Model Description and Evaluation of the Mark-Recapture Survival Model Used to Parameterize the 2012 Status and Threats Analysis for the Florida Manatee (*Trichechus manatus latirostris*)

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Contents

Abbreviations

Barker RD	Barker Robust Design model
cv	coefficient of variation
CBM	Core Biological Model
CJS	Cormack-Jolly-Seber (model)
FWRI	Fish and Wildlife Research Institute (Florida Fish & Wildlife Conservation Commission)
MIPS	Manatee Individual Photo-identification System
Mote	Mote Marine Laboratory
m-r	mark recapture
RD	robust design closed-population model
TA	Threats Analysis
TRACE	TRAnsparent and Comprehensive model Evaluation
USFWS	U.S. Fish & Wildlife Service
USGS	U.S. Geological Survey

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1 Introduction

This report provides a TRAnsparent and Comprehensive model Evaluation (TRACE; Grimm and others, 2014) of the **mark-recapture**[3] (m-r) **survival estimation model** used to parameterize components of the 2012 status and threats analysis for the Florida manatee (*Trichechus manatus latirostris*). The aim of a TRACE document is to provide researchers and decisionmakers with clear and transparent information about the quality, suitability, and utility of a given model to address a specific management objective. Rykiel (1996) lists two questions critical to model evaluation: (1) does the model realistically mimic the real world and is therefore suitable for its intended purpose; and (2) how much confidence can be placed in inferences about the real world that are based on model results? To answer these questions, the TRACE evaluation is partitioned into eight elements: problem formulation, model description, data evaluation, conceptual model evaluation, implementation verification, model output verification, model analysis, and model output corroboration. Standardized protocols are used for evaluation reports, which allow researchers to (1) communicate to resource managers consistent evaluation information over time; (2) build understanding and expertise on the structure and function of the model; (3) document changes in model structures and applications in response to evolving management objectives, new biological and ecological knowledge, and new statistical advances; and (4) provide greater transparency for management and research review.

Here, we provide supporting details and evidence for the rationale, validity, and efficacy of a new m-r model, the Barker **Robust** Design (Barker RD, Kendall and others, 2013), to estimate regional manatee survival rates and temporal variability necessary to parameterize components of the 2012 version of the manatee **Core Biological Model** (CBM, version 5.03) and Threats Analysis (TA). The CBM and TA provide scientific analyses on population viability of the Florida manatee subspecies for U.S. Fish and Wildlife Service (USFWS) 5-year reviews of

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[1] U.S. Geological Survey.

[2] American Journal Experts, Calle Los Alpes, Quinta Pata-Pata, Prados del Este, Caracas, Miranda, 1080-A, Venezuela.

[3] Terms in bold are defined in the Glossary.

the status of the West Indian manatee species (*Trichechus manatus*) as listed under the Endangered Species Act. Results of the 2012 CBM and TA were published in

Runge, M.C., Langtimm, C.A, Martin, J., and Fonnesbeck, C.J., 2015, Status and threats analysis for the Florida manatee (*Trichechus manatus latirostris*), 2012: U.S. Geological Survey Open-File Report 2015–1083, 23 p. [Also available at http://dx.doi.org/10.3133/ofr20151083.**]**

The scientific basis of the Barker RD model has been thoroughly vetted in peer reviewed scientific journals and applied to manatee m-r **photo-identification** monitoring data. Given the recent development of the model and its first application in an analysis in a management decision context, a review and evaluation of issues specific to its application in the CBM and TA are warranted.

The manatee survival reporting protocols used here were developed from the original TRACE rationales first introduced by

Schmolke A., Thorbek, P., DeAngelis, and D.L., Grimm, V., 2010, Ecological modelling supporting environmental decision making—A strategy for the future: Trends in Ecology and Evolution, v. 25, p. 479–486.

and the updated standard document structure and online templates in

Grimm, V., Augusiak, J., Focks, A., Frank, B., Gabsi, F., Johnston, A.S.A., Kułakowska, K., Liu, C., Martin, B.T., Meli, M., Radchuk, V., Schmolke, A., Thorbek, P., and Railsback, S.F., 2014, Towards better modelling and decision support—Documenting model development, testing, and analysis using TRACE: Ecological Modelling, v. 280, p. 129–139.

and

Augusiak, J., Van den Brink, P.J., and Grimm, V., 2014, Merging validation and evaluation of ecological models to “evaludation”—A review of terminology and a practical approach: Ecological Modelling, v. 280, p. 117–128.

TRACE protocols were designed for the evaluation of ecological projection models. Mark-recapture survival models differ in a number of ways, but most importantly in that they provide retrospective estimation and inference, which then can be used in a wide variety of models to project population dynamics under different management and environmental scenarios. To better document and evaluate applications of survival models in general, and Florida manatee applications specifically, some modifications were made to the original TRACE elements in descriptions and format of intended content. We identify this initial standardized reporting protocol as TRACE–MANATEE SURVIVAL and this evaluation specifically as TRACE–MANATEE SURVIVAL, Barker RD version 1. As survival modeling efforts in support of management decisions increase in complexity and specificity to management objectives, undoubtedly revisions and refinements to these protocols will be necessary, similar to the first TRACE protocols (Schmolke and others, 2010; Grimm and others, 2014).

