from dual-observer counts and estimated the number of individuals within groups by removal sampling. Our model is unique in that we jointly analyzed group and individual counts using assumptions that allow probabilities of group detection to depend on group size. Ours is the first analysis of manatee aerial surveys to model spatial and temporal abundance of manatees in association with habitat type while accounting for imperfect detection. We conducted the study in the Ten Thousand Islands area of southwestern Florida, USA, which was expected to be affected by the Picayune Strand Restoration Project to restore hydrology altered for a failed real-estate development. We conducted 11 surveys in 2006, spanning the cold, dry season and warm, wet season. To examine short-term and seasonal changes in distribution we flew paired surveys 1–2 days apart within a given month during the year. Manatees were sparsely distributed across the landscape in small groups. Probability of detection of a group increased with group size; the magnitude of the relationship between group size and detection probability varied among surveys. Probability of detection of individual manatees within a group also differed among surveys, ranging from a low of 0.27 on 11 January to a high of 0.73 on 8 August. During winter surveys, abundance was always higher inland at Port of the Islands (POI), a manatee warm-water aggregation site, than in the other habitat types. During warm-season surveys, highest abundances were estimated in offshore habitat where manatees forage on seagrass. Manatees continued to use POI in summer, but in lower numbers than in winter, possibly to drink freshwater. Abundance in other inland systems and inshore bays was low compared to POI in winter and summer, possibly because of low availability of freshwater. During cold weather, maps of patch abundance of paired surveys showed daily changes in manatee distribution associated with rapid changes in air and water temperature as manatees sought warm water with falling temperatures and seagrass areas with increasing temperatures. Within a habitat type, some patches had higher manatee abundance suggesting differences in quality, possibly due to freshwater flow. If hydrological restoration alters the location of quality habitat, postrestoration comparisons using our methods will document how manatees adjust to new resources, providing managers with information on spatial needs for further monitoring or management. Total abundance for the entire area was similar among survey dates. Credible intervals however were large on a few surveys, and may limit our ability to statistically detect trends in total abundance. Additional modeling of abundance with time- and patch-specific covariates of salinity, water temperature, and seagrass abundance will directly link manatee abundance with physical and biological changes due to restoration and should decrease uncertainty of estimates. © 2011 The Wildlife Society.[†]

KEY WORDS abundance estimation, aerial surveys, dual-observer sampling, Everglades restoration, Florida manatee, habitat covariates, hierarchical models, removal sampling.

The Comprehensive Everglades Restoration Plan (CERP) was authorized by the United States Congress in 2000 with the goal of restoring the hydrological characteristics of the Everglades while simultaneously supplying the water needs of south Florida's urban and natural areas. Although

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[1] *E-mail: clangtimm@usgs.gov*

[2] *Present Address: U.S. Fish and Wildlife Service, 4401 N Fairfax Dr., MBSP 4107, Arlington, VA 22203, USA.*

implementation of the restoration was stalled for many years, construction on the Picayune Strand Restoration Project (U.S. Army Corps of Engineers and South Florida Water Management District 2004) just North of the Ten Thousand Islands National Wildlife Refuge (TTINWR) in southwest Florida was expedited with Congressional authorization in 2007 and funding in 2009. Monitoring and assessment of the response of endangered and protected species to this and other restoration projects is a major component of the adaptive management framework of CERP (reviewed in National Research Council 2008). One focal species for CERP is the endangered Florida manatee (*Trichechus manatus latirostris*), a marine mammal that lives at the marine-freshwater interface of the coasts of the southeastern United States. The manatee population is likely to be affected by hydrologic restoration because individual manatees move among critical resources in response to changes in water temperature, salinity, and tide (Hartman 1979, Deutsch et al. 2003, Stith et al. 2011). As a tropical species, manatees are limited in distribution by cold temperatures. In Florida, during cold periods <20°C, manatees must find warmer water to escape cold stress and possible death (Hartman 1979). Because manatees are primary consumers of submerged aquatic vegetation, hydrologic changes that affect seagrass quality, abundance, and distribution also may induce changes in manatee distributions, fecundity, and population growth rates. The main objective of our research was to provide managers with a monitoring and analysis design to assess the impact of the Picayune Strand Restoration on manatees in the area.

Aerial surveys are the most cost effective and timely means of monitoring the distribution and abundance of manatees. However, the development of statistically rigorous surveys and estimators of abundance have been problematic because of issues concerning imperfect detection. Detection errors, if unaccounted for, may yield biased estimates of abundance and unreliable estimates of trends in abundance. Lefebvre et al. (1995) described the following sources of bias in manatee surveys: 1) availability bias, as not all animals are near enough to the surface to be seen; 2) perception bias, as observers will not detect and count all animals available to be seen; and 3) sample frame bias, as not all manatees occupy the survey area and are available to be seen.

Previous surveys have been designed to address some, but not all sources of bias. Miller et al. (1998) employed a strip transect approach with dual observers to address perception bias and sample frame but did not account for availability. Using this design, total abundance was estimated by multiplying the estimate of the number of manatee groups by mean group size. Edwards et al. (2007) employed a design to estimate the different components of manatee detection separately using both mark-resight data and dive profiles of telemetry data. However, this design was labor intensive and calibrations were specific to one aggregation site and period of study. Fonnesbeck et al. (2009) improved the calibration analysis by combining the sources of monitoring data into an integrated hierarchical modeling framework that estimated all parameters simultaneously. Craig and Reynolds (2004) also used a hierarchical Bayesian approach, but modeled availability and detection jointly. Pollock et al. (2006) developed a design for surveys in Australia of dugongs (*Dugong dugon*, a related genus), which used dual observers to estimate perception probability and artificial dugong models and depth recorders on live dugongs to estimate availability probabilities across the heterogeneous environment.

Although these approaches yielded improved estimates of abundance and variance, we sought an approach that not only accounts for detection errors but more importantly allows spatial and temporal variation in abundance to be modeled using covariates that are thought to affect abundance and distribution of manatees. In this way we could model abundance–habitat relationships and with the use of covariates assess or predict changes in the manatee population with changes in salinity, water temperature, and depth simulated from numerical models of hydrodynamics that have and are being developed to assess Everglades restoration (Wang et al. 2007, Swain and Decker 2009). We also sought an approach with the flexibility to model abundance at either the local scale for managers of various parks and refuges in the Greater Everglades (Biscayne Bay National Park, Everglades National Park [ENP], Big Cypress National Preserve, and TTINWR) or at the regional scale for state and federal assessments of manatee recovery. Federal assessments currently rely on Population Viability Analysis based on regional population models that primarily employ estimates of survival and reproduction obtained by analyzing repeated photo-documented sightings of individually recognizable manatees (Kendall et al. 2004, Langtimm et al. 2004, Runge et al. 2007*a*,*b*). Data for manatees in the Greater Everglades are lacking. With the extension of aerial surveys into ENP, estimates of trends in manatee abundance could be used to estimate population growth rate and to construct population models for this underrepresented region.

Hierarchical (state-space) modeling offered us the flexibility to model ecological processes that influence distribution and abundance in conjunction with several types of sampling errors (Royle and Dorazio 2008). To provide managers with baseline information prior to hydrological restoration, we were interested in estimating manatee abundance in conjunction with manatee habitat requirements for offshore forage (seagrass), inland fresh drinking water, and warm-water winter refuge. Restoration could alter the location and quality of these resources resulting in postrestoration changes in manatee distribution and abundance. To address detection errors we particularly were interested in accounting for variation in detection related to group size. Manatee diving behavior confounds accurate counts of manatees by affecting both availability and perception (Edwards et al. 2007). In shallow areas manatees at or below the surface under clear water conditions are easily within view and available for counting. However in deeper water manatees can stay submerged out of view for up to 20 min before coming up for a breath (Hartman 1979). Glare, wind, and turbidity can decrease detection further. With the formation of groups, as is common in feeding areas and warm water aggregations, diving behavior further confounds counting. Larger groups may be more easily detected but accurate counts of the number of individuals in the group may be more difficult. Furthermore, estimation of abundance is confounded because detection of groups is dependent on group size. With hierarchical models we could estimate manatee abundance by applying the modeling approach described by Royle and Dorazio (2006) separately to group counts and individuals counts and then calculate abundance as the product of estimates of group abundance and group size, but this approach fails to specify the dependence between the two. To address these issues we developed a new hierarchical model and modified an existing manatee aerial survey design to meet the data requirements and assumptions of the new model.

Our new aerial survey protocol and method of analyses included: 1) a dual-observer sampling protocol to estimate the number of manatee groups while accounting for perception errors; 2) a removal sampling protocol to estimate the number of manatees in each group while accounting for availability errors; 3) a model for linking the dual-observer counts and removal counts; 4) use of habitat covariates to model spatial variation in abundance and detection; and 5) a modern Bayesian approach that provides estimates of manatee abundance and credible intervals (CrI) at spatial and temporal scales useful for managers.

STUDY AREA

We conducted the aerial-survey study in the Ten Thousand Islands (TTI) area of southwestern Florida, USA. The area encompassed TTINWR, a portion of Rookery Bay National Estuarine Research Reserve, and the western edge of ENP (Fig. 1). Manatee aerial surveys flown in the early 1990s and again in the 2000s documented that manatees in the region frequented the inland tidal creeks, inshore bays, inter-island waterways, and near-shore seagrass beds. A telemetry study further documented individual manatees making regular distant movements from the near-shore seagrass beds to inland tidal creeks to drink freshwater and in winter to find thermal refuge in deep water basins and canals (Stith et al. 2011). A major center of activity for manatees was the inland basin of Port of the Islands (POI; Fig. 1) on the Faka Union Canal. In winter the deep canal and hydrological processes at POI maintained warmer temperatures than the Gulf or bays and was used as a major manatee winter refuge during cold fronts (Stith et al. 2011). A weir, which separated inland freshwater from tidal seawater, was thought to provide freshwater overflow or leakage for drinking water for manatees.

