Evaluating Methods for Estimating Delaware Bay *Limulus polyphemus* Abundance

by

Emily Margaret Merritt

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Approved by

Conor McGowan, Chair, U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit Assistant Leader and Assistant Research Professor of Wildlife Sciences
David Smith, Biological Statistician, U.S. Geological Survey
Matthew Catalano, Assistant Professor of Fisheries, Auburn University

Abstract

Monitoring is an essential component of wildlife management. In the United States, Atlantic horseshoe crabs (*Limulus polyphemus*) are harvested and relied upon by several user groups in mid-Atlantic states, and managers have used offshore trawl surveys to monitor the species. However, this monitoring method is expensive and has an uncertain future in management efforts. Utilization and analysis of volunteer-collected, mark-recapture data may serve as a more feasible monitoring alternative. Our objectives were to evaluate the utility of a hierarchical, state-space modeling approach within a Bayesian framework for estimating the Delaware Bay spawning population using 2003 and 2004 volunteer-collected data. We compared our model's analysis of those data to trawl survey data analyses of those years. We also evaluated the effects of increasing tagging and recapture effort on our model's estimates. Our estimates were comparable to those of past trawl surveys, and our approach may be a viable monitoring alternative.

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Introduction and Justification

HORSESHOE CRAB INTRODUCTION

Biology

Horseshoe crabs are ancient, benthic marine arthropods that have remained physiologically unchanged for over 200 million years (ASMFC 1998, Walls et al. 2002). Despite their common name, they are more closely related to spiders (*Chelicerata spp.*) than other marine arthropods, and are the closest living relatives of the now extinct trilobite class of marine arthropods (Shuster 1982, ASMFC 1998). They are ecological and behavioral generalists that tolerate fluctuating environmental conditions (Walls et al. 2002). Four species of horseshoe crab are found in two regions of the world, but the Atlantic horseshoe crab (*Limulus polyphemus*) – our species of focus – is found along the Atlantic Coast of North America from Maine to the Yucatan Peninsula (Shuster 1982). It is most abundant from Virginia to New Jersey, but the data used for this thesis were collected on the Delaware Bay population of *L. polyphemus* (hereafter horseshoe crab).

Horseshoe crabs of both sexes have a hard, dome-shaped carapace, and males are generally smaller than females (Botton and Ropes 1988, as cited in Walls et al. 2002). Both sexes can live up to 17 to 19 years, and reach sexual maturity and full size in 9 to 11 years, although males mature faster than females (Shuster 1950, as cited in ASMFC 1998; Botton and Ropes 1988, as cited in Walls et al. 2002; Smith et al. 2009).

A 2003 mark-recapture estimate reported that there were approximately 13,730,000 (8,780,000 – 19,400,000; 90% CI) adult males and 7,350,000 (4,520,000 – 10,160,000; 90% CI) adult females in the Delaware Bay spawning horseshoe crab population (Smith et al. 2006). Another analysis using trawl survey data collected after the spawning season near the mouth of the Delaware Bay in the Atlantic Ocean estimated that there were 6,530,000 (3,340,000 – 9,730,000; 95% CI) adult males and 3,030,000 (1,560,000 – 4,490,000; 95% CI) adult females in the population in 2003(D. Hata and E. Hallerman, Virginia Polytechnic Institute and State University, unpublished data). Additionally, that analysis estimated that there were 5,690,000 (2,220,000 – 9,150,000; 95% CI) adult males and 2,560,000 (1,360,000 – 3,750,000; 95% CI) adult females in 2004. However, all of these estimates and their wide credible intervals may have been biased by their methods of data collection and analysis (McGowan et al. 2009). The Delaware Bay sex ratio of adult males to females is male-skewed at 2.2:1 (M:F; Smith et al. 2006). This difference between males and females could be due to the quicker maturation rate of males or higher fishing and natural mortality of females (Smith et al. 2009).

Each spring, millions of adult horseshoe crabs migrate from the deep waters of Delaware Bay and the continental shelf to spawn on beaches, and then return to deep waters after the spawning season to overwinter (Shuster and Botton 1985, Anderson and Shuster 2003). Horseshoe crabs prefer sandy estuarine beaches, such as those on Delaware Bay, for spawning due to their low wave energy environments that reduce risk of stranding for adults, optimal thermal, salinity, and oxygen content conditions for egg development, and abundance of food resources for hatchlings (Anderson and Shuster 2003).

In the mid-Atlantic region horseshoe crabs begin spawning in April or May when water temperatures are consistently above 15º C (Smith and Michels 2006). Intensity of spawning activity is correlated with lunar phase and weather events. Barlow et al. (1986) observed that peak spawning activity commonly takes place during the highest high tides of new and full moons (spring tides) in May and June. Smith et al. (2010) showed that 55% of spawning activity took place during the three days around each spring tide. However, many horseshoe crabs spawn for several days in succession throughout the lunar cycle during high tides, typically returning to the same beach or others close by (Botton 1982, as cited in Shuster and Botton 1985; Swan 2005; Smith et al. 2010). No spawning occurs during low tides (Barlow et al. 1986). Inter-annually, horseshoe crabs exhibit little site fidelity to spawning beaches, and may migrate between estuarine beaches within the region (King et al. 2005, Swan 2005, Smith et al. 2010). Heavy weather activity with waves greater than 0.3 m can negatively affect spawning by disturbing spawning sites, washing animals off the beach, breaking up spawning pairs, and preventing individuals from coming on to the beach (Shuster 1982, Smith et al. 2002).