2 How to Use This Document

Eight evaluation elements are presented in sections 3–10 below: (3) problem formulation within the decisionmaking context, (4) mark-recapture model description, (5) data evaluation, (6) model evaluation, (7) model implementation verification, (8) model output verification, (9) model analysis evaluation, and (10) model output corroboration. Supporting information for each element was derived from peer-reviewed scientific publications of past manatee analyses, classic biometrics papers at the foundation of m-r models, the recent publications outlining development of the Barker RD model, specifics on the implementation of the model in 2012, and assessments of the quality and quantity of the data analyzed and the model output.

At the beginning of each element is a short explanation of the element and what content is provided for evaluation. A short overview follows summarizing the supporting information. Full details and discussion are contained in the body of the element.

The target audience for this document consists of a diverse group of users at varying levels of scientific expertise, including resource managers, researchers, policy makers, stakeholders, and the public. We have attempted to make the material accessible to all users, but there is still considerable technical language and terminology. A glossary of terms is provided at the end of the document. The first use of each term in the text is highlighted in bold. Hyperlinks embedded in the document provide easy navigation from the table of contents to the element headings and Glossary.

3 Problem Formulation Within the Decisionmaking Context

This TRACE element provides supporting information on the decisionmaking context in which the model will be used; a precise specification of the objective of the analysis, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Overview

Adult manatee survival probabilities and female breeding probabilities, estimated from photo-identification data of marked individuals monitored state-wide over the course of decades, provide the empirical foundation for the manatee CBM and TA. The CBM and TA project future growth and population viability under different management and environmental scenarios. Outcomes under the different scenarios are considered by the USFWS as part of their 5-year reviews of the Florida subspecies, which are required under the Endangered Species Act. Population viability analyses in general project future population growth based on empirical estimates of past temporal variation around mean survival rates and breeding rates. Population growth rates are most sensitive to even small changes in adult survival. Therefore, adult survival is the most critical demographic parameter in the CBM, and unbiased and accurate estimates are essential to status assessments. The Barker RD model used to estimate survival for the 2012 analysis corrects for a bias in manatee survival rates identified prior to the first 5-year review in 2007 (Langtimm and others, 2004; Runge and others, 2007b; Langtimm, 2009). The survival parameters required for the CBM take the form of (1) region-specific mean annual survival estimated over the years of available monitoring data, and (2) temporal variance in survival caused by environmental fluctuations. Estimates of mean and variance are

region- and time-specific; extrapolations to other locations and time periods should be considered with caution.

Unbiased and **accurate** estimates of regional survival are required for the manatee CBM and TA (regions are defined later). Previous analyses have demonstrated that population growth rates for large, long-lived vertebrates such as the California condor (*Gymnogyps californianus*) (Mertz, 1971), killer whales (*Orcinus orca*) (Brault and Caswell, 1993), cheetahs (*Acinonyx jubatus*) (Crooks and others, 1998), and the Florida manatee (Runge and others, 2007a, b) are most sensitive to a change in the adult survival rate compared to the same amount of change in calf or subadult survival rates or the female breeding rate.

M-r models were first applied to Florida manatee photo-identification data to estimate adult survival probabilities in the 1990s (O'Shea and Langtimm, 1995; Langtimm and others, 1998). M-r models are highly regarded in the research and management community and have been used to estimate survival probabilities for innumerable animal species (and some plants) when individuals can be monitored by naturally occurring or artificially applied unique marks (Williams and others, 2002). Directly estimating **detection probabilities** of individuals is a hallmark of m-r models and key to estimating survival, because the monitoring of individuals during each sampling period is imperfect. If estimation procedures do not account for individuals that are alive but not detected, survival and other **parameters** can be biased. This **bias** can lead to false interpretations of true survival rates or trends in survival and can adversely influence management decisions. Detection of marked individuals can be affected by multiple factors, including sampling error (that is, observer error, less than ideal survey conditions), and natural processes such as permanent dispersal of individuals to another area, temporary movements making the individual unavailable for detection, or life history strategies in which individuals use spatially separated resources during different monitoring periods. Different types of detection issues are inherent to different populations and biological systems.

Over time, more advanced m-r models have been developed with greater realism to model, estimate, and account for imperfect detection under the various processes just described. The Barker RD model (Kendall and others, 2013) used for the 2012 CBM addressed a detection problem that can bias survival estimates for the most recent years at the end of the monitoring **time series**. This terminal bias was specifically identified with manatees but can be common to many large, long-lived, mobile vertebrates with high annual survival rates (Langtimm, 2009; Bromaghin and others, 2015). More detailed description and discussion of the problem and the solutions are provided in other elements herein.

Adult survival parameters required for the CBM take the form of (1) mean annual survival estimated over the years of available monitoring data, and (2) the variance in annual survival caused by fluctuations in the environment (technical term: "temporal or process variance"). Population viability analyses in general project future survival on the basis of empirical estimates of past temporal variation around the mean survival rate (McGowan and others, 2011). For the 2012 TA, separate estimates of mean annual survival and **temporal variance** were required for the four Florida manatee management regions (Northwest, Southwest, Atlantic Coast, and Upper St. Johns River) modeled in the CBM. The estimates represent variation in survival as a result of all sources of mortality. Additional estimates were required for the Southwest region, where mortality events from toxic red-tide algal blooms occur on a frequent basis. The Southwest component of the CBM projects future impacts of these severe events with random introductions of a major red-tide year into the analysis, in which survival in that year represents red-tide mortality in addition to mortality experienced in non-event years. The range of possible values for the additional effect of red tide is estimated for known event years relative to baseline estimates of survival under nonevent years.