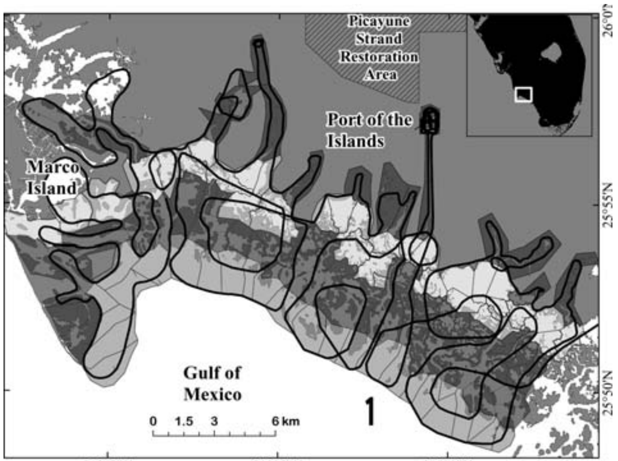

Figure 1. Aerial survey design for Florida manatees in the Ten Thousand Islands area of southwest Florida, USA, in 2006, showing the fixed flight path (dark line) and individual patches for the 5 habitat types: Offshore (light gray), inter-island travel corridors (medium gray), near-shore bays (white), inland canals and tidal creeks (dark gray), and Port of the Islands (POI). Seagrass used as forage by manatees are found offshore, whereas warm-water refuge and fresh drinking water are found at POI and inland rivers. Hydrological restoration in the Picayune Strand north of POI should alter hydrology and habitat for the manatees.

The survey area was expected to be affected by the Picayune Strand Restoration Project, designed to restore the hydrology altered by the Golden Gate Estates project north of POI (Fig. 1; U.S. Army Corps of Engineers and South Florida Water Management District 2004). After construction of drainage canals for the housing project, water was diverted from western bays which became hypersaline in the dry season, while Faka Union Bay received unnaturally high pulses of freshwater. The restoration project planned to fill or plug these canals and divert water toward the western bays with the objective to restore the historic quantity and duration of sheet flow through Picayune Strand State Forest and TTINWR to the coastal estuaries (U.S. Army Corps of Engineers and South Florida Water Management District 2004).

METHODS

Aerial Surveys

General flight methods.– We conducted surveys from a Cessna 172 or 182 (Cessna Aircraft Co., Wichita, KS) at an altitude of approximately 183 m traveling 120–140 km/hr. The flight path was originally developed for county-wide distribution surveys in the late 1980s and early 1990s (Ackerman 1995) and we modified it to provide coverage of all manatee habitat within the study area. Based on satellite tracking of individual manatees the path covered almost all manatee habitat (B. M. Stith, unpublished report). Flight regulations for the single engine aircraft restricted flight to near shore within gliding distance back to land (approximately 2 km) and a section of seagrass southeast of Cape Romano extended beyond the flying limit. Because of the complex water landscape of TTI, strip transect surveys were of limited use and a fixed path following the inter-island waterways, shorelines, bays, tidal creeks, and canals offered the best coverage (Fig. 1). The circuitous flight path allowed unobstructed views from the plane across narrow waterways and larger bays by observers sitting on the right side of the plane. We recorded the flight path on a Garmin GPS III Global Positioning System.

To maximize detection we standardized flying conditions. We began all surveys in the morning and flew them during incoming or high tides, as some habitat was not accessible to manatees during low tide. To enhance surface and subsurface viewing we ran surveys when wind speeds were <20 km/hr, cloud cover was minimal, and there was little or no precipitation. We also categorized and recorded viewing conditions such as turbidity, water surface condition, and cloud cover, as conditions often varied during of the flight. Although we could model detection to include viewing condition covariates, we focused on development of new methods (below) and assumed bias from variability in viewing conditions was minimal under our standardized flying conditions.

We flew 11 surveys in 2006. During each flight we sampled all manatee habitat patches (Fig. 1). To examine short-term and seasonal changes in distribution we flew paired surveys 1–2 days apart within a given month during the year. We flew cold, dry season flights on 10 and 11 January, 7 and 9 February, and 30 and 31 March. We flew warm, wet season flights on 27 and 29 July, 8 August (mechanical problems prevented the second Aug survey), and 17 and 18 October.

Two experienced observers, one in the front seat next to the pilot and a second in the back seat behind the first observer, collected data. Observers recorded manatee locations and additional data on 1:40,000 scale navigational charts from the National Oceanic and Atmospheric Administration. We later translated map locations to latitude and longitude as we entered the data into Arcmap9.2.

Dual-observer protocol.– Two observers worked independently to detect groups of manatees. As the plane followed the flight path, both observers searched the area for manatees out to the edge of the waterway being flown. Detection can decline with distance of the target species from the plane and can be modeled using line-transect distance-sampling (Buckland et al. 2004). With the frequent turns and circuitous flight path required to sample the irregular-shaped water bodies, however, it was difficult to consistently maintain a formal transect protocol. Additionally, within the narrow channels, canals, and tidal creeks a distance effect was probably minimal. Therefore, for this analysis we assumed detection was constant across the width of the view although in some of the larger water bodies detection may have declined with distance.

When a sighting was made, the observer waited until the group had been passed and the other observer had adequate time for viewing. At that time, the observers would confer and record whether the group was sighted by 2 observers, by the front observer only, or by the back observer only. The pilot then turned back and circled the group to collect data needed to estimate group size (see below) and, after circling was completed, returned to the flight path to continue the dual-observer protocol.

Removal protocol.– Circling a manatee group to allow individuals to surface into view is a standard technique used in manatee surveys to determine group size (Ackerman 1995). Usually a group is circled until repetitive counts are consistent and one count is recorded as the best estimate of the total number (Lefebvre et al. 1995). In our study the pilot followed a similar flight protocol, but we recorded sighting data with each complete circle. The initial number of observed individuals we recorded from the first sighting under the dual-observer protocol. In instances where we only observed a mud plume, indicating a disturbance from a manatee or other species, we recorded the initial number as zero. Both observers then worked together while circling to identify and record the number of new individuals sighted with each completed pass. As some individuals rose toward the surface and came into view, others would dive and move out of view. Recording the sighting history of each individual manatee, as is done in a classic capture–recapture design for closed populations (Williams et al. 2002), was not reliable with groups of >4 manatees. However, with the small group sizes in our study (1–12) and a tight flight circle, which allowed almost continual viewing of a group, observers believed they could reliably identify the appearance of previously unseen individuals based on their position relative to individuals that had already been seen or had recently submerged out of sight. Because we removed previously sighted individuals from counts of subsequent circles, our data corresponded to those of a classic removal design (Williams et al. 2002). We made 1–7 circles at the discretion of the observers depending on viewing conditions, the number of individuals initially seen, and observer confidence in the counts. A key difference of our protocol compared to previous protocols described by Lefebvre et al. (1995) is that our removal estimation procedure did not require circling to continue until we thought all individuals were counted. Unlike the dual-observer protocol for group detection, which accounted for variation in experience between observers, our removal protocol did not estimate observer error; therefore bias could be introduced with inexperienced observers. In our study 2 experienced observers (TJD conducted every survey) worked jointly to identify individuals, reducing, but probably not eliminating, error.

Structuring Data for Analysis

Defining sample units.– Our statistical analysis assumed that abundance and detection varied among spatial sample units (patches) owing to differences in habitat characteristics of the patches. To define sample units we established patch boundaries such that habitat characteristics were homogeneous within a patch and, given known manatee behavior and movements, the size of the patch was small enough to survey while not violating closure assumptions (i.e., we assumed no movement of manatees among patches in the time required to sample a patch).

We divided the surveyed landscape into patches consisting of discrete landscape features used by manatees (Fig. 1). We delineated patches manually by digitizing polygons on-screen using Arcmap 9.2, with digital orthophoto quarter quadrangles (DOQQs) as background images (2-m ground resolution). Patches varied in size ($\bar{x} = 112.05$ ha) due to differences in landscape features or physiography. Natural boundaries that served to delineate patches included river basins and canals, oyster reefs or other shallow water barriers to movement, deep channels separating shoals, and interfaces between features such as river systems, bays, mangrove islands, and offshore shoals. We flew all 130 manatee habitat patches in the study area for each survey in 2006 and used those data in this analysis.

Covariates.– Based on known biology and findings from the satellite telemetry study, the habitat characteristics we were most interested in assessing with regard to abundance were habitat type, water temperature, salinity, and seagrass. However, the period of record for the regional hydrodynamic model did not include our study year, so patch- and survey-specific covariates were not available for this analysis. In lieu of the hydrologic covariates, habitat type was discernable from aerial photographs and nautical charts that provided a broad index of relative differences in water temperature, salinity, and presence of seagrass. We divided the entire study area into 5 general habitat types (Fig. 1): 1) offshore seagrass areas, 2) travel corridors between islands, 3) inshore bays and estuaries, 4) inland rivers, canals, and lakes, and 5) POI. The artificial basin at POI with its winter thermal properties warranted a separate habitat designation due to its unrivaled heavy use by manatees (Stith et al. 2011). We assigned each patch a fixed habitat type, which did not vary among surveys.