As female horseshoe crabs migrate to spawning beaches, males use visual and chemical cues to find and clasp on to females (called amplexus; Botton and Loveland 1989, Hassler and Brockmann 2001). Unattached males come to spawning beaches as well, looking for females and to crowd around mating pairs in “satellite” groups (Brockmann and Penn 1992, Penn and Brockmann 1994). Males spawn more often than females, which creates a male-biased operational sex ratio — much greater than the 2.2:1 population sex ratio — and promotes male-male mating competition (Brockmann 1990, ASMFC 2009, Smith et al. 2010). Females dig nests approximately 15 cm (±3.5 SD) deep in moist sand where they deposit clusters of eggs (Weber and Carter 2009). Each female lays approximately 22 egg clusters per season, with an average of approximately 5,786 (±2,834) eggs per cluster (Shuster and Botton 1985, Weber and Carter 2009). They spawn for 3 to 4 tides, laying approximately 88,000 eggs annually (Shuster 1982, Shuster and Botton 1985). Attached and unattached males release free-swimming sperm into the water to fertilize the eggs (Brockmann 1990). Waves and the burrowing action of other nesting females brings many eggs to the surface (Nordstrom et al. 2006, Smith et al. 2009). These eggs would not survive if left exposed, but shorebirds take advantage and consume large quantities of them (Botton et al. 1994). Eggs that remain buried develop successfully in environments with appropriate conditions (Shuster 1982).

Ecological and Economic Value

During the horseshoe crab spawning season, hundreds of thousands of migratory shorebirds spend approximately two weeks from mid-May to early-June in the Delaware Bay region (Myers 1986, Clark et al. 1993, ASMFC 1998). At least 11 different species of migratory shorebirds gather there to exploit the widely abundant, energy-rich horseshoe crab eggs (Myers 1986, Berkson and Shuster 1999). In preparation for the completion of their journey from South American wintering areas to Arctic breeding grounds, the shorebirds regain mass largely from the eggs they consume during their stopover (Shuster 1982, Myers 1986). The shorebirds, including red knot (*Calidris canutus rufa*), ruddy turnstones (*Arenaria interpres*), semipalmated sandpipers (*C. pusilla*), and sanderlings (*C. alba*), will supplement their diet with other food sources as needed (Botton 1984, Myers 1986). It is hypothesized that alternative food resources cannot support the energetic needs of migrating shorebirds, and a very large quantity of eggs are required to ensure their survival (Botton et al. 1994, Niles et al. 2009). However, other research (e.g., McGowan et al. 2011*a*) suggests that changes in arctic breeding ground conditions may have a greater impact on their annual survival. Regardless, the Delaware Bay region and horseshoe crab spawning season are thought to be very important to migratory shorebirds (Myers 1986, ASMFC 1998). Additionally, evidence suggests red knots recently experienced steep population reductions, and as of 2014, the red knot was listed as "threatened" under the U.S. Endangered Species Act (FWS 2014).

Historically, Native Americans used horseshoe crabs for food, as tools, and as fertilizer (Kreamer and Michels 2009). From the mid- to late-1800s, European settlers used millions of horseshoe crabs for fertilizer and to supplement livestock feed, but this practice ended mid-twentieth century after chemical-based fertilizers were developed. In the early 1900s, the horseshoe crab's large, compound eye and simple nervous system were used for research, and in the late 1900s, the use of horseshoe crabs as bait for eel and whelk fisheries dramatically increased (Walls et al. 2002, Kreamer and Michels 2009). Although horseshoe crabs had been harvested for over 100 years, they were considered a "trash fish" not deserving of careful population management until the 1980s (Walls et al. 2002).

Currently, the biomedical industry extracts blood from horseshoe crabs to create Limulus Ameobocyte Lysate (LAL; Hall 1992). LAL is used in testing for bacterial contamination in injectable drugs and intravenous devices. Horseshoe crab blood has inimitable bacterial detection capacity and the application of LAL to medical testing has greatly improved safety. Previously, it was common to test drugs on rabbits, but since its discovery, LAL has substituted test rabbits and its use in tests of pharmaceutical and biomedical products is currently required by the U.S. Food and Drug Administration (Novitsky 1984, Walls et al. 2002, Odell et al. 2005). In the late 1990s, the annual LAL-associated economy generated approximately $60 million and created about 440 to 540 jobs along the Atlantic Coast (Manion et al. 2000).

With a tremendous increase in whelk (*Busycon spp.*) and American eel (*Anguilla rostrada*) demand around 1990, the commercial horseshoe crab fishery increased as well and became centered around mid-Atlantic coastal waters (ASMFC 1998, Berkson and Shuster 1999). The fishery is active today and annually catches hundreds of thousands of male and female horseshoe crabs by trawl, dredge, hand, and gillnet along certain portions of the Atlantic Coast (ASMFC 1998). Eels are attracted to the chemical odors of gravid (egg-laden) females, making them the preferred horseshoe crab by eel pot fishers (Walls et al. 2002). The whelk fishery uses both sexes. Currently, there is no alternative bait for these fisheries as effective as horseshoe crabs. The whelk and eel fisheries annually generated approximately $21 million and created about 340 to 440 jobs for the mid-Atlantic region in the late 1990s (Manion et al. 2000).

In addition to use by shorebirds, the biomedical industry, and commercial fisheries, horseshoe crabs are used for education and simple enjoyment (Walls et al. 2002). Public aquariums and coastal educational centers use them in touch tanks and as the subject of extension and educational programs for students of all ages. Locals and preservationists appreciate their intrinsic value and enjoy observing the horseshoe crabs during spawning. Additionally, thousands of tourists and birders visit Delaware Bay beaches to witness and enjoy the annual horseshoe crab and shorebird spectacle. This ecotourism-related economy greatly contributes to local economies, and in the late 1990s brought in approximately $7 to $10 million and created about 120 to 180 jobs annually (Manion et al. 2000).