Survival estimates from a sample of known individuals at specific major winter **aggregation sites** in each region are used to infer survival rates for the broader population of adults in the region. The sample of individuals used to estimate adult survival is obtained from manatees cataloged in the **Manatee Individual Photo-identification System (MIPS)**. Each individual can be identified by its unique scar patterns, which are primarily created by collisions with watercraft. Because unscarred individuals are not recognizable and therefore cannot be monitored with photo-identification, they are not represented in the analyses. A question posed is whether survival estimates are biased if they are only estimated from scarred individuals identifiable by marks that can evolve over time; a full discussion of this question is presented in the data evaluation element.

Statistical estimates of survival probabilities are only applicable to adult manatees. Young individuals (calves and subadults) have a low probability of having healed scars that meet the criteria for cataloging in MIPS; thus, data are not sufficient to estimate survival for these age classes. We followed conservative criteria for defining adult status, because we expect differences in mortality risks among calves, subadults, and adults (see O’Shea and Langtimm, 1995, for discussion and definitions of age classes).

Photo-identification data analyzed were collected during specific time periods at specific aggregation sites in each management region and thus under specific environmental conditions. It may not be possible to extrapolate these estimates to new conditions without further justification. A specific case in point is the mortality events from severe cold that occurred during the winters of 2009–10 and 2010–11. Although photographs and monitoring data had been collected during those years, the extensive postprocessing of data required to accurately identify individuals (see data evaluation element) had not yet been completed at the time of the 2012 CBM. Given the large number of dead manatees documented during those events, extrapolation as to their effect on survival is not realistic.

4 Mark-Recapture Model Description

This TRACE element provides supporting information on the model. It provides a detailed model description and justifies the modeling approach and the degree of complexity. Model users should learn what the model is, how it works, and what guided the design or selection of the model for this particular analysis and management question.

Overview

The m-r model used for survival analysis is the Barker RD. Detailed documentation for the model is reported in Kendall and others (2013) and a summary is described in this section. The model uses repeated encounters of known individuals and jointly models three types of data: (1) photo-documented sightings of marked live individuals at the primary monitoring areas during winter, (2) auxiliary resightings of those individuals at any locations and times other than the standard winter monitoring framework, and (3) any identification of individuals from dead recoveries. The model reduces bias in survival estimates at the end of the time series by incorporating additional information on true

survival (dead recoveries or additional sightings of live individuals at times and places outside the winter sampling frame).

Justification of the modeling approach and its complexity. The Barker RD model (Kendall and others, 2013) used for the 2012 CBM addressed a detection problem that can bias survival estimates for the most recent years at the end of the monitoring time series. Langtimm and others (2004) identified a decline in adult manatee survival estimates on the Atlantic Coast that was probably due to a recent series of warmer winters during which manatees were less likely to use the monitored thermal refuges as aggregation sites. Further analyses of both the real data and data simulated specific to known survival and individual movement rates confirmed the decline was an artifact of the modeling effort (Langtimm, 2009). Bias occurred when some individuals did not return the following years to the annually monitored sites. Because survival is high, many individuals eventually can return alive to the monitoring areas and estimates made for the earlier years were shown to be unbiased; however, at the end of the time series, additional information was needed to determine the fate of individuals not seen during the last few periods. After conducting a **simulation study** to compare and contrast the utility of modeling the standard winter monitoring data using several types of additional data (Peñaloza and others, 2014), the Barker RD model offered the best solution and flexibility to address terminal bias for the Florida manatee system.

Description of the conceptual model and the represented processes. The Barker RD model combines robust design capture data (that is, more than one sampling period per **primary sampling period** of interest) collected at focal study sites, with dead recoveries and **auxiliary** live observations that can occur outside these focal sites. With this model, survival and two types of emigration can be estimated: **permanent emigration**, whereby an individual that leaves the study area has zero probability of returning (for example, dispersal); and **temporary emigration**, whereby an individual that leaves the study area has a positive probability of returning (for example, manatees that may not return to a site only used during colder winters). The model design incorporating multiple secondary monitoring periods embedded within each primary monitoring period (winter season in the case of manatees) was first introduced by Pollock (1982) and identified as the robust design, because analyses under a variety of sampling conditions showed that results were resistant (robust) to moderate departures from model **assumptions**. The design has since proved useful in extending m-r models to estimate a wide variety of population parameters, such as temporary emigration (Kendall and others, 1997).

The Barker RD model is an extension of the Lindberg model (Lindberg and others, 2001), which combined the robust design closed population model (RD; Kendall and others, 1997) with information on known dead individuals (Burnham, 1993), and the Barker model (Barker, 1997, Barker and others, 2004), which combined data on known deaths with auxiliary live sightings of marked individuals. The Lindberg model and the Barker model were first developed to model survival and dispersal of annually hunted waterfowl and fish populations.

The Barker RD model jointly analyzes three types of data. For the Florida manatee, those data for the 2012 CBM analysis consisted of (1) live sightings of individuals photographed within the formal winter monitoring design, which is defined by region-specific **primary aggregation sites** *and* a winter primary period that is divided into two **secondary sampling periods**, (2) auxiliary resightings of those individuals identified at other times or places, and (3) dead recoveries of those individuals from any location, at any time. A discussion of the data available under those categories is covered below under data evaluation.

The parameters estimated by the model. The full likelihood for the model and the parameter definitions are presented in Kendall and others (2013). Here, we describe the parameters and summarize how they are estimated.