Air and water temperatures are important predictors of manatee movement during winter (Deutsch et al. 2003). Gulf temperatures are colder than inshore temperatures for most of the winter. Following cold fronts Gulf temperatures often drop sufficiently ($<20^\circ$C) to drive manatees from offshore seagrass beds to inshore winter refuges (Stith et al. 2011). We expected to see survey-specific differences in distribution and abundance due to temperature changes, but patch-specific and survey-specific temperature data were not available in all patches, precluding a covariate analysis for this variable. Instead we summarized survey-specific air and water temperature from monitoring stations at a Gulf location near Naples, Florida and inshore at POI to provide ancillary information to interpret abundance results.

Statistical Analysis

We developed a statistical model that exploited the fact that our sampling protocols to count groups of manatees and individuals within groups (dual-observer and removal sampling, respectively) allowed us to estimate group abundance and group size (no. of manatees per group) while accounting for errors in detection. Because detection of a group should depend on the number of manatees in the group (i.e., the larger the group the more likely it is to be detected) the two types of counts are not independent. We developed a model for joint analysis of dual-observer counts and removal counts that formalized the dependence between the 2 types of counts. Because manatee abundance should vary among patches owing to differences among habitat types (offshore, corridor, bay, inland, and POI) we developed an approach to spatially reference estimates of abundance and uncertainty to patches based on habitat type.

Hierarchical model of dual-observer counts.– We may use the multinomial distribution to model the counts of 2 observers, say A and B, who independently detect groups of manatees. For example, we may summarize their observations using 3 counts: y_{AB} = number of groups seen by both observers, y_{A0} = number of groups seen only by observer A, and y_{0B} = number of groups seen only by observer B. Under the multinomial model, we assume

$$y_{\mathrm{AB}}, y_{\mathrm{A0}}, y_{\mathrm{0B}} | M, p_{\mathrm{A}}, p_{\mathrm{B}} \sim \mathrm{Multinom}\,(M, p_{\mathrm{A}}p_{\mathrm{B}}, p_{\mathrm{A}}(1-p_{\mathrm{B}}), (1-p_{\mathrm{A}})p_{\mathrm{B}} \qquad (1)$$

where p_{A} and p_{B} denote observer-specific probabilities of group detection. The multinomial index M denotes the unknown total number of groups. In this model $y_{00} = M - (y_{\mathrm{AB}} + y_{\mathrm{A0}} + y_{\mathrm{0B}})$ denotes the number of groups that were available for detection but were not detected by either observer; therefore, estimating M is equivalent to estimating y_{00}.

In our case we needed to modify this model of group detections so that we assume detection probabilities to differ not only between observers but also among groups, depending on the number of manatees in the group. Therefore, we began by redefining the observation of an individual group as a 4×1 vector $\boldsymbol{y}$ whose value corresponds to 1 of 4 possible types of detections:

$$\mathbf{y} \in \begin{cases} (1,0,0,0), & \mathrm{AB} \\ (0,1,0,0), & \mathrm{A0} \\ (0,0,1,0), & \mathrm{0B} \\ (0,0,0,1), & 00 \end{cases}$$

Note that only the first 3 values of $\boldsymbol{y}$ are observable; the fourth corresponds to a group that is available but not detected by either observer. We analyzed these group detection histories using a technique called parameter expanded, data augmentation (Royle et al. 2007; J. A. Royle and R. M. Dorazio, U.S. Geological Survey, unpublished report), wherein we augmented the observed values of $\boldsymbol{y}$ by an arbitrarily large number of all-zero detection histories [00 or $\boldsymbol{y} = (0,0,0,1)$ in our notation] and reparameterized the original model for the augmented data. This technique was developed originally to simplify the analysis of capture–recapture models with individual effects in which the dimension of the parameter space (i.e., no. of unknowns) is itself unknown. In our application, the individual effect is the effect of manatee group size on group detection probability.

In using data augmentation, we fixed the dimension of the parameter space by embedding the complete data (wherein M is known) into a larger data set of fixed dimension (say, G). We analyzed this larger, augmented data set using a new model that effectively yielded a reparameterization of M in the conventional model of the observed (unaugmented) data. We can view this new model as a zero-inflated version of the conventional model, which we can easily fit using modern methods of Bayesian computation (e.g., Gibbs sampling). By fitting the new (zero-inflated) model, we can estimate the number of augmented detection histories that are sampling zeros (i.e., detection histories that belong to groups that are members of the population exposed to sampling) and thereby obtain an estimate of the parameter M of the conventional model (Eq. 1). The remaining all-zero detection histories, which we refer to as structural zeros, are not of scientific interest, as they correspond to detection histories of groups that are not members of the population exposed to sampling.

To illustrate the model of augmented group detections in more concrete terms, clarifying the role of spatial referencing and the effects of habitat on manatee abundance, we let the index i correspond to 1 of G groups nested within each of the n patches sampled on any survey date. Therefore, the collection of augmented data set includes nG observation vectors $\boldsymbol{y}_i$ ($i = 1, \ldots, G, G + 1, \ldots, 2G, 2G + 1, \ldots, nG$) that correspond to nG groups of manatees. We choose the number of manatee groups per patch, G, to be sufficiently large that it greatly exceeds the number of groups actually exposed to sampling in each of the n patches. At first, the subjective choice of G may seem to be a limitation of this approach; however the adequacy of any assumed value of G is easily diagnosed as part of the analysis (Royle et al. 2007). If necessary, the analysis can always be repeated using a higher value of G to ensure that estimates of group abundance are not biased (negatively) by the choice of G.

Given our notation, the multinomial model of the ith group's observation is

$$\mathbf{y}_i|w_i,\ p_{i\mathrm{A}},\ p_{i\mathrm{B}} \sim \mathrm{Multinom}\left(w_i{\textstyle\prod}_{i\mathrm{AB}},\ w_i{\textstyle\prod}_{i\mathrm{A}0},\ w_i{\textstyle\prod}_{i0\mathrm{B}},\ w_i{\textstyle\prod}_{i00}, +1-w_i\right) \qquad (2)$$

where $\prod_{i\mathrm{AB}} = p_{i\mathrm{A}}p_{i\mathrm{B}}$, $\prod_{i\mathrm{A}0} = p_{i\mathrm{A}}(1 - p_{i\mathrm{B}})$, $\prod_{i0\mathrm{B}} = (1 - p_{i\mathrm{A}})\, p_{i\mathrm{B}}$, $\prod_{i00} = (1 - p_{i\mathrm{A}})\,(1 - p_{i\mathrm{B}})$. In Equation 2, w_i is a latent parameter that indicates whether the ith group is a member of the population exposed to sampling ($w_i = 1$). If the group is not a member of the population, then $w_i = 0$. The multinomial cell probabilities also depend on group- and observer-specific detection probabilities $p_{i\mathrm{A}}$ and $p_{i\mathrm{B}}$. Note that for each value of w_i the multinomial cell probabilities in Equation 2 must sum to 1 given our definition of the observation vector $\boldsymbol{y}$; therefore, the multinomial index parameter equals 1 and need not be specified explicitly. Also note that by conditioning on the latent parameter w_i in Equation 2, we automatically specify whether an undetected group, whose observation vector is $\boldsymbol{y} = (0,0,0,1)$, corresponds to a sampling zero or a structural zero. For example, if the ith group is a member of the population exposed to sampling but is undetected by observers A and B, then $\Pr(\boldsymbol{y}_i = (0,0,0,1) \mid w_i = 1) = (1 - p_{i\mathrm{A}})\,(1 - p_{i\mathrm{B}})$. On the other hand, if the ith group is not exposed to sampling, then $\Pr(\boldsymbol{y}_i = (0,0,0,1) \mid w_i = 0) = 1$ that is, manatees that are not members of the population are unobserved with probability 1 under our modeling assumptions. Therefore, by estimating the value of w for each group, we can estimate manatee abundance in a way that naturally excludes the structural zeros in the augmented data (see below).

To estimate w for each group of manatees, we need a model of their inclusion in the population. We assume the probability that the ith group is a member of the population exposed to sampling to depend on the habitat in which the group occurs. In other words we assume occurrence of manatees to depend on habitat. Recall that we categorized each patch into 1 of 5 habitat types; therefore, we let $\psi_x(x\in\{1,2,3,4,5\})$ denote the probability that a group from habitat type x is a member of the population of manatees exposed to sampling. Because the value of x is patch-specific, it is known for all manatee groups (both observed and augmented). Using x_i to denote the ith group's value of x, we specify the model of w_i as follows:

$$w_i|x_i \sim \mathrm{Bernoulli}\ (\psi_{xi}) \qquad (3)$$

which provides an explicit connection between the habitat of a patch and the number of manatee groups present in that patch. In addition, estimates of w_i allow us to estimate total number of manatees present in each of the 5 habitat types (see below).

The multinomial cell probabilities in Equation 2 include detection parameters $p_{i\mathrm{A}}$ and $p_{i\mathrm{B}}$ that depend on both group (i) and observer (A or B). As noted earlier, we assume detectability of a group to increase with its size. To specify this dependence and the effect of observer, we make the following assumptions:

$$\mathrm{logit}\,(p_{i\mathrm{A}}) = \alpha_{0\mathrm{A}} + \alpha_1 z_{i1} \qquad (4)$$

$$\mathrm{logit}\,(p_{i\mathrm{B}}) = \alpha_{0\mathrm{B}} + \alpha_1 z_{i1} \qquad (5)$$

where $\alpha_{0\mathrm{A}}$ and $\alpha_{0\mathrm{B}}$ parameterize the effects of observers A and B, respectively, on group detection and α_1 parameterizes the increase in detectability (i.e., assuming $\alpha_1 > 0$) associated with observing z_{i1} manatees during the first removal of the ith group of individuals. Note that we assume α_1 to be the same for both observers and we include it to allow detection probabilities to be higher for larger groups of manatees. This functional dependence between group detection probability and z_{i1} expresses a formal connection between the group-level data $\boldsymbol{y}_i$ and the individual-level data z_{i1}. We could have assumed that a group's detectability depended on the total number of manatees in the group. However, this assumption seems inconsistent with the sampling protocol used by the dual observers. Group detections by observers A and B were influenced by the number of manatees visible from the plane, not by the total number of manatees in the group, which includes manatees not visible from the plane.