Management

In the late 1980s, state and federal fishery resource agencies, conservation organizations, and other fisheries interests on the Atlantic coast began expressing concern over the increasing exploitation of horseshoe crabs and lack of knowledge about their total abundance, but harvest remained largely unregulated (ASMFC 1998). It was not until the late 1990s that a collective effort was made to increase understanding of horseshoe crab population dynamics to manage them effectively. The Atlantic States Marine Fisheries Commission (ASMFC) is made up of the 15 Atlantic Coast states who work together to help manage and conserve shared coastal fishery resources within state and federal waters. In 1998, the Horseshoe Crab Management Board of the ASMFC created the "Interstate Fishery Management Plan for Horseshoe Crab." They proposed a coordinated and consistent effort to "identify management, monitoring, and information needs to ensure the continued role of the horseshoe crab resource in the ecology of coastal ecosystems, while providing the opportunity for commercial, recreational, medical, scientific, and educational use over time" (ASMFC 1998:1). The ASMFC used best scientific information available to inform management actions, and today those actions are still shaped by new information that is provided by scientists of the Horseshoe Crab Technical Committee (ASMFC 1998). Representatives of fishers, the bait packing industry, and conservation organizations form the Horseshoe Crab Advisory Panel, which uses panel member perspectives to inform management actions (Walls et al. 2002). Depending on new information, the Management Board adjusts harvest restrictions and management actions to achieve conservation objectives (ASMFC 1998).

Since its creation, the Plan provided coordinated and consistent monitoring, management, and regulation of horseshoe crabs over the long-term, and caused a stabilization of the population (ASMFC 1998, Smith et al. 2009). However, concerns over struggling shorebird populations persisted and many advocates blamed horseshoe crab harvest. In an attempt to improve management and conservation of horseshoe crabs and migratory shorebirds along the mid-Atlantic coast, the ASMFC commissioned and subsequently adopted an adaptive management framework for horseshoe crabs in 2012 that is limited by red knot conservation objectives (McGowan et al. 2009, ASMFC 2012). Adaptive management is “a structured approach to decision making that emphasizes accountability and explicitness in decision making” and is useful when there is a lot of uncertainty regarding ecosystem functionality (Williams et al. 2007:4).

It is hypothesized that red knot populations are dependent on horseshoe crab eggs and that effective horseshoe crab harvest management and regulation may benefit red knot conservation efforts (McGowan et al. 2011*b*). However, there are alternative hypotheses regarding the causes of red knot decline and the ecological interactions between these two species (McGowan et al. 2009, 2011*a*; Fraser et al. 2013). Adaptive management was applied to the mid-Atlantic Coast horseshoe crab harvest decision process so that harvest policies could be made and alternative management actions could be evaluated considering all competing objectives and ecological uncertainty (i.e., the alternative hypotheses; Williams et al. 2002, 2007; McGowan et al. 2009, 2011*b*). A critical component of an adaptive management program is monitoring the managed system to make annual decisions and learn how the system responds to management actions (i.e., how accurate are model predictions?; Lyons et al. 2008). Standardized studies, such as trawl and spawning surveys, are conducted so that accurate data can be collected and to allow for statistical modeling that links population dynamics between horseshoe crabs and red knots (McGowan et al. 2011*b*). These studies also inform harvest policy and alternative management action decisions. An adaptive management framework can improve understanding of a resource system's function and achieve complicated management objectives for both horseshoe crab and shorebird populations (Williams et al. 2007).

PROJECT JUSTIFICATION

Until the fall of 2013, Delaware Bay horseshoe crab population monitoring data were primarily collected through offshore trawl surveys (Hata and Berkson 2004, McGowan et al. 2009). Those data were supplemented with land-based spawning surveys (spatially and temporally replicated counts on beaches during spawning), and harvest reports (horseshoe crab landings from fishermen; ASMFC 2013). Prior to the late 1990s, trawl and spawning surveys occurred but did not have standardized methodologies or produce sufficient indicators of horseshoe crab population status (ASMFC 1998). Standard horseshoe crab survey procedures have since been developed and improved for both methods, and are now commonplace (Smith et al. 2002, Hata and Berkson 2003). However, there are positives and negatives to trawl and spawning surveys.

The offshore trawl surveys, conducted by Virginia Polytechnic Institute and State University (VPI) between 2002 and 2013, were expensive to operate (at least $250,000 per year; E. Hallerman, VPI, personal communication), and used nets that may have biased capture rates or been inefficient at capturing horseshoe crabs (ASMFC 1998, Walls et al. 2002, Hata and Berkson 2003). However, all ocean-based surveys for horseshoe crabs are subject to imperfect catchability. While these surveys attempt to estimate population abundance through stratified random sampling and spatial extrapolation, there are concerns about temporal variability and effective spatial coverage (Hata and Berkson 2003); results of the trawl survey are often uncertain and have limited utility. Furthermore, funding for trawl surveys was discontinued in 2012 and future funding is highly uncertain (C. P. McGowan, U.S. Geological Survey, personal communication).

Spawning surveys occur on accessible beaches at the height of horseshoe crab spawning, utilize volunteer help, and require less effort than trawl surveys (Smith and Michels 2006). Additionally, the monetary costs associated with this method have never been quantified, but it is assumed that the annual costs of labor and database management would be much less than those required to operate trawl surveys (C. P. McGowan, personal communication). Surveys are limited to only 12 or 15 occasions within a spawning season, and take place during spring tides in May and June to coincide with peak spawning activity (Shuster and Botton 1985). Surveys occur on beaches throughout the Delaware Bay on nighttime high tides 2 days before, the day of, and 2 days after new and full moons (Smith et al. 2002, 2010). Volunteers count all spawning male and female horseshoe crabs within 100 1-m^2 quadrats along a 1 km transect at the hide tide line

(Smith et al. 2002). Because volunteers execute the counts, there is concern about observer error, and surveys are occasionally cancelled when volunteers do not show up or when weather is bad, which causes gaps in the data. Additionally, horseshoe crab distributions vary weekly due to weather events that shift spawning, and annually due to migration between beaches within the region, both of which create sampling error and uncertainty (Berkson and Shuster 1999, Smith et al. 2002, King et al. 2005, Swan 2005, Smith and Michels 2006). Furthermore, the 100-m^2 survey area along 1 km of beach may not capture a representative sample of the spawning population during a survey, especially if abundance is high (Berkson and Shuster 1999, Weber and Carter 2009, Smith and Robinson 2015). However, the spawning survey method and data, if used in an unbiased estimation context that accounts for sampling uncertainties and detection probability, may replace the discontinued trawl surveys.