- *Probability of temporary emigration and probability of* ***availability****.* Nonrandom temporary emigration away from the primary monitoring area is the main source of bias in manatee terminal survival rate estimates. Identifying the fate (technical term: "state") of these individuals (dead, alive and available for detection, temporarily unavailable, or permanently unavailable at a focal study area) is key to estimating true survival (*S*), the primary demographic parameter of interest for the CBM analysis, separate from temporary emigration and dispersal. The model accomplishes this by estimating the complement of temporary emigration, which is the probability of availability for detection at the winter site. Annual availability is estimated for two individual states: one in which individuals available for detection in the study area the previous winter survived to the current winter and remained faithful to the winter site (*a*"); and another in which those individuals away the previous year (and thus unobservable) survived to the current year and remained faithful to the winter site (*a*'). By defining the current year's availability specific to whether an individual was a temporary emigrant or not the previous year, subsequent estimates of dead recovery rates and auxiliary live resighting rates can be used to draw inferences about the fate of individuals not sighted in the last primary periods. The probability of temporary emigration is then estimated as a transition from one year to the next from an observable state at the aggregation site to an unobservable state away from the site.
- *Detection probabilities.* The ability to estimate the probability that an individual is at the primary monitoring area and thus available for detection is predicated upon the ability to estimate resighting probabilities of individuals from the two secondary periods within each annual primary winter period (*p*). Probability of dead recovery (*r*) and probability of auxiliary live resighting of an individual (*R*, given it survived to the next period; and *R'*, given it dies before the next period and is not recovered) are estimated between primary periods.
- ***Fidelity*** *to the primary study site and its complement, permanent emigration.* Permanent emigration, defined here as ceasing to use the focal winter monitoring sites, with zero chance of returning, would negatively bias survival estimates throughout the time series if unaccounted for in the model. We don't believe this phenomenon is likely for manatees. The Florida manatee is a nearshore species that forages in shallow waters that support their primary food source—submerged aquatic vegetation. They rarely cross deep waters, preferring to follow coastlines and natural features, and are limited in distribution by accessibility to warm water during cold weather. However, the collection of **ancillary data** on sightings of manatees at other sites during the winter and during other times of the year, in addition to dead recoveries, provides the direct information on survival needed to mitigate bias that would be induced by permanent emigration.

5 Data Evaluation

This TRACE element provides supporting information on the quality and sources of monitoring data analyzed, the criteria and rationale for selecting data for estimation, and an assessment of the validity of the sample to infer estimates for the larger regional population and to compare populations. This evaluation will allow model users to assess the scope and the uncertainty of the model output as it relates to monitoring processes, post-sampling data processing, data selection, and sound statistical inference from the sample to the region.

Overview

We analyzed long-term data on individual manatees uniquely marked and identifiable by scars acquired in the wild and "captured" by photographs during annual monitoring at winter aggregation sites. Such data can be subject to misidentification and error, but data processing procedures, described below, effectively minimize errors. We provide a full discussion regarding possible bias in estimates, given that the sample population for inference consists of individuals primarily marked by healed injuries. The number of years of data available for analysis varied among regions and did not include years of the most recent mortality events of unknown cause in the Indian River Lagoon in northeastern Florida or years of severe cold throughout Florida.

Data processing protocols and quality. Data for these analyses were accessed from the MIPS, a database established in 1978 and maintained since 1995 as a cooperative partnership with U.S. Geological Survey (USGS) **Sirenia Project**, Florida's Fish and Wildlife Research Institute (FWRI), and Mote Marine Laboratory (Mote). Since the last manatee 5-year review in 2007, the database managers at USGS, FWRI, and Mote have completed a major overhaul of MIPS, which has resulted in common protocols for collecting and processing data and storing data in a common database. Since 2004, digital cameras have been used to photo-document individual sightings; legacy images prior to that time have been digitized, increasing efficiency and accuracy in data processing and matching photographs to cataloged MIPS individuals. These data collection and processing improvements ensure data are comparable among geographic regions.

Individuals in MIPS are identified by healed scars, mutilations, or deformities, typically the result of one or more boat strikes, but also by distinct characteristics remaining from healed lesions caused by cold damage, injuries caused by entanglements, or other causes. Protocols and procedures to process field data for entry into MIPS were designed to minimize misidentification and ensure data quality and consistency for analyses. A requirement for inclusion of an individual manatee into MIPS is complete photographic documentation of the trunk and tail, detailing healed features that are unique enough to be recognized upon subsequent resighting, whether that be in the general area of its first capture or an unusual dispersal, such as to Cuba (Alvarez-Aleman and others, 2010) or Chesapeake Bay, Maryland (Beck and others, 2011). Each resighting of a photographically documented individual is verified by at least two experienced observers, and data for each sighting are proofed prior to entry into MIPS.

The features used for identification may be present in multiple areas on the manatee. Each healed, permanent feature is coded specifically by type (scar, mutilation, and so forth), by location on the manatee (region: flipper, head, trunk, or tail; position: right, left, or dorsal), and described subjectively by size (small, medium, or large), and precisely by number (1, 2-3, or 4 or more), color (gray or white), and shape (blotch or line). The resulting explicit feature code may be common to multiple manatees, but having multiple identical codes assigned to multiple manatees is a rare occurrence. Although multiple features may have the same feature code, the feature itself has a unique outline or shape that will distinguish it from others upon scrutiny of the photographs. Up to five feature codes may be entered into a query of the MIPS user interface to generate a list of potential candidates. A wildcard option may be entered for any character(s) in the code, and results may be further censored by sex, region, or specific area. A long list of potential identifications may thus be reduced to a shorter list for evaluation and ultimate determination of a match.