Hierarchical model of removal counts.–To estimate the sizes of both observed and unobserved groups of manatees, we need to specify a model of the counts of individual manatees observed within each group. We let $\mathbf{z}_i = (z_{i1}, z_{i2}, \ldots, z_{iJ_i})$ denote the sequence of counts of manatees first observed in each of J_i successive removals of the ith group. We assume these counts to have a multinomial distribution

$$z_{i1},\ z_{i2},\ \ldots,\ z_{iJ_i}|N_i,\ p \sim \mathrm{Multinom}\ (N_i,\ p,\ p\,(1-p),\ \ldots,\ p\,(1-p)^{J_i-1}) \qquad (6)$$

where p denotes probability of detection of an individual manatee during each successive pass (i.e., given that the group has been detected) and N_i denotes the unknown number of manatees in the group. Note that N_i includes both observed and unobserved individuals and that each group must contain ≥ 1 manatee. Therefore, we modeled group sizes using a truncated-Poisson distribution with probability mass function

$$g(N_i|\lambda) = \frac{\lambda^{N_i}\exp(-\lambda)}{N_i!\{1-\exp(-\lambda)\}} \tag{7}$$

where λ denotes the average number of manatees in a group. Modeling the distribution of group sizes is important because it keeps the number of parameters to be estimated from growing with the sample size. More importantly, the model of group sizes allows us to estimate values of z_{i1} when the ith group is not actually observed. Recall that we need z_{i1} to specify the probability of detecting the ith group (see Eqs. 4 and 5). If the ith group is observed, then we use the observed value of z_{i1} to evaluate group detection probabilities $p_{i\mathrm{A}}$ and $p_{i\mathrm{B}}$; however, if the ith group corresponds to an augmented observation, then we predict z_{i1} from the model-based estimates of N_i and p (see Appendix).

Estimation of model parameters and manatee abundance.– The hierarchical model we described contains many latent parameters. We could fit the model by maximizing the marginal likelihood obtained by removing all the latent parameters by integration. However, this approach would be technically challenging to implement and counter-productive because we need estimates of several latent parameters, such as w_i and N_i, to estimate manatee abundance. We therefore opted for a Bayesian approach to inference and estimation using modern methods of Bayesian computation (Markov chain Monte Carlo). Our inferences are based on an arbitrarily large sample of the joint posterior distribution of the model's parameters (see Appendix).

Once we calculate a sample of the joint posterior, the estimation of manatee abundance in each patch or in groups of patches (e.g., patches of similar habitat) is a straightforward calculation. We let the sequence $1, 2, \ldots, G$ index the G groups of manatees associated with one patch. Some of these groups are observed; the others correspond to groups added via data augmentation. Fitting the model to the data provides estimates of w_i, an indicator of whether the ith group is a member of the population, and N_i, the abundance of manatees in the ith group, for $i = 1, 2, \ldots, G$. Therefore, an estimator of the total number of manatees in the patch is simply $\sum_{i=1}^{G} w_i N_i$. We can estimate the total number of manatees in a specific habitat type or in the entire population similarly, the only difference being the indexes we use in the summation. Our Bayesian approach to inference yields the entire posterior distribution of the parameters w_i and N_i. From this posterior distribution we can summarize abundance for specific spatial and temporal scales. We were interested in total abundance for the region, spatial distribution by season and habitat types, and patch-specific abundance over time. Comparison of patch-specific abundance was best illustrated with time-specific maps of abundance estimates. Because abundance estimates were highly skewed toward low values, we used the geometrical interval method in Arcmap 9.2 to select levels of abundance for mapping, rounding the endpoints to integers for ease of interpretation: <1 (i.e., a partial individual that we estimated to account for detection errors for patches with no manatee counts), 1–2 individuals (the predominant group size among counts), 2–15 individuals (moderate abundance), and >15 individuals (high abundance).

RESULTS

Manatees were sparsely distributed across the landscape in small groups. During any given survey the raw counts included many patches with no observed manatees and few patches with >1 group. The number of manatees initially detected in each group (i.e., at first sighting) often included only 1 or 2 individuals, but ranged as high as 17 individuals in winter at POI.

Estimates of detection probabilities showed that groups and individual manatees were missed during surveys. Modeling the dual-observer data for each patch and survey showed that probability of detection of a group, while traveling the flight path, increased with group size (Fig. 2A), although the magnitude of the relationship between group size and detection probability varied among surveys

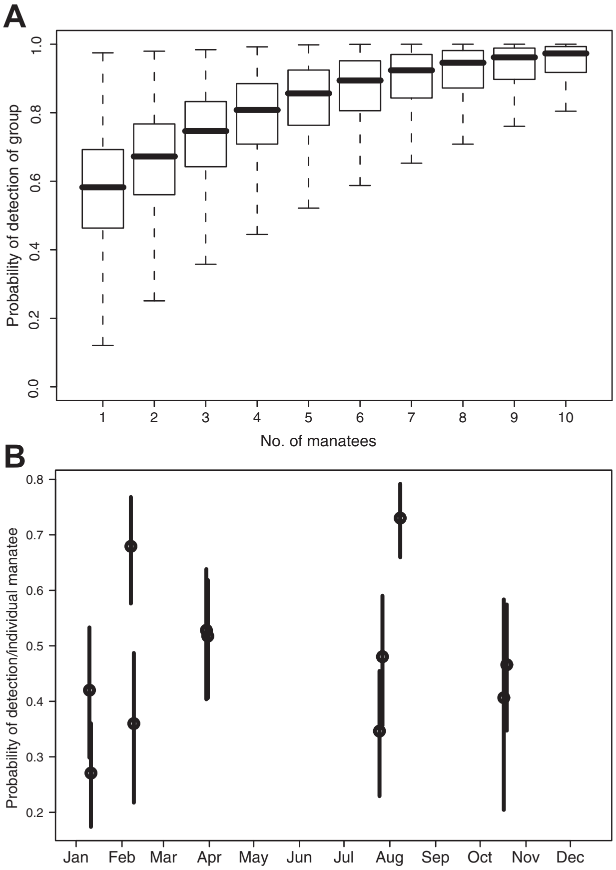

Figure 2. A: Estimates of group detection probability as a function of the initial no. of manatees obs in a group for 11 January during aerial surveys conducted in the Ten Thousand Islands area of southwest Florida, USA, in 2006. We flew paired surveys (1–2 days apart) throughout the year. We documented increasing detection with group size for all 11 surveys flown in 2006. B: Posterior mean and 95% credible interval for probability of detection/individual manatee based on removal sampling. Detection varied among surveys.

Table 1. Posterior mean ($\bar{x}$) and 95% credible interval (CrI) for logit-scale increase in probability of group detection (α_1) associated with the no. of Florida manatees initially obs in the group during 11 aerial surveys we conducted in TTI Florida, 2006.

Date	$\bar{x}$	95% CrI
10 Jan	0.24	−0.17–0.69
11 Jan	0.38	−0.01–0.85
07 Feb	0.25	−0.12–0.71
09 Feb	0.23	−0.48–1.17
30 Mar	0.31	−0.06–0.68
31 Mar	0.25	−0.07–0.65
25 Jul	0.24	−0.23–0.76
27 Jul	0.27	−0.09–0.70
08 Aug	0.16	−0.03–0.43
17 Aug	0.19	−0.22–0.62
19 Oct	0.17	−0.02–0.39

(Table 1). Detection of individual manatees within a group, estimated from removal counts, also differed among surveys (Fig. 2B) and showed higher variability than group detection, ranging from a low of 0.27 on 11 January to a high of 0.73 on 8 August.

Spatial distribution of manatees among patches and habitat types changed with time. Within each habitat type estimates of total abundance varied seasonally (Table 2). During winter surveys (Jan, Feb, and late Mar) abundance was always higher at POI, the warm-water aggregation site (range 59–160), than in the other habitat types. During warm-season surveys (Jul–Oct), highest abundances were estimated in the offshore habitat type where manatees forage on seagrass (range 68.3–172.6). Manatees continued to use POI in summer, but in lower numbers than in winter (range 12–50). Abundance in inland rivers, canals and lakes in summer was low (range 0.2–11.3) compared to winter (range 7.1–58.4).

Several consistent features of patch-specific habitat use were evident in the maps of manatee abundance (Fig. 3). With the exception of 1 or 2 surveys, we found the highest abundances at POI (and the canal leading to POI) and off the tip of Cape Romano in the southwestern portion of the study area. Within the inter-island corridors, we consistently estimated patches to have <1 individual. For inland river systems, estimates were usually low (<1 or 1–2 individuals). Greater variability in abundance occurred both spatially and temporally among offshore patches and bays.