Another potential benefit of spawning surveys is the heretofore incidental collection of mark-recapture data during surveys. Mark-recapture analysis approaches can be useful for estimating population size and other demographic parameters (Schwarz and Seber 1999, Williams et al. 2002). For horseshoe crabs, this approach requires an intense effort of tag (or mark) application onto a portion of the population (as described by Swan 2005; Seber 1965). The U. S. Fish and Wildlife (USFWS) service distributes standard tags with unique identification numbers to various programs and projects that conduct these tagging efforts every year on beaches or from boats in the Delaware Bay region (D. R. Smith, U.S. Geological Survey, personal communication). The tagged horseshoe crabs disperse and some are “recaptured” during spawning surveys. Surveyors record their tag numbers and the USFWS maintains that information in a database. From those data, individual capture histories are built and analyzed. This approach involves a large amount of tagging and recapture effort, and analyses potentially yield low recapture rates and biased estimates of abundance, regardless of effort (Royle 2004). Nevertheless, annual tagging efforts coupled with annual spawning surveys provides an opportunity for mark-recapture data analysis.

For this thesis, we developed an alternative analysis method to trawl surveys that utilizes spawning survey and mark-recapture data for the estimation of Delaware Bay horseshoe crab abundance. This new method is used within a Bayesian framework and consists of a hierarchical, state-space model that is a modified version of Jolly-Seber (Jolly 1965, Seber 1965) mark-recapture models and was developed by Crosbie and Manly (1985) and Schwarz and Arnason (1996; CMSA). The CMSA model can be easily altered and analyze data from an open population. Our method also contains a binomial model for count data that allows for varying marked-to-unmarked ratios throughout the season. The relaxed qualities of these models makes our application of them to horseshoe crab data possible. In Chapter 1, we assessed the accuracy and precision of our method using a simulated data set. Additionally, we compared our method’s analysis of 2003 and 2004 data to trawl survey data estimates from those years. In Chapter 2, we used a simulated data set that mimics the mark-recapture data from Chapter 1 to evaluate the effects of increasing tagging and recapture effort on the precision and relative bias of abundance estimates. We wrote both chapters as independent manuscripts.

LITERATURE CITED

Anderson, L. I., and C. N. Shuster, Jr. 2003. Throughout geologic time: where have they lived? Pages 189-224 *in* Shuster Jr., C.N. et al., editors. The American horseshoe crab. Harvard University Press, Cambridge, Massachusetts, USA.

Atlantic States Marine Fisheries Commission (ASMFC). 1998. Interstate fishery management plan for horseshoe crab. Fishery management report no. 32. ASMFC, Washington, D.C., USA.

_____. 2009. Horseshoe crab stock assessment for peer review. Stock assessment report no. 09-02 (supplement A). ASMFC, Washington, D.C., USA.

_____. 2012. Addendum VII to the interstate fishery management plan for the horseshoe crab for public comment: adaptive resource management framework. ASMFC, Washington, D.C., USA.

_____. 2013. 2013 horseshoe crab stock assessment update. ASMFC, Washington, D.C., USA.

Barlow, R. B., M. K. Powers, H. Howard, and L. Kass. 1986. Migration of *Limulus* for mating - relation to lunar phase, tide height, and sunlight. Biological Bulletin 171:310-329.

Berkson, J., and C. N. Shuster. 1999. The horseshoe crab: the battle for a true multiple-use resource. Fisheries 24:6-10.

Botton, M. L. 1984. Diet and food preferences of the adult horseshoe crab, *Limulus polyphemus*, in Delaware Bay, New Jersey. Marine Biology 81:199-207.

Botton, M. L., and R. E. Loveland. 1989. Reproductive risk - high mortality associated with spawning by horseshoe crabs (*Limulus polyphemus*) in Delaware Bay, USA. Marine Biology 101:143-151.

Botton, M. L., R. E. Loveland, and T. R. Jacobsen. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of horseshoe crab (*Limulus polyphemus*) eggs. Auk 111:605-616.

Brockmann, H. J. 1990. Mating behavior of horseshoe crabs, *Limulus polyphemus*. Behavior 114:206-220.

Brockmann, H. J., and D. Penn. 1992. Male mating tactics in the horseshoe crab, *Limulus polyphemus*. Animal Behavior 44:653-665.

Clark, K. E., L. J. Niles, and J. Burger. 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. Condor 95:694-705.

Crosbie, S. F., and B. F. Manly. 1985. A new approach for parsimonious modelling of capture-mark-recapture experiments. Biometrics 41:385-398.

Fish and Wildlife Service (FWS). 2014. Endangered and threatened wildlife and plants: threatened species status for the *rufa* red knot. Department of the Interior, Federal Register 79(238).

Fraser, J. D., S. M. Karpanty, J. B. Cohen, and B. R. Truitt. 2013. The red knot (*Calidris canutus rufa*) decline in the western hemisphere: is there a lemming connection? Canadian Journal of Zoology 91:13-16.

Hall, W. R., Jr. 1992. The horseshoe crab - a reminder of Delaware's past. University of Delaware, Sea Grant Marine Advisory Service, Newark, Delaware, USA.

Hassler, C., and H. J. Brockmann. 2001. Evidence for use of chemical cues by male horseshoe crabs when locating nesting females (*Limulus polyphemus*). Journal of Chemical Ecology 27:2319-2335.

Hata, D., and J. Berkson. 2003. Abundance of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay area. Fishery Bulletin 101:933-938.

Hata, D., and J. Berkson. 2004. Factors affecting horseshoe crab *Limulus polyphemus* trawl survey design. Transactions of the American Fisheries Society 133:292-299.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both dead and immigration-stochastic model. Biometrika 52:225-247.