It is not uncommon for manatees to acquire one or more new features during their sighting history. New features in a previously unmarked area on the manatee add useful information for subsequent identification. However, new features also may obscure or change the appearance of an existing feature, which can make re-identification problematic and could result in missing a match to a known individual or misidentification of the individual as another manatee. Nonetheless, we believe errors are minimal because nearly all manatees have multiple features useful for identification on different areas of the body. Analysis of the database in 2012 showed that most individuals have at least five features to aid in identification (range 1-21, mean 6.9, mode 5). Annual resighting rates are high, allowing acquisition of new marks to be documented and coded quickly to assist with subsequent identification, and independent verification of all matches by two staff members is required before data are accepted in MIPS.

Inferring survival probabilities from a sample population of scarred manatees: possible bias. Given that MIPS consists of individuals primarily marked by permanent scars from multiple watercraft encounters, there is the question of whether the estimates are representative of the larger population containing both scarred and unscarred adults. The effects of an individual’s past collisions with boats on future mortality are unknown. Four scenarios are possible: (1) there is no difference between scarred and unscarred individuals with regard to future mortality risk and survival estimates are unbiased; (2) scarred individuals recover with chronic or debilitating sublethal conditions that reduce future survival, and thus estimates are negatively biased relative to survival probabilities in the larger population; (3) scarred individuals display behavior that reduces the probability of future watercraft encounters, and therefore estimates are positively biased; or (4) scarred individuals have survived past injuries because they are the stronger individuals in the population (weaker animals die) and better able to survive future threats; therefore, estimates are positively biased. At this point in time, we cannot resolve this question. Nonetheless, scarred individuals composed a significant fraction of the population in each region, so the magnitude of the bias, if it exists, cannot be large.

Data availability for the 2012 CBM. The number of years of data available for analysis varied among regions on the basis of when consistent monitoring began. For the 2012 CBM, the backlog of photographs remaining for processing was reduced but not eliminated. Post-processed field data encompassing the winters of 2009–10 and 2010–11, when a large number of manatees died from severe cold, were not available for analysis. Data availability was as follows:

Northwest (NW):	1982–83 through 2008–09
Southwest (SW):	1995–96 through 2008–09
Atlantic Coast (AC):	1982–83 through 2008–09
Upper St. Johns River (USJR):	1985–86 through 2008–09

The formal winter monitoring design targeted the primary winter aggregation sites within each region that were historically monitored and the focus of past survival analyses (Langtimm and others, 1998; Langtimm and others, 2004; Runge and others, 2007b). **Secondary sites** that do not provide warm water during the coldest days and were not systematically monitored in the past were excluded from the **winter sampling frame**. However photo-documented sightings at secondary sites were available for use as auxiliary observations described below. As in past analyses, the primary time period for winter monitoring spanned 90 days during the coldest part of the year when manatees seek warm water and are most easily photographed. The 90-day period yielded an adequate sample of individuals for analysis and excluded early and late transients that show strong fidelity over years to other refuge sites. The primary period was region-specific and based on evaluations of available data from previously published survival analyses (Langtimm and others, 2004). The start of the monitoring period varied by region, because of temporal differences in the arrival of the first cold fronts that draw manatees to the primary winter monitoring sites.

Auxiliary data consist of all resightings of those individuals identified at the major winter monitoring sites at any locations and times outside of the formal winter monitoring design. These resightings can be opportunistic, incidental sightings made at any time or place and submitted to MIPS by partners, the public, and colleagues; or targeted sightings based on the monitoring plans of MIPS partners. Targeted sightings include (1) sightings at the primary aggregation sites before or after the winter primary period, mostly when cold fronts draw individuals to the **refugia**, (2) sightings at secondary sites photographed if time is available during winter after the primary sites have been covered, and (3) sightings at secondary “shoulder” areas where manatees stage seasonally to move between winter and summer habitat (identified by telemetry, aerial surveys, and past photo-identification experience).

Photographs of dead manatees recovered in Florida were provided by the FWRI Carcass Recovery Program. Photographs of dead individuals outside of Florida were provided by the USFWS and members of the marine mammal stranding network. Carcass images were reviewed for a match to a MIPS ID in the same manner as images of live sightings. Features on badly decomposed carcasses, even if visible, often precluded identification because of loss of color or shape.

6 Model Evaluation

This TRACE element provides supporting information on the simplifying assumptions underlying a model’s design, both with regard to empirical knowledge and general, basic principles. It includes explanations relating how the various parts of the model mimic known features of the target biological system, and it evaluates model assumptions and criteria for censoring data to meet assumptions. This critical evaluation allows model users to understand that model design was not *ad hoc* but based on carefully scrutinized considerations.

Overview

The Barker RD is built on proven and widely used m-r models. It provides greater realism and more accurate and precise estimates of survival for Florida manatees than models used in past analyses. The structure allows for the use of all available data, not just those collected during the standard winter monitoring design. Analysis of real data (Kendall and others, 2013) and a simulation study (Peñaloza and others, 2014) demonstrated the ability of the new model to reduce bias in survival estimates at the end of the time series.