Shifts in distribution with changing winter temperatures are discernable by comparing the maps of abundance for the paired winter surveys with water temperature differences between the Gulf and inland hydrology stations. We conducted February surveys during a prolonged cold front (Fig. 4). On the first survey date (7 Feb), abundance was at low to moderate levels in some offshore patches, but on the next survey two days later (9 Feb), we estimated abundance offshore at <1 and moderate to high only at POI and adjacent inland areas (Fig. 3). The January surveys occurred during a warming trend following a strong cold front that peaked on 8 January, with increasing Gulf temperatures during the 10–11 January surveys (Fig. 4). Maps of abundance during this 2-day period indicated that manatees moved from the warm water aggregation at POI into the adjacent inland bays and river systems (Fig. 3). March surveys occurred during a warming trend following a strong cold front that peaked on 27 March, with Gulf temperatures fluctuating near or above 20°C during the 30–31 March surveys (Fig. 4). Maps of abundance during this 2-day period indicated a shift in abundance away from bays and inland river systems out to offshore seagrass beds. Warm season maps (Fig. 3) showed consistently high abundance in patches within the Cape Romano seagrass beds.

Although patch-specific abundance changed over time, total abundance for the entire area was similar among survey dates. CrI, however, were large for winter and October surveys (Fig. 5).

DISCUSSION

Ours is the first analysis of manatee aerial survey data to model the spatial and temporal abundance of manatees in association with habitat type, while accounting for imperfect detection. The results provided baseline information on the distribution and abundance of manatees in the TTI area prior to hydrologic restoration planned for the Picayune Strand. Our abundance estimates indicated 2 widely separated habitat types of major importance to manatees: Offshore shoals and the inland canal and boat basin at POI. Seagrass in these offshore shoals provided food for the herbivorous manatee year round. Repeated high abundance off Cape Romano, compared to other offshore patches, suggests

Table 2. Posterior mean ($\bar{x}$) and 95% credible interval (CrI) for total abundance of Florida manatees in each of 5 habitat types during aerial surveys we conducted in TTI Florida, 2006.

	Port of the Islands		Inland		Bay		Corridor		Offshore	
Date	$\bar{x}$	95% CrI	$\bar{x}$	95% CrI	$\bar{x}$	95% CrI	$\bar{x}$	95% CrI	$\bar{x}$	95% CrI
10 Jan	88	62–156	12.2	5–39	68	47–137	9.9	2–38	14.2	4–47
11 Jan	160	96–304	58.4	26–144	152	97–301	25.2	7–77	39.3	14–110
07 Feb	59	52–75	31.9	29–42	12	10–21	6.1	4–14	22.1	18–34
09 Feb	102	81–158	23.2	13–53	11	7–26	0.5	0–7	0.5	0–7
30 Mar	98	56–167	30.4	11–78	41	13–106	38.0	10–104	59.3	28–129
31 Mar	84	69–114	7.1	3–19	17	10–34	20.1	12–41	76.0	60–116
25 Jul	45	31–66	9.7	5–19	26	17–41	26.0	20–38	138.5	115–179
27 Jul	12	9–21	4.4	2–12	28	20–46	4.4	2–12	112.9	93–152
08 Aug	27	24–36	0.2	0–3	29	24–41	18.2	16–26	156.4	149–172
17 Oct	43	12–148	11.3	1–63	15	4–69	28.2	6–126	68.3	26–254
19 Oct	50	26–111	6.5	1–27	23	7–69	15.8	5–49	172.6	124–307

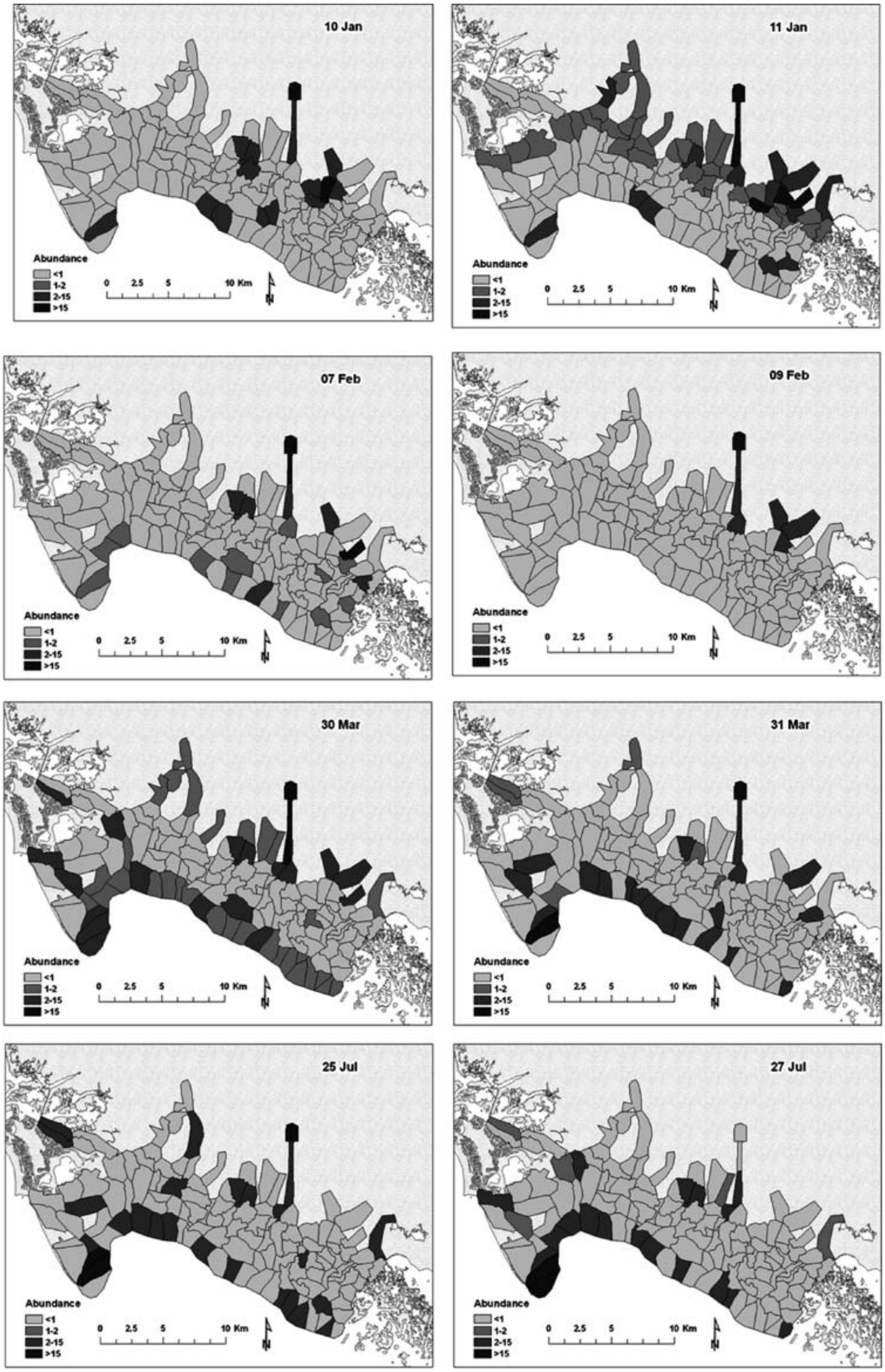

Figure 3. Patch-specific maps of posterior mean abundance of manatees during aerial surveys we conducted in the Ten Thousand Islands area of southwest Florida, USA, in 2006. During colder periods manatee abundance was higher inland at warmer sites; during warmer periods abundance was higher at foraging areas offshore.

that seagrass abundance and quality may be higher there, supporting larger numbers of manatees. Offshore manatee abundance decreased during winter, as manatees delayed feeding during cold periods to remain in warmer water at POI. Chronic cold stress quickly leads to a cascade of pathological effects compromising metabolic, nutritional, and immune systems (Bossart et al. 2003). No other patches in our study area approached cold season abundance estimated at POI. Research based on a manatee telemetry study and analysis of hydrological data demonstrated that POI provided manatees with warmer water than the Gulf of Mexico and inshore bays, because formation of a halocline prevented mixing and cooling of bottom water (Stith et al. 2011).

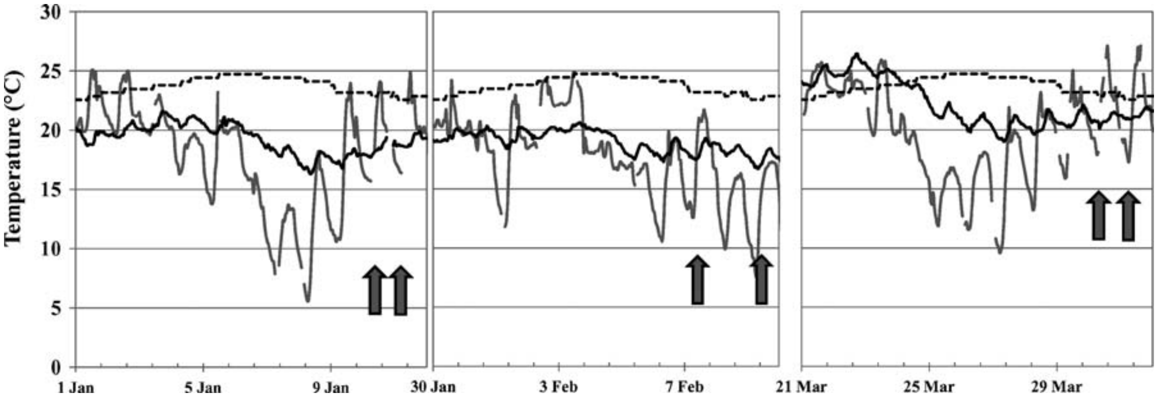

Figure 4. Air temp (°C, solid gray line) and water temp (°C) in the Gulf of Mexico (solid black line) and at the manatee winter refuge at Port of the Islands (POI; dashed lines) during the winter aerial surveys in the Ten Thousand Islands area of southwest Florida, USA, in 2006. Survey dates are indicated by arrows. When Gulf water temp <20°C manatees aggregated at the warmer waters of POI.