King, T. L., M. S. Eackles, A. P. Spidle, and H. J. Brockmann. 2005. Regional differentiation and sex-biased dispersal among populations of the horseshoe crab *Limulus polyphemus*. Transactions of the American Fisheries Society 134:441-465.

Kreamer, G., and S. Michels. 2009. History of horseshoe crab harvest on Delaware Bay. Pages 299-313 *in* J.T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. The Journal of Wildlife Management 72:1683-1692.

Manion, M. M., R. A. West, and R. E. Unsworth. 2000. Economic assessment of the Atlantic Coast horseshoe crab fishery. Division of Economics, U. S. Fish and Wildlife Service, Arlington, Virginia, USA.

McGowan, C. P., J. E. Hines, J. D. Nichols, J. E. Lyons, D. R. Smith, K. S. Kalasz, L. J. Niles, A. D. Dey, N. A. Clark, P. W. Atkinson, C. D. Minton, and W. Kendall. 2011*a*. Demographic consequences of migratory stopover: linking red knot survival to horseshoe crab spawning abundance. Ecosphere 2(6):1-22.

McGowan, C., D. Smith, J. Sweka, J. Martin, J. Nichols, R. Wong, J. Lyons, L. Niles, K. Kalasz, and J. Brust. 2009. A framework for adaptive management of horseshoe crab harvest in the Delaware Bay constrained by red knot conservation. Stock assessment report no. 09-02 (supplement B) of the Atlantic States Marine Fisheries Commission. Washington, DC, USA.

McGowan, C. P., D. R. Smith, J. A. Sweka, J. Martin, J. D. Nichols, R. Wong, J. E. Lyons, L. J. Niles, K. Kalasz, J. Brust, M. Davis, and B. Spear. 2011*b*. Multispecies modeling for adaptive management of horseshoe crabs and red knots in the Delaware Bay. Natural Resource Modeling 24:117-156.

Myers, J. P. 1986. Sex and gluttony on Delaware Bay. Natural History 95:68-77.

Niles, L. J., J. Bart, H. P. Sitters, A. D. Dey, K. E. Clark, P. W. Atkinson, A. J. Baker, K. A. Bennett, K. S. Kalasz, N. A. Clark, J. Clark, S. Gillings, A. S. Gates, P. M. Gonzalez, D. E. Hernandez, C. D. T. Minton, R. I. G. Morrison, R. R. Porter, R. K. Ross, and C. R. Veitch. 2009. Effects of horseshoe crab harvest in Delaware Bay on red knots: are harvest restrictions working? Bioscience 59:153-164.

Nordstrom, K. F., N. L. Jackson, D. R. Smith, and R. G. Weber. 2006. Transport of horseshoe crab eggs by waves and swash on an estuarine beach: implications for foraging shorebirds. Estuarine, Coastal and Shelf Science 70:438-448.

Novitsky, T. J. 1984. Discovery to commercialization - The blood of the horseshoe crab. Oceanus 27:13-18.

Odell, J., M. E. Mather, and R. M. Muth. 2005. A biosocial approach for analyzing environmental conflicts. A case study of horseshoe crab allocation. Bioscience 55:735-748.

Penn, D., and H. J. Brockmann. 1994. Nest-site selection in the horseshoe crab, *Limulus polyphemus*. Biological Bulletin 187:373-384.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860-873.

Schwarz, C.J., and G.A. Seber. 1999. Estimating animal abundance: review III. Statistical Science 14:427-456.

Seber, G. 1965. A note on the multiple-recapture census. Biometrika 52:249-259.

Shuster Jr, C. N. 1982. A pictorial review of the natural history and ecology of the horseshoe crab *Limulus polyphemus*, with reference to other *Limulidae*. Progress in Clinical and Biological Research 81:1.

Shuster, C. N., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L), in Delaware Bay. Estuaries 8:363-372.

Smith, D. R., L. J. Brousseau, M. T. Mandt, and M. J. Millard. 2010. Age and sex specific timing, frequency, and spatial distribution of horseshoe crab spawning in

Delaware Bay: insights from a large-scale radio telemetry array. Current Zoology 56:563-574.

Smith, D. R., and S. F. Michels. 2006. Seeing the elephant. Fisheries 31:485-491.

Smith, D. R., M. J. Millard, and R. H. Carmichael. 2009. Comparative status and assessment of *Limulus polyphemus* with emphasis on the New England and Delaware Bay populations. Pages 361-386 *in* J. T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Smith, D. R., M. J. Millard, and S. Eyler. 2006. Abundance of adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay estimated from a bay-wide mark-recapture study. Fishery Bulletin 104:456-464.

Smith, D. R., P. S. Pooler, B. L. Swan, S. F. Michels, W. R. Hall, P. J. Himchak, and M. J. Millard. 2002. Spatial and temporal distribution of horseshoe crab (*Limulus polyphemus*) spawning in Delaware Bay: implications for monitoring. Estuaries 25:115-125.

Smith, D. R., and T. J. Robinson. 2015. Horseshoe crab spawning activity in Delaware Bay, USA, after harvest reduction: a mixed-model analysis. Estuaries and Coasts: 1-10.

Swan, B. L. 2005. Migrations of adult horseshoe crabs, *Limulus polyphemus,* in the Middle Atlantic Bight: a 17-year tagging study. Estuaries 28:28-40.

Weber, R. G., and D. B. Carter. 2009. Distribution and development of *Limulus* egg clusters on intertidal beaches in Delaware Bay. Pages 249-266 *in* J. T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Walls, E. A., J. Berkson, and S. A. Smith. 2002. The horseshoe crab, *Limulus polyphemus*: 200 million years of existence, 100 years of study. Reviews in Fisheries Science 10:39-73.

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

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2007. Adaptive management: the U.S. Department of the Interior technical guide. Adaptive Management Working Group, Washington, DC, USA.