The Barker RD model provides greater realism and more accurate and precise estimates than past efforts with other models. Estimates using the Cormack-Jolly-Seber (CJS) model are interpreted as apparent survival, because true survival and temporary or permanent emigration cannot be separated. The RD closed population model can directly estimate true survival separate from temporary emigration with the exception of the last time period. To estimate the last survival rate, the last emigration probability, which is not estimable, must be constrained to equal an estimable emigration probability (Kendall and others, 1997). Langtimm (2009) showed that for manatees with high annual survival and relatively high probability of nonrandom temporary emigration, an inappropriate constraint can produce sufficient bias to warrant ignoring the most recent survival estimates when making management decisions. The Barker RD can separately estimate true survival, temporary emigration, and permanent dispersal because of the use of resightings made at times and locations outside of the winter sampling frame.

As previously described, the Barker RD is built on proven and widely used existing models (Barker, 1997; Kendall and others, 1997; Lindberg and others, 2001; Barker and others, 2004). The model integrates the salient features of the underlying models to provide greater realism specific to manatees but is also applicable to other species. Kendall and others (2013) demonstrated the utility of the new model by comparing analyses of the same set of manatee encounter histories under models that considered only robust design data (RD model), robust design combined with dead recoveries (Lindberg model), and robust design combined with dead recoveries and auxiliary resightings (Barker RD model). Additional supporting evidence was provided by Peñaloza and others (2014) in analyses of simulated data generated under known values of survival, temporary emigration, and detection probabilities that compared the utility of joint analyses of several types of ancillary data to reduce terminal bias. This simulation study is discussed in more detail under the model analysis evaluation element.

The value of available manatee auxiliary data for the Barker RD model. Although manatee photo-identification monitoring was not originally designed for the Barker RD model, data were available for auxiliary resightings. The original objective of the monitoring program was to provide individual histories to understand individual movement patterns and to characterize population traits of reproduction (gestation period, interbirth interval, litter size, fecundity, and crude birth rate) and return rates of individuals as an index of annual survival (O’Shea and Hartley, 1995; Rathbun and others, 1995; Reid and others, 1995). As a matter of practicality, field photographers focused regular monitoring on the coldest days at the largest aggregations when manatees were most easily photographed. Additional sites were soon targeted for opportunistic monitoring as aerial surveys and telemetry studies identified other areas that manatees frequented during warmer winter days and (or) where manatees staged in smaller groups before moving between summer and winter ranges (Deutsch and others, 2003). These auxiliary data are useful for determining the fate of individuals undetected at the primary sites and are easily collected compared to other species that disperse more widely or migrate long distances such as sea turtles or waterfowl (Peñaloza and others, 2014). Additional opportunistic photos of manatees taken by the public or local management and research groups in and outside of Florida provide additional information.

Evaluation of model assumptions. The underlying assumptions of the model are similar to those of the models from which it was derived (Kendall and others, 2013):

- The population available for capture within a primary period is demographically closed during the primary period (no births, deaths, emigration, or immigration). To best meet this assumption, we restricted the primary winter period to 90 days during the coldest part of the year, which allowed an adequate sample to be collected before reproduction began in the spring and ensured that transients moving to their preferred warm-water refuges had already moved through the area. Some deaths do occur during the primary period;

however, Kendall (1999) demonstrated that closed RD is robust to violations of this assumption.

- Within each group (region), state (available or unavailable), mixture, or detection status (previously detected within a primary period or not), each individual has the same probability of detection and state transition. To meet this assumption, we carefully developed criteria for structuring encounter histories. For example, by restricting the analyses to adults that only frequented the largest consistently monitored aggregation sites, we expected detection to be similar among individuals, as opposed to including adults at secondary sites that are only subject to opportunistic monitoring. Restricting the primary time period to the coldest days of the year ensured that transient individuals (having a low probability of returning the following year compared to winter residents) would be few.
- Identifying marks are retained, recorded correctly, and do not affect survival or behavior. Protocols for data collection and post processing minimize errors and ensure individuals are still identifiable, even after acquiring new scars. Because manatee identification data are "captured" as a digital image, individuals are not physically handled and data collection does not disrupt manatee behavior.

7 Model Implementation Verification

This TRACE element provides supporting information on (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, and so forth) and to facilitate future installation, modification, and maintenance.

Overview

Model structure and statistical likelihoods for the Barker RD were officially published by Kendall and others (2013) after the completion of the 2012 CBM and TA analyses. The model, however, had already been coded and implemented in Program MARK (White and Burnham, 1999), the most comprehensive and widely used software application currently available to analyze m-r data. Estimates for the 2012 survival analyses were conducted using MARK. Program code was thoroughly tested and minor problems reported by coauthors and users were corrected and are documented on the MARK Web page (http://warnercnr.colostate.edu/~gwhite/mark/mark.htm**). The entire history of changes to MARK since 1998 is available on the Web page (includes development of the Robust Design, Lindberg, and Barker models). MARK is widely used, and continued maintenance and incorporation of new statistical and research approaches and models are supported by several institutions and numerous researchers. The MARK Web page also includes downloading and installation instructions for the free software, program documentation, recent changes, and reported known problems. A constantly evolving online user's guide, Program MARK: A Gentle Introduction (**http://www.phidot.org/software/mark/docs/book/**), and the online analysis forum, Phi-dot (**http://www.phidot.org/forum/index.php**), provide technical, theoretical, and user support on the MARK user interface, core analytical functions, and specific models and applications. Estimates of mean survival and temporal variance were calculated according to the method**

of Burnham and others (1987), as model output from the variance components estimator in MARK. The program allows the user to specify the range of estimates for output or include a covariate for specific event years to estimate added or reduced mortality during those events. For the Southwest region, we used the covariate option to estimate the additional effect in major red-tide years.