During warm season manatees continued to use POI, perhaps because of availability of freshwater. Manatees are the only marine mammal known to frequently drink freshwater (Ortiz 2001). Port of the Islands and its connection to the coast (Faka Union canal and Faka Union Bay) showed higher warm season abundance than other inland freshwater rivers and their inshore bays, even those west of POI that are closer to the Cape Romano seagrass beds. Compared to POI, these rivers and bays frequently turn hypersaline in the cold, dry season, and freshen during the warm, rainy season (U.S. Army Corps of Engineers and South Florida Water Management District 2004). The higher certainty of access to freshwater for drinking at POI may make it more attractive to manatees than other freshwater rivers. This may change with the Picayune Strand Restoration as it is expected to increase freshwater flow to the rivers and bays west of POI (U.S. Army Corps of Engineers and South Florida Water Management District 2004).

Movement and redistribution of the local manatee population among habitats and patches was fluid, even over 2 days, and was not unexpected for a highly mobile species. This fluidity may be more pronounced in TTI compared to other Florida habitat because of the distance among feeding areas, fresh drinking water, and thermal refuges. The most pronounced changes occurred in cold season when rapid changes in air and water temperatures led to rapid changes in abundance and distribution. Maps of patch-specific abundance (Fig. 3) provided static snapshots of the dynamics of movement of the entire population during the passage of cold fronts. Similar movements in TTI have been documented by 5 yr of satellite telemetry of 33 individuals (Stith et al. 2011; B. M. Stith, unpublished report; J. P. Reid, U.S. Geological Survey, personal communication). As a cold front moved in, individuals dispersed across the landscape converged at the warmer water at POI. As the front retreated and temperatures edged higher, manatees moved into shallow bays that warmed more quickly than the deeper Gulf and were closer to seagrass beds. Highest abundance in bays occurred after passage of a cold front as manatees made their way toward the feeding areas. Once temperatures climbed, they moved out to feed offshore. In summer when cold stress was not an issue, manatees settled into a home range pattern with greater dependence on offshore foraging habitat. Although they continued to move among patches and between offshore marine habitat and inshore freshwater habitat, telemetry showed individuals would move independently rather than en masse in response to temperature changes.

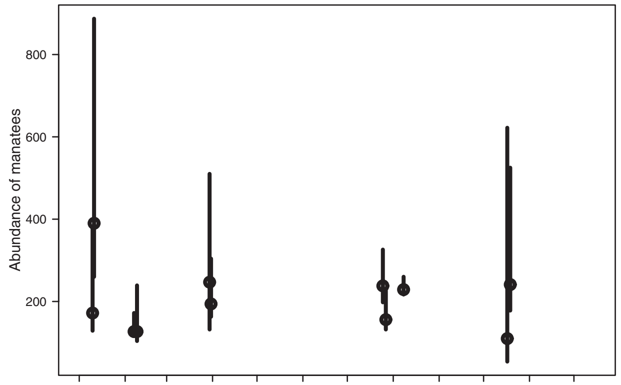

Figure 5. Posterior medians and 95% credible intervals for total abundance of manatees we estimated from aerial surveys we conducted in 2006 for the Ten Thousand Islands area of southwestern Florida, USA.

Our statistical treatment of variation in group detection with group size is a major advance in aerial surveys of wildlife populations. In other analyses of manatee surveys, a dual-observer approach was used to estimate the number of groups and this estimate was multiplied by mean group size to compute an estimate of abundance (Miller et al. 1998). However, it makes intuitive sense that the larger the group the larger the probability of group detection. This intuition has motivated development of statistical methods for modeling group detection probability as a function of observed group size (Samuel et al. 1987, Buckland et al. 2004, Royle 2009). Our statistical approach differs from previous approaches because we used both observed and estimated group sizes to model the dependence between group-level detections based on the dual-observer sampling and individual-level detections based on removal sampling. Using this approach we estimated a positive effect of group size on manatee group detection probability (Fig. 2A; Table 1). By

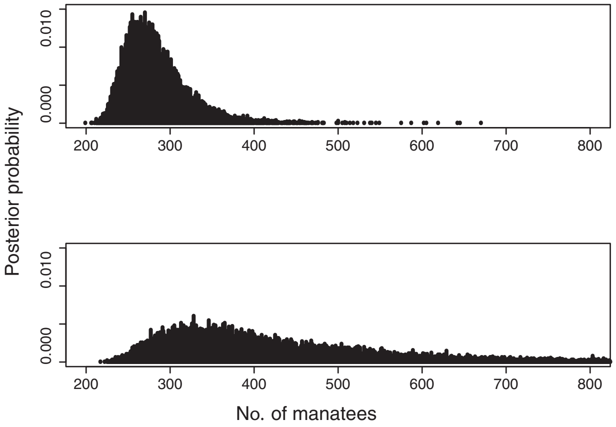

Figure 6. Posterior distributions of total abundance of manatees in all 130 patches we estimated for the aerial survey we conducted 11 January in the Ten Thousand Islands area of southwestern Florida, USA in 2006. We computed posteriors using 2 modeling assumptions: Group detection is fixed (top panel); group detection probability increases with no. of manatees detected in each group (bottom panel).

comparing the posterior distributions of total abundance from a model with group detection fixed versus a model with variable detection, we can see the dramatic effects of group size on estimates of abundance (Fig. 6). Because groups of 1–2 individuals dominate the landscape but are the most likely groups to go undetected, the large effect on abundance seems reasonable. Not accounting for group size will negatively bias estimates of manatee abundance under our survey design.

Our distribution maps successfully captured dynamic movements of manatees also detailed from satellite telemetry (Fig. 3) but abundance estimates and uncertainty changed substantially over time, sometimes with large CrI (Figs. 4 and 5). Our estimates of total abundance, however, generally were consistent with maximum counts of manatees in the area from past surveys (T. J. Doyle, U.S. Fish and Wildlife Service [USFWS], and Florida Fish and Wildlife Research Institute, unpublished data). Uncertainty was larger during the winter surveys when manatees aggregated in larger numbers at POI and in October when individual manatees may be moving from summer to winter home range areas (Deutsch et al. 2003). When manatees were dispersed across offshore habitat in August CrI were narrow. This suggests that our approach may be more robust to situations where animals occur in low densities across the landscape.

Some of the variability in estimates and CrI undoubtedly was due to the distance between critical resources and the highly mobile nature of manatees. Good habitat existed adjacent to the study area and manatees could move to these areas, violating the closure assumption. Expanding coverage to a broader area might reduce the influence of random movement on abundance estimates. However, the survey area and flight duration was at the limit of practicality for a single-day-single-plane survey that surveyed all patches. Development of a stratified random sample based on habitat type would increase the area that could be surveyed and allow inferences to be made across a larger region.

One factor that may have a marked effect on uncertainty in estimates was our use of only one simple covariate, habitat type, to model spatial variation. Although analysis revealed continual redistribution of manatees among habitat types, we were forced to interpret the expected causes of those movements using ancillary temperature data collected at fixed monitoring stations within the region. We expect manatee occurrence in the patches to vary with temperature, salinity, and seagrass quality and quantity. The U.S. Army Corps of Engineers and South Florida Water Management District (2004) documented differences in salinity and freshwater flow to rivers and bays across the TTI landscape, thus we expect manatees are less likely to occur in some of those western waterways. Additionally, we know from telemetry data that some patches within the inter-island corridors are more heavily used for travel than others. In our analysis, we applied patch-specific abundance estimates to all patches within the habitat type. If the number of patches truly without manatees is high, but positive abundance values are inferred based on the application of detection estimated for non-zero patches, this could create bias and inflate CrI. Inclusion of time and habitat patch-specific covariates from telemetry data and from simulations of the new hydrologic model (Swain and Decker 2009) should improve precision of the estimates to provide better base-line estimates for postrestoration assessments. This approach would also provide managers with better information on factors affecting abundance and allow us to infer and predict smaller scale patterns of manatee distribution with greater accuracy.

Our observers noted that accurate identification of new individuals during the removal phase of the survey was more difficult, but not unmanageable, with large groups. Larger aggregations formed at POI in winter and sometimes in offshore seagrass areas. However, at POI most groups were small because they were dispersed across 11 distinct canals within the boat basin. Larger group sizes have been documented at other winter aggregation sites. For instance Edwards et al. (2007) reported groups of up to 50 animals at the TECO Big Bend power plant in Tampa Bay. However, the presence of a few groups too large to sample with the removal protocol should not bias estimates. If observers feel they cannot track individuals as they appear in each circle (due to size or other complication), the initial group size is still valid for inclusion in the abundance analysis. We can exclude the successive count data and calculate total group size using the probability of detection estimated from the removal data of all remaining groups. Nonetheless, our approach would be most appropriate for areas and seasons when manatees are dispersed across the landscape. Alternative methods, such as repeated counts, may be more effective at winter aggregation sites with large groups.

Dual observers allowed us to account for imperfect detection given that manatee groups were within view and available for counting. However, some groups of manatees may have been submerged and out of view as the plane made its initial pass. We suspect smaller groups of 1–2 manatees are more frequently unavailable for viewing, as submersion of all manatees of the group at the same time would be less likely with increasing group size. With additional time circling within a patch, or replicate flights over segments of the flight path, observers did identify some missed groups, but whether they were unavailable or missed by both observers was unknown. Although we had little evidence for large availability bias due to submerged groups, if such bias is high, then reflights of segments of the flight path allowing 20–30 min for new groups to emerge into view and old groups to drop out of view would provide data to estimate detection error and account for this aspect of availability bias.