Chapter 1: Modified Mark-Recapture Analysis Using a Hierarchical Modeling Approach

ABSTRACT

Effective and consistent monitoring is an essential component of any management effort for exploited wildlife populations. In the United States, Atlantic horseshoe crabs (*Limulus polyphemus*) are harvested and relied upon by several user groups in the mid-Atlantic states (i.e., Delaware, New Jersey, Maryland, and Virginia), and managers have used offshore trawl surveys to monitor the species and inform management decisions. However, this monitoring method is expensive and, due to a lack of funding, has an uncertain future in horseshoe crab management efforts. Utilization and analysis of volunteer-collected spawning survey count and tag-recapture data may serve as a more feasible monitoring alternative. For this study, we evaluated the efficacy of a hierarchical modeling approach within a Bayesian framework in analyzing data collected on adult male horseshoe crabs during Delaware Bay spawning surveys in 2003 and 2004. Among other parameters, we estimated male abundance of 6,328,000 (2,044,000 – 10,320,000; 95% CI) in 2003 and 3,293,000 (1,721,000 – 5,802,000; 95% CI) in 2004. These estimates are comparable to those of past trawl survey data analyses, and our model produced abundance estimates that were close to the known value within a simulation study. Use of spawning survey data and our modeling approach could be a useful monitoring alternative to the trawl survey method.

INTRODUCTION

Monitoring is an essential component of effective wildlife management, especially for exploited populations (Williams et al. 2002). Often, competing management objectives, limited management options, and uncertainty in how wildlife populations will respond to management produce challenges for managers in the decision-making process (Lyons et al. 2008). Monitoring aids decision-making by providing managers with information that they can use to develop objectives, evaluate the effects of management actions, suggest alternative actions, and address uncertainty. Additionally, managers attempting to reach desired levels of abundance or harvest for a species can analyze data collected from monitoring efforts to determine the status of a population (Williams et al. 2002, Lyons et al. 2008). Management of Atlantic horseshoe crabs, *Limulus polyphemus*, on the East Coast of the United States incorporates consistent monitoring effort and is one example of how monitoring is used to inform management and aid the decision-making process.

Atlantic horseshoe crabs, *L. polyphemus* (hereafter horseshoe crab), are found along the Atlantic Coast of North America, but are most abundant in the Delaware Bay region (Shuster 1982). Horseshoe crabs have a unique physiology and reproductive strategy that make them an important ecological and economic multiple-use resource (Berkson and Shuster 1999, Smith et al. 2009). Each spring, millions of male and female horseshoe crabs migrate to the sandy estuarine beaches of Delaware Bay to spawn (Shuster and Botton 1985). During peak spawning, migratory shorebirds traveling to Arctic breeding grounds stop in the Delaware Bay region for several weeks to take advantage of the widely abundant, energy-rich horseshoe crabs eggs available on beaches

(Niles et al. 2009, Mizrahi and Peters 2009). Availability of eggs during this stopover period may have in impact on survival of some species of migratory shorebird, including the red knot (*Calidris canutus rufa*; Botton et al. 1994, Baker et al. 2004, Niles et al. 2009, McGowan et al. 2011*a*). The biomedical industry extracts blood from hundreds of thousands of horseshoe crabs annually to create Limulus Ameobocyte Lysate (LAL), which is used in testing for bacterial contamination in injectable drugs and intravenous devices (Hall 1992, ASMFC 1998). The use of LAL in medical testing has greatly improved safety, and the U.S. Food and Drug Administration currently requires the LAL test on pharmaceutical and biomedical products before their distribution (ASMFC 1998, Walls et al. 2002). Commercial whelk (*Busycon spp.*) and American eel (*Anguilla rostrada*) fisheries catch hundreds of thousands of horseshoe crabs each year along certain portions of the Atlantic Coast for use as bait (ASMFC 1998). Horseshoe crabs are the preferred and most effective bait for these fisheries, which generate millions of dollars and hundreds of jobs for the mid-Atlantic region (Manion et al. 2000, Walls et al. 2002).

The Horseshoe Crab Management Board of the Atlantic States Marine Fisheries Commission (ASMFC) created the “Interstate Fishery Management Plan for Horseshoe Crab” in 1998 to satisfy the needs of all user groups and effectively manage horseshoe crabs (ASMFC 1998). They proposed a coordinated and consistent effort to manage and monitor horseshoe crabs in a way that maintains their role in the ecosystem while ensuring long-term use of them by all stakeholders. The plan was successful for horseshoe crabs, but there were concerns about the negative effects of horseshoe crab harvest on shorebird populations (Smith et al. 2009, ASMFC 2012). In an attempt to improve management and conservation of both horseshoe crabs and migratory shorebirds along the mid-Atlantic Coast, the ASMFC adopted an adaptive management framework for horseshoe crabs in 2012 that is limited by red knot conservation objectives (McGowan et al. 2009, ASMFC 2012). Adaptive management was applied to the horseshoe crab harvest decision process so that harvest policies could be made and alternative management actions could be evaluated considering all competing stakeholder objectives, best available scientific data, and ecological uncertainty surrounding horseshoe crabs and red knots (Williams et al. 2002, 2007; McGowan et al. 2009, 2011*b*; Smith et al. 2013).

A critical component of the adaptive management program is annual monitoring of Delaware Bay horseshoe crabs to learn how their population responds to management actions (Lyons et al. 2008, ASMFC 2012). Data from horseshoe crab monitoring programs, specifically an offshore trawl survey and standardized spawning surveys, have been utilized for statistical modeling that linked population dynamics between horseshoe crabs and red knots (Smith and Michels 2006, McGowan et al. 2011*a*). Data from the monitoring programs also enable analysts to assess the state of the horseshoe crab population, and these studies help inform harvest policy and alternative management decisions (ASMFC 2012).