8 Model Output Verification

This TRACE element provides supporting information on how well model output matches observations.

Overview

Model output matched several observations of severe mortality events and known behavior.

Although the Barker RD can estimate permanent emigration to new areas outside of Florida, true dispersal for manatees is rare (see discussion under model description element). Therefore, Kendall and others (2013) expected and confirmed that a candidate model that precluded permanent emigration (F=1.0) would be the best supported model based on model selection criteria.

Years of lower survival rates were observed during years having known major red-tide mortality events. Additional years of photo-identification data added since the 2012 CBM and subsequently analyzed showed the expected result that uncertainty in the annual estimates decreased in magnitude with additional years of data.

Comparisons among regions showed the expected survival differences based on differences in known risk among regions.

9 Model Analysis Evaluation

This TRACE element provides supporting information on (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Overview

The relative contribution of dead recoveries and auxiliary live observations to reduce terminal bias in manatee survival estimates has been evaluated using real data (Kendall and others, 2013) and simulated data (Peñaloza and others, 2014). Both analyses showed auxiliary resightings reduced bias the most. Surprisingly, dead recoveries were least effective, essentially because of the small number of individuals that die within populations having high survival rates such as those of Florida manatees. Nonetheless, increased precision in estimates was realized when either data type was included in the analysis. The simulation study showed that models using RD and auxiliary resightings reduce but do not necessarily eliminate terminal bias, particularly for the very last estimate. Simulations with higher auxiliary resighting probabilities showed less absolute bias and higher precision. Research and evaluation of the quality and quantity of the real data available for auxiliary resightings have not yet been conducted and will be required to

understand and evaluate any remaining terminal bias in the regional survival rates. Nonetheless, the published studies demonstrate that with additional years of monitoring data, those terminal survival estimates change and stabilize, and the estimates become more precise as the fate of additional undetected individuals in those years is determined.

Analysis of real data. Kendall and others (2013) compared annual survival estimates and coefficients of variation (cv) in survival and availability under models that considered (1) only robust design data (RD model), (2) robust design data combined with dead recoveries (Lindberg model), and (3) robust design data combined with dead recoveries and auxiliary resightings (Barker RD model) for a 20-year manatee dataset and the same dataset truncated at 9 years. Declines in annual survival in later years were most pronounced in the RD only and the Lindberg model as compared to the Barker RD model. With respect to **precision**, the cv for survival was typically lowest for the Barker RD model and highest for the RD model.

Analysis of simulated data. The simulation study by Peñaloza and others (2014) generated individual encounter histories under population values for survival, temporary emigration, and detection probabilities specified to mimic conditions previously identified by Langtimm (2009) as creating pronounced terminal bias in manatee survival estimates. They then evaluated the performance of various estimation models that jointly analyzed the encounter history robust design data and one additional source of ancillary data. Additional data types included dead recoveries, auxiliary resightings, telemetry locations of a small sample of individuals (providing information on movements away from the monitoring site), or covariates indicative of the magnitude of temporary emigration (that is, winter temperature). The ancillary data were simulated using several different levels of detection, or predictive environmental covariates, to explore the magnitude of improvements in bias and precision with increasing information.

Although dead recoveries provided direct information on survival, the effect on bias was minimal, even if all dead individuals were recovered. With high survival probabilities, few individuals died, providing little information on the fate of individuals. Auxiliary observations of live individuals also provided direct information on survival, but constituted a potentially larger source of information. Unlike recoveries, live individuals can be observed during all future occasions, whereas the identification of a carcass can occur only once at death (Kendall and others, 2013). Simulations with higher auxiliary resighting probabilities showed less absolute bias and higher precision.

The results of all three studies (Langtimm, 2009; Kendall and others, 2013; Peñaloza and others, 2014) showed that models using robust design and auxiliary resightings reduce bias the most. Simulations with higher auxiliary resighting probabilities showed less absolute bias and higher precision. Furthermore, the separate or combined use of auxiliary resighting data and carcass data improved the precision of the survival estimates and other estimates such as temporary emigration and detection probabilities. It is important to note that these data did not necessarily eliminate terminal bias, particularly for the very last estimate, but with additional years of monitoring data, those terminal survival estimates changed and stabilized. The estimates became more precise as the fate of additional undetected individuals in previous years was determined. For the 2012 CBM, we felt some bias still was possible, and we excluded the last estimable survival rate when calculating region-specific mean and temporal variance. Research and evaluation of the quality and quantity of the real data available for auxiliary resightings have not yet been conducted and will be required to understand and evaluate any remaining terminal bias in the regional survival rates.

10 Model Output Corroboration

This TRACE element provides supporting information on how model outputs compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence that, in addition to model output verification, indicates the model is structurally realistic and provides results that can be trusted to some degree.

Overview

The mean survival rates estimated for each region for incorporation into the 2012 CBM and TA are presented below in table 1, as published in Runge and others (2015). The estimates were higher than those estimated in previous studies using other m-r models based on fewer years of data (Langtimm and others, 2004; Runge and others, 2007b), but there was no evidence of a positive trend in survival rates between the last analysis in 2007 and the one in 2012. The higher mean survival estimated for the 2012 analysis is the result of implementing the new Barker RD model, which directly estimates and accounts for annual variation in manatee use of warm-water sites that bias survival estimates. We now have a more realistic survival model that accounts for important movement processes that affects our ability to monitor manatees. Higher estimates caused by the implementation of new models that address bias have been documented in other studies (Lebreton, 2006). High adult survival estimates are not unusual for other long-lived vertebrates, as reported for several studies by population biologists using quantitative techniques.