There are multiple detection problems inherent to manatee surveys, nearly all with potential fixes. The question is what are the most important issues and what fixes reduce bias and uncertainty to levels acceptable to management objectives within given cost and logistical constraints. We addressed some of the most important issues. Although our design and hierarchical modeling approach is specific to manatees, we believe it has broader application to other surveys, specifically in situations where animals occur in low densities across the landscape, where mobile species can show shifts in distribution without changes in abundance, where estimates may be confounded by variation in detection of groups of individuals with group size, and where habitat configurations are not amenable to surveys using line-transect techniques. For the USFWS this monitoring approach contains essential elements for Strategic Habitat Conservation, a landscape approach for the agency to manage resources into the future within a structured decision making framework (USFWS 2006, 2008). It can model population-habitat relationships and is spatially-explicit at multiple temporal and spatial scales. Estimates of abundance (a major descriptor of current population state) and variance allow for comparisons of population state in future surveys. The abundance estimates and distribution patterns can easily be incorporated into population and ecosystem models to describe or assess past outcomes or predict future outcomes under various restoration plans, management actions, or natural events.

MANAGEMENT IMPLICATIONS

Our results modeling manatee abundance–habitat relationships indicate that manatees in TTI travel to different habitat types for different critical resources. Within a habitat type, some patches had higher manatee abundance suggesting differences in quality, possibly due to freshwater flow. If hydrological restoration alters the location of quality habitat, postrestoration comparisons using our methods will document how manatees adjust to new resources, providing managers with information on spatial needs for further monitoring or management. Large CrI, however, limit our ability to statistically detect trends in total abundance, particularly in winter. Large changes in population size may be evident, but detection of smaller changes most likely would be swamped by the uncertainty of some estimates. Additional modeling of abundance with time- and patch-specific covariates of salinity, water temperature, and seagrass abundance will directly link abundance to physical and biological changes due to restoration and should decrease uncertainty of estimates. Datasets to provide these covariates are currently under development.

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LITERATURE CITED

Ackerman, B. B. 1995. Aerial surveys of manatees: A summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, H. F. Percival, editors. Population biology of the Florida manatee. Information and technology report 1. National Biological Service, Washington, D.C., USA.

Bossart, G. D., R. A. Meisner, S. A. Rommel, S.-J. Ghim, and A. B. Jenson. 2003. Pathological features of the Florida manatee cold stress syndrome. Aquatic Mammals 29:9–17.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2004. Advanced distance sampling. Oxford University Press, Oxford, United Kingdom.

Craig, B. A., and J. E. Reynolds, III. 2004. Determination of manatee population trends along the Atlantic coast of Florida using a Bayesian approach with temperature-adjusted aerial survey data. Marine Mammal Science 20:386–400.

Deutsch, C. J., J. P. Reid, R. K. Bonde, D. E. Easton, H. I. Kochman, and T. J. O'Shea. 2003. Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States. Wildlife Monographs 151.

Edwards, H. H., K. H. Pollock, B. B. Ackerman, J. E. Reynolds, III, and J. A. Powell. 2007. Estimation of detection probability in manatee aerial surveys at a winter aggregation site. Journal of Wildlife Management 71:2052–2060.

Fonnesbeck, C. J., H. H. Edwards, and J. E. Reynolds, III. 2009. A hierarchical covariate model for detection, availability and abundance of Florida manatees at a warm water aggregation site. Pages 563–578. *in* D. L. Thomson, E. G. Cooch, M. J. Conroy, editors. Modeling demographic processes in marked populations. Environmental and Ecological Statistics 3. Springer, New York, New York, USA.

Gilks, W. R., A. Thomas, and D. J. Spiegelhalter. 1994. A language and program for complex Bayesian modelling. The Statistician 43:169–177.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publication 5.

Kendall, W. L., C. A. Langtimm, C. A. Beck, and M. C. Runge. 2004. Capture–recapture analysis for estimating manatee reproductive rates. Marine Mammal Science 20:424–437.

Langtimm, C. A., C. A. Beck, H. H. Edwards, K. J. Fick-Child, B. B. Ackerman, S. L. Barton, and W. C. Hartley. 2004. Survival estimates for Florida manatees from the photo-identification of individuals. Marine Mammal Science 20:438–463.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial surveys as a technique for estimating trends in manatee population size – Problems and prospects. Pages 63–74. *in* T. J. O'Shea, B. B. Ackerman, H. F. Percival, editors. Population biology of the Florida manatee. Information and technology report 1. National Biological Service, Washington, D.C., USA.

Miller, K. E., B. B. Ackerman, L. W. Lefebvre, and K. B. Clifton. 1998. An evaluation of strip-transect aerial survey methods for monitoring manatee populations in Florida. Wildlife Society Bulletin 26:561–570.

National Research Council. 2008. Progress toward restoring the Everglades: The second biennial review, 2008. National Academies Press, Washington, D.C., USA.

Ortiz, R. M. 2001. Osmoregulation in marine mammals. Journal of Experimental Biology 204:1831–1844.

Pollock, K. H., H. D. Marsh, I. R. Lawler, and M. W. Alldredge. 2006. Estimating animal abundance in heterogenous environments: An application to aerial surveys of dugongs. Journal of Wildlife Management 70:255–262.

Robert, C. P., and G. Casella. 2004. Monte-Carlo statistical methods. Second edition. Springer-Verlag, New York, New York, USA.

Royle, J. A. 2009. Analysis of capture–recapture models with individual covariates using data augmentation. Biometrics 65:267–274.

Royle, J. A., and R. M. Dorazio. 2006. Hierarchical models of animal abundance and occurrence. Journal of Agricultural, Biological, and Environmental Statistics 11:249–263.

Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. Academic Press, San Diego, California, USA.

Royle, J. A., R. M. Dorazio, and W. A. Link. 2007. Analysis of multinomial models with unknown index using data augmentation. Journal of Computational and Graphical Statistics 16:67–85.

Runge, M. C., C. A. Sanders-Reed, and C. J. Fonnesbeck. 2007*a*. A core stochastic population projection model for Florida manatees (*Trichechus manatus latirostris*). U.S. Geological Survey Open-File Report 2007-1082, http://www.pwrc.usgs.gov/resshow/manatee/documents/OFR2007-1082.pdf. Accessed 21 Apr 2009.

Runge, M. C., C. A. Sanders-Reed, C. A. Langtimm, and C. J. Fonnesbeck. 2007*b* A quantitative threats analysis for the Florida manatee (*Trichechus manatus latirostris*). U.S. Geological Survey Open-File Report 2007-1086, http://www.pwrc.usgs.gov/resshow/manatee/documents/OFR2007-1086.pdf. Accessed 21 Apr 2009.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in north central Idaho. Journal of Wildlife Management 51:622–630.

Stith, B. M., J. P. Reid, C. A. Langtimm, E. D. Swain, T. J. Doyle, D. H. Slone, J. D. Decker, and L. E. Soderqvist. 2011. Temperature inverted haloclines provide winter warm-water refugia for manatees in southwest Florida. Estuaries and Coasts 34:106–119.

Swain, E. D., and J. D. Decker. 2009. Development, testing, and application of a coupled hydrodynamic surface-water/ground-water model (FTLOADDS) with heat and salinity transport in the Ten Thousand Islands/Picayune Strand restoration project area, Florida. U.S. Geological Survey Scientific Investigations Report 2009-5146, Reston, Virginia, USA.

Tanner, M. A. 1996. Tools for the statistical inference: Methods for the exploration of posterior distributions and likelihood functions. Third edition. Springer-Verlag, New York, New York, USA.

U.S. Army Corps of Engineers and South Florida Water Management District. 2004. Comprehensive Everglades Restoration Plan, Picayune Strand Restoration (formerly Southern Golden Gate Estates Ecosystem Restoration). Final integrated project implementation report and environmental impact statement. http://www.evergladesplan.org/pm/projects/docs_30_sgge_pir_final.aspx. Accessed 21 Apr 2009.

U.S. Fish and Wildlife Service. 2006. Strategic habitat conservation: Final report of the National Ecological Assessment Team. U.S. Fish and Wildlife Service, USA. http://www.fws.gov/science/doc/SHC_FinalRpt.pdf. Accessed 30 May 2009.

U.S. Fish and Wildlife Service, 2008. Strategic habitat conservation handbook: A guide to implementing the technical elements of strategic habitat conservation (version 1.0). U.S. Fish and Wildlife Service, USA. http://www.fws.gov/science/doc/SHCTechnicalHandbook.pdf. Accessed 30 May 2009.

Wang, J. D., E. D. Swain, M. A. Wolfert, C. D. Langevin, D. E. James, and P. A. Telis. 2007. Application of FTLOADDS to simulate flow, salinity, and surface-water stage in the southern Everglades, Florida. U.S. Geological Survey Scientific Investigations Report 2007-5010, Reston, Virginia, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

APPENDIX—Computations for Fitting the Model

We fit the model we described using a Bayesian approach to inference. We used modern methods of Bayesian computation (Markov chain Monte Carlo) to compute an arbitrarily large sample from the joint posterior distribution of the model's parameters. In principle, we can use popular software packages, such as WinBUGS (Gilks et al. 1994) to calculate a sample from the joint posterior. In practice, however, WinBUGS cannot produce a sufficiently large sample of the posterior for our data given the memory limitations of current desktop computers. Therefore, we developed and implemented a Gibbs sampling algorithm (Robert and Casella 2004) based on random draws from the full conditional distributions described in the following paragraphs.