Since the early 2000s, horseshoe crab population monitoring data were primarily collected through offshore trawl surveys (trawl net pulled by boat) conducted by Virginia Polytechnic Institute and State University (VPI) near the mouth of the Delaware Bay in the fall of each year (Hata and Berkson 2004, McGowan et al. 2009). Analyses of those data were used to inform management, however, these surveys were expensive to operate (at least $250,000 per year; E. Hallerman, VPI, personal communication), and used nets that may have biased capture rates or been inefficient at capturing horseshoe crabs (ASMFC 1998, Walls et al. 2002, Hata and Berkson 2003). However, all ocean-based surveys for horseshoe crabs are subject to imperfect catchability. While these surveys attempt to estimate population abundance through stratified random sampling and spatial extrapolation, there are concerns about temporal variability and effective spatial coverage (Hata and Berkson 2003); results of the trawl survey are often uncertain and have limited utility. Furthermore, funding for trawl surveys was discontinued in 2012 and future funding is highly uncertain (C. P. McGowan, U.S. Geological Survey, personal communication).

Since the late 1990s, standardized spawning surveys (spatially and temporally replicated counts) have taken place on Delaware Bay beaches during the horseshoe crab spawning season and require less effort than trawl surveys (Smith and Michels 2006). Additionally, the monetary costs associated with this method have never been quantified, but it is assumed that the annual costs of labor and database management would be much less than those required to operate trawl surveys (C. P. McGowan, personal communication). Surveys are limited to only 12 or 15 occasions within a spawning season, and take place during spring tides in May and June to coincide with peak spawning activity (Shuster and Botton 1985). Volunteers conduct the surveys on nighttime high tides 2 days before, the day of, and 2 days after new and full moons (spring tides; Smith et al. 2002, 2010). Ten to 11 days separate surveys between spring tide periods, and 2 days separate each of the 3 surveys conducted around a new or full moon. Volunteers collect data on the number of male and female horseshoe crabs counted within 100 1-m^2 quadrats along a 1 km transect at the hide tide line (Smith et al. 2002). Because volunteers execute the counts, there is concern about detection error, and surveys are occasionally cancelled when volunteers do not show up or when weather is bad, which causes gaps in the data. Additionally, horseshoe crab distributions vary weekly due to weather events that shift spawning activity, and annually due to migration between beaches within the region, both of which create sampling error and uncertainty (Berkson and Shuster 1999, Smith et al. 2002, King et al. 2005, Swan 2005, Smith and Michels 2006). Furthermore, the 100-m^2 survey area along 1 km of beach may not capture a representative sample of the spawning population during a survey, especially if abundance is high (Berkson and Shuster 1999, Smith and Robinson 2015). However, the spawning survey method and data, if used in an unbiased estimation context that accounts for sampling uncertainties and detection probability, could substitute the discontinued trawl surveys.

Another potential benefit of spawning surveys is the heretofore incidental collection of mark-recapture data during spawning surveys. Mark-recapture analysis approaches are useful for estimating population size and other demographic parameters (Williams et al. 2002). For horseshoe crabs, this approach requires an intense effort of tag (or mark) application onto a portion of the population (as described by Swan 2005; Seber 1965). The U.S. Fish and Wildlife (USFWS) service distributes standard tags with unique identification numbers to various programs and projects that conduct these tagging efforts every year on beaches or from boats in the Delaware Bay region (D. R. Smith, U.S. Geological Survey, personal communication). The tagged horseshoe crabs disperse and some are “recaptured” during spawning surveys. Surveyors record their tag numbers and the USFWS maintains that information in a database. From those data, individual capture histories are built and analyzed. This approach involves a large amount of tagging and recapture effort, and analyses potentially yield low recapture rates and biased estimates of abundance, regardless of effort (Royle 2004). Nevertheless, annual tagging efforts coupled with annual spawning surveys provides an opportunity for mark-recapture data analysis.

To date, no effort has been made to incorporate an entire season's worth of spawning survey and mark-recapture data for the estimation of Delaware Bay horseshoe crab abundance. Attempting this is necessary for effective population management in the absence of trawl survey efforts. Here, we developed a hierarchical, state-space model and assessed its performance within a Bayesian framework using one simulated data set and two, whole-season data sets from 2003 and 2004. Our model is a modified version of Jolly-Seber (Jolly 1965, Seber 1965) mark-recapture models developed by Crosbie and Manly (1985) and Schwarz and Arnason (1996; CMSA), and is similar to one developed by J. E. Lyons et al. (USFWS, unpublished report) for use with red knot data (Appendix A). This model uses data augmentation and allows for varying marked-to-unmarked ratios and spawning population size throughout the season – an open population. The ability of the CMSA superpopulation model to be altered and accommodate an open population makes our application of it to horseshoe crab data possible.

METHODS

Data Collection

We used data collected by U.S. Geological Survey (USGS) volunteers on Delaware Bay beaches during spring tide spawning surveys (described above) in May and June of 2003 and 2004, and analyzed data from each year (season) separately. We used male-only count and recapture data because males have higher detection rates than females due to their active, aboveground spawning behavior (Smith et al. 2006). Count data included counts of unmarked male horseshoe crabs, quadrats surveyed, beach surveyed, and survey date. Fifteen surveys were conducted on 22 beaches from 29 April to 1 June 2003, and 12 surveys were conducted on 23 beaches from 2 May to 19 June 2004. For both years, we pooled count data from all beaches together for each survey occasion because our data analysis did not allow for individual beach assessments.