Table 1. Florida manatee mean adult survival rates by region.

[From Runge and others (2015). In all cases, data were analyzed through the winter of 2008–09, but 1–2 annual estimates at the end of the timeseries were dropped, owing to concerns about bias. Note that the estimate for the Southwest is for years in which there was not a major red-tide event. SE, standard error]

Region	Mean	SE	Years	Source
Atlantic	0.967	0.004	1983–2007	Langtimm and others, this analysis
Upper St. Johns	0.975	0.004	1986–2006	Langtimm and others, this analysis
Northwest	0.977	0.003	1983–2007	Langtimm and others, this analysis
Southwest	0.971	0.004	1996–2007	Langtimm and others, this analysis

Eberhardt (2002) and Gaillard and others (1998, 2003) reviewed published literature for studies estimating adult female survival rates from m-r data for long-lived vertebrates. The estimates they reported for a diverse group of mammalian species showed the higher survival estimates obtained through this analysis are within the range of those found for large long-lived vertebrates where m-r data have been analyzed.

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Glossary

accurate The extent to which a measurement or estimate approaches the true value.

aggregation sites See **refugia**, below.

ancillary data Data types considered in analyses in addition to those collected under standard or specified monitoring protocols; for example, dead recovery data, telemetry data, and capture data.

availability The probability that an individual is in the study area and available for detection during the primary monitoring period.

assumption A simplified representation or description of a system or complex entity, especially one designed to facilitate calculations and predictions (see statistical model).

auxiliary sightings Live sightings obtained outside of the primary winter monitoring period either at secondary sites or during a nonwinter period.

bias A systematic difference between a measured or estimated value and the true value.

Core Biological Model (CBM) A population model for the Florida manatee developed to project population status over 50 to 150 years and to examine the potential impact of different threat scenarios.

detection probability In mark-recapture **statistical models** (see below), the probability that an animal will be detected (that is, captured, sighted, or resighted) during the study period.

fidelity The tendency of some species or individuals to annually return to the same site or range, usually at the end of a seasonal **migration** (see below); also known as philopatry.

mark-recapture A class of statistical models and related studies based on the estimation of life history parameters from multiple re-encounters of marked individually recognizable animals.

migration A periodic, relatively long-distance movement of animals, usually on an annual or seasonal basis, triggered by a variety of environmental and (or) endogenous factors.

Manatee Individual Photo-identification System (MIPS) A computerized database of manatee life history records and images providing sighting histories used for manatee population and survival modeling.

parameter A population characteristic, usually unknown, that is estimated in a statistical model with a precision indicated by the standard error and related confidence interval.

permanent emigration or dispersal A term used in population biology studies where an individual that leaves the study area has a zero probability of returning.

photo-identification The identification of individual animals based on photographs showing distinctive external markings or characteristics.

precision The extent to which repeated measurements or estimates of a value produce similar results.

primary sampling period A region-specific time period of 90 consecutive days during the coldest time of year when manatees are most easily photographed at warm-water refugia.

primary monitoring site A major warm-water aggregation site where manatees have historically been monitored during cold winter periods.

Program MARK A software application for estimating population parameters in a wide variety of mark-recapture statistical models, using individual encounter histories as the basic input.

refugia Natural or artificial warm-water areas where manatees consistently aggregate during cold winter periods.

robust Statistical methods that produce valid results under a variety of sampling conditions by being resistant to outliers and moderate departures from model assumptions.

secondary sampling periods Consecutive 45-day subdivisions of a primary winter sampling period during which targeted primary sites should be monitored at least once.

secondary site Any locality outside of the primary winter aggregation sites that is monitored for auxiliary sightings throughout the year, usually at a reduced level of effort.

shoulder area A secondary site where manatees temporarily gather prior to migrating between summer and winter ranges.

simulation study The use of computer-generated samples based on predetermined parameter values to evaluate the behavior and robustness of statistical models under varying sampling scenarios.

Sirenia Project The research project (1978-present) established by U.S. Fish & Wildlife Service to support management of manatees and dugongs (scientific classification: Order Sirenia) after Congress authorized and listed sirenians under the Endangered Species Act and the Marine Mammal Protection Act. The Sirenia Project became part of the U.S. Geological Survey, the research arm of the Department of Interior, after a major reorganization of the Department in 1996.

statistical model A mathematical equation describing the relationship between two or more variables with parameters that can be used for hypothesis testing and predicting future events. Most statistical models are based on underlying assumptions that must be met for resulting inferences to be valid, with robust models less sensitive to violations (see **robust**, above).

survival estimation model A statistical model used for estimating survival in a population over time and evaluating the relative importance of factors affecting survival.

temporary emigration A term used in population biology studies where an individual that leaves the study area has a positive probability of returning (for example, manatees, which may not use the site during warmer winters or female sea turtles, which return to monitored nesting beaches after several years when in breeding condition).

time series Data collected through repeated observations of the same individuals and (or) study sites over a period of time.

temporal variance An estimate of the variation in annual survival rates (after removing variance caused by sampling error), owing to fluctuations in the environment.

unbiased See **bias**, above.

winter sampling frame A temporal and spatial term corresponding to a primary winter sampling period at primary aggregation sites.