The Bayesian approach to inference requires prior distributions to be specified for the model parameters. We generally use a set of mutually independent priors that are proper and place nearly equal probability (or probability density) across the range of parameter values. By specifying prior indifference in the magnitude of any particular parameter value, inferences should be insensitive to the prior. For some parameters our choice of prior implies a conditional posterior distribution that has a familiar form and is easily sampled. For example, we assume a uniform (0,1) prior for ψ_x and its conditional posterior distribution is

$$\psi_x|\cdot \sim \text{Beta}(1 + \sum_{i:x_i=x} w_i, 1 + \sum_i I(x_i = x) - \sum_{i:x_i=x} w_i) \qquad (1)$$

Where $I(\cdot)$ denotes an indicator function which evaluates to 1 for true arguments and to 0 otherwise. We take the summations in Equation 1, and in all subsequent equations, over all nG groups of manatees in the augmented data set.

The conditional posterior distribution of w_i depends on the value of $\boldsymbol{y}_i$. For $\boldsymbol{y}_i = (0,0,0,1)$ (i.e., the ith group of manatees is not detected), the conditional posterior distribution is

$$w_i|\cdot \sim \text{Bernoulli}\left(\frac{\psi_{x_i}(1-p_{iA})(1-p_{iB})}{\psi_{x_i}(1-p_{iA})(1-p_{iB}) + 1-\psi_{x_i}}\right) \qquad (2)$$

For any other value of $\boldsymbol{y}_i$, the ith group is detected and we can show that $w_i = 1$ with probability 1 (proof omitted). Note that the values of $p_{i\mathrm{A}}$ and $p_{i\mathrm{B}}$ used in Equation 2 depend on the value of z_{i1} because

$$p_{i\mathrm{A}} = \frac{1}{[1 + \exp\{-(\alpha_{0A} + \alpha_1 z_{i1})\}]} \qquad (3)$$

$$p_{i\mathrm{B}} = \frac{1}{[1 + \exp\{-(\alpha_{0B} + \alpha_1 z_{i1})\}]} \qquad (4)$$

by definition. However, because the ith group is undetected when $\boldsymbol{y}_i = (0,0,0,1)$, no removal counts are available and z_{i1} is unobserved; therefore, we must compute z_{i1} as part of the Gibbs sample by taking a random draw from its conditional posterior, a Binomial (N_i, p) distribution. In practice, we scale the values of z_{i1} used in Equations 3 and 4 to have zero mean and unit variance using the sample mean and variance of removal counts of observed groups of manatees. This scaling improves estimation and implies that α_{0A} and α_{0B} parameterize the average, logit-scale detection probabilities of the 2 observers, whereas α_1 parameterizes a deviation from these averages.

The conditional posterior distributions of $\alpha_{0\mathrm{A}}$, $\alpha_{0\mathrm{B}}$, and α_1 also depend on z_{i1}, although z_{i1} may be observed (if the *i*th group is detected) or estimated as part of the Gibbs sample (if the *i*th group is not detected). By assuming a uniform (0,1) prior distribution for $\alpha_{0\mathrm{A}}$ and $\alpha_{0\mathrm{B}}$ transformed to the probability scale (i.e., by inverting the logit transformation) we induce a probability density function (pdf) of the form, $\exp(\alpha)/(1 + \exp(\alpha))^2$, for each parameter's prior. This yields conditional posterior distributions of $\alpha_{0\mathrm{A}}$ and $\alpha_{0\mathrm{B}}$ with the following unnormalized pdfs:

$$[\alpha_{0\mathrm{A}}|\cdot] = \frac{\exp(\alpha_{0\mathrm{A}})}{\{1+\exp(\alpha_{0\mathrm{A}})\}^2}\prod_i p_{i\mathrm{A}}^{w_i(y_{i1}+y_{i2})}(1-p_{i\mathrm{A}})^{w_i(y_{i3}+y_{i4})} \tag{5}$$

$$[\alpha_{0\mathrm{B}}|\cdot] = \frac{\exp(\alpha_{0\mathrm{B}})}{\{1+\exp(\alpha_{0\mathrm{B}})\}^2}\prod_i p_{i\mathrm{B}}^{w_i(y_{i1}+y_{i3})}(1-p_{i\mathrm{B}})^{w_i(y_{i2}+y_{i4})} \tag{6}$$

We use a random-walk, Metropolis sampler with Gaussian proposal to update $\alpha_{0\mathrm{A}}$ and $\alpha_{0\mathrm{B}}$ using Equations 5 and 6, respectively, as the target density functions. For the parameter α_1 which denotes the effect of a group's size on its probability of detection, we assume a normal $(0,\sigma^2)$ prior distribution with high variance ($\sigma^2 = 1{,}000$), which yields a conditional posterior with unnormalized pdf:

$$\begin{aligned}[\alpha_{0\mathrm{A}1}|\cdot] &= \sigma^{-1}\exp\left(-\frac{0.5\alpha_1^2}{\sigma^2}\right)\\ &\times\prod_i p_{i\mathrm{A}}^{w_i(y_{i1}+y_{i2})}(1-p_{i\mathrm{A}})^{w_i(y_{i3}+y_{i4})}p_{i\mathrm{B}}^{w_i(y_{i1}+y_{i3})}(1-p_{i\mathrm{B}})^{w_i(y_{i2}+y_{i4})}\end{aligned} \tag{7}$$

We use a random-walk, Metropolis sampler with Gaussian proposal to update α_1 using Equation 7 as the target density function.

We assume a uniform (0,1) prior distribution for p and this yields a conditional posterior distribution that is easy to sample:

$$p|\cdot \sim \mathrm{Beta}\,(1+\sum_{i:J_{i>0}} z_{i\cdot},\ 1+\sum_{i:J_{i>0}} J_i\,(N_i - z_{i\cdot}) - z_{i\cdot} + \sum_{j=1}^{J_i} j z_{ij}) \tag{8}$$

where $z_{i\cdot} = \sum_{j=1}^{J_i} z_{ij}$ denotes the total number of manatees detected in J_i passes (i.e., removals) of the *i*th group of manatees. Note that this distribution depends only on the removal counts and latent abundances of groups of manatees that were actually detected. This dependence also holds for the conditional posterior of λ, but the distribution of this parameter is more difficult to sample. We assume a Gamma (a,b) prior for λ with equal shape and inverse-scale parameters ($a = b = 0.1$), which yields a conditional posterior for λ with unnormalized pdf

$$p(\lambda|\cdot) = \lambda^{\alpha-1+m}\exp\{-\lambda(b+n)\}\{1-\exp(-\lambda)\}^{-n} \tag{9}$$

where $n = \sum_i I(J_i > 0)$ denotes the number of manatee groups in the sample that were actually observed and $m = \sum_{i:J_i>0} N_i$ denotes the total abundance of manatees in these groups. Notice that the right side of Equation 9 resembles the kernel of a Gamma ($a + m$, $b + n$) distribution. Therefore, we use this distribution, which has unnormalized pdf

$$q(\lambda) = \lambda^{\alpha-1+m}\exp\{-\lambda\,(b+n)\} \tag{10}$$

as a candidate for generating independent proposed values of λ. Initially we attempted to compute samples of the conditional posterior of λ using a Metropolis-Hastings algorithm. However, the probability of accepting a proposed value of λ, say λ^*, via Metropolis-Hastings is $[\{1 - \exp(-\lambda)\}/\{1 - \exp(-\lambda^*)\}]^n$. Notice that this acceptance probability tends to 0 as $\lambda \to 0$ or as $n \to \infty$; therefore, the Metropolis-Hastings algorithm is unsuitable for computing draws from the conditional posterior of λ. As an alternative, we used a sampling-importance-resampling (SIR) algorithm (Tanner 1996), which requires more computation than Metropolis-Hastings but yields accurate samples from the conditional posterior of λ. The SIR algorithm proceeds as follows:

1. Randomly draw an arbitrarily large number of proposed values of λ, say $\lambda_1^*, \lambda_2^*, \ldots, \lambda_S^*$, from the Gamma ($a + m$, $b + n$) proposal distribution.
2. Compute an importance ratio $r(\lambda^*) = \frac{p(\lambda^*|\cdot)}{q(\lambda^*)} = \{1-\exp(-\lambda^*)\}^{-n}$ for each proposed value of λ.
3. Compute an importance weight $w(\lambda^*) = r(\lambda^*)/\sum_{s=1}^{S} r(\lambda_S^*)$ for each proposed value of λ.
4. Randomly select 1 value from the set of proposals λ_S^* using their importance weights as sampling probabilities; then assign the selected value as the new value of λ.

The SIR algorithm reliably produces random draws from the conditional posterior distribution of λ.

The conditional posterior distribution of N_i depends on the value of $\boldsymbol{y}_i$. For $\boldsymbol{y}_i = (0,0,0,1)$ (i.e., the *i*th group of manatees is not detected) the conditional posterior distribution of group abundance is a truncated-Poisson distribution with probability mass function $g(N_i\,|\lambda)$ On the other hand, if the *i*th group of manatees is observed in the sample, then the number of manatees that were not detected in J_i passes, say z_{i0}, has a Poisson $(\lambda(1-p)^{J_i})$ distribution, which is easily sampled. A random draw from conditional posterior of N_i is obtained by adding the randomly drawn value of z_{i0} to z_i the total number of manatees detected in the removal sample of the *i*th group.

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