We coupled these USGS spawning survey data with additional recapture data (obtained from the USGS) on male horseshoe crabs marked by various agencies prior to the spawning surveys of 2003 and 2004, and recaptured by the USGS during spawning surveys in those years. In other words, recapture data consisted of marked individuals who were recaptured during spawning surveys, and had been marked in years prior to or right before those surveys began. Most of these recaptured individuals were tagged by the USGS during an early-spring (March and April) trawl survey effort within the waters of the Delaware Bay (Smith et al. 2006). We generated individual capture histories from those recapture data and included marked individuals found both in- and outside of the quadrats sampled. The exact number marked individuals that were alive, part of the Delaware Bay spawning population, and available for recapture was unknown for 2003 and 2004, and we conducted our analyses accordingly. However, the USGS tagged 12,505 males in 2003 and 7,276 males in 2004 in Delaware Bay before spawning surveys began (D. R. Smith, personal communication), thus at least that many were potentially available for recapture. We did not use these data because if our analysis method was applied to data from other years, the total number marked may not be known; a lack of consistent tagging effort and horseshoe crab survival and movement make determining the actual number of marked individuals in any given year difficult.

We added a fixed amount of all-zero capture histories to each year's recapture data, a process known as parameter-expanded data augmentation (PX-DA; Royle and Dorazio 2008, 2012). PX-DA overcomes the problem of not knowing the total number of marked individuals that are alive, members of the population, and available for recapture by incorporating a pseudo-population (i.e., all-zero capture histories) into a data set before analysis. This pseudo-population must be made large enough to avoid right-truncation of the posterior distribution of the abundance estimate (Kery and Schaub 2012), and consists of a "known" number individuals that may or may not have been available for recapture (as determined by the PX-DA parameter and inclusion probability, see Model Structure section; Royle and Dorazio 2008). The augmented data set (including actual recaptures and the pseudo-population) is analyzed with a reparameterized mark-recapture model. PX-DA does not affect estimates, helps account for imperfect detection, and aids the modeling process; however, it increases computation time (Kery and Schaub 2012, Royle and Dorazio 2012). For both years, we incorporated data augmentation into our capture history data sets. To avoid arbitrarily choosing and testing various amounts of data augmentation to add, we used estimates of marked individuals produced in preliminary analyses of 2003 and 2004 data to guide our choice (see Analyses and Results sections below).

Model Structure

Our method uses the CMSA superpopulation approach of Royle and Dorazio (2008) and includes a hierarchical, state-space model with data augmentation, and a binomial model for count data (Appendix A). Hierarchical state-space models describe capture history data with a model for the unobservable or partially observable state process (conditional on ecological or individual variation), and a model for the observation process (conditional on detection error and the state process; Fig. 1.1; Kery and Schaub 2012).

The state process of our analysis consists of a model for occasion-specific spawning probabilities. Horseshoe crabs arrive in Delaware Bay before spawning surveys start, and come to beaches from the water variably (i.e., dependent on water temperature, wave height, tides, etc.) and repeatedly for several days to weeks throughout the spawning (and survey) season (Shuster and Botton 1985, Brousseau et al. 2004, Smith et al. 2010). Male horseshoe crabs exhibit independent spawning probabilities from other males during this time (Hassler and Brockmann 2001). Additionally, horseshoe crabs may depart Delaware Bay after they have completed spawning while surveys are still occurring (Anderson and Shuster 2003, Brousseau et al. 2004). Our occasion-specific spawning probability model accounts for these factors by allowing horseshoe crabs to spawn at various times throughout the season, and considers that when the animals are not spawning, they are unavailable for detection. We modeled spawning probability as a beta-distributed parameter with a uniform prior probability distribution for each sampling occasion,

$$s_t \sim Beta(1,1) \tag{1}$$

where s_t is the probability of a male spawning at survey occasion *t*. A second part of the state process determines the state of an individual (i.e., spawning or not spawning) at each survey occasion. In our model, the parameter $z_{i,t}$ determines the state and is modeled as a Bernoulli-distributed random variable,

$$z_{i,t} \sim Bernoulli(s_t) \tag{2}$$

where the Bernoulli trial is 1 if individual *i* is spawning at occasion *t*, and 0 if it is not.

Marked males are specified by our model using w_i, the PX-DA parameter. This parameter determines if a male is marked and available for sampling according to the inclusion probability, ψ, and a Bernoulli random variable,

$$w_i \sim Bernoulli(\psi) \tag{3}$$

Inclusion probability is the probability that an individual is included in the augmented data set and a member of the Delaware Bay spawning population (superpopulation). We did not make the inclusion probability occasion-specific because that parameter relates only to augmented capture history data, which are compiled after a survey season is complete and do not vary during the estimation procedure.

We restricted the survival (φ) and detection (p) parameters to remain constant throughout the season. Survival probability is less than 100% (Butler 2012), and although it may change at random throughout the season due to weather and other environmental factors, those factors are stochastic and not temporally correlated (i.e., temporal changes in survival and detection are attributed to estimated variance, not time-specific estimates of survival or detection). Detection probability varies throughout the season because of environmental conditions and observation error (e.g., storms make it hard for surveyors to work, experience and numbers of volunteers throughout the season, or incomplete quadrat counts; Zippin 1958, Royle and Kery 2007). However, we used a constant detection probability to save computing time in our analyses and to overcome issues of parameter non-identifiability (Schwarz and Arnason 1996). As a result, our model assumes that variability due to detection probability is constant but that variation in observations of marked and unmarked individuals is attributable to temporal variation in spawning probabilities. Given these restrictions, we made the probability of recapturing a marked male ($w_{i=1}$) on a beach during a survey, $\mu_{i,t}$, a function of whether or not the horseshoe crab was alive (φ), spawning (s_t), and detected (p),

$$\mu_{i,t} = w_i \times \varphi \times s_t \times p \tag{4}$$

Recapturing a marked, alive, and spawning male on a beach during a survey was determined according to a Bernoulli random variable,

$$y_{i,t} \sim Bernoulli(\mu_{i,t}) \tag{5}$$

where 1 means the individual was detected during a survey and 0 indicates otherwise. This equation references the augmented data set. Equations 4 and 5 are the models for the observation process. The states of our analysis are: (1) in the study area (Delaware Bay) but not spawning, (2) in the study area, spawning, but not detected, and (3) in the study area, spawning, and detected (Fig. 1.1).

We calculated the total number of marked males in Delaware Bay for a season by summing the number of marked ($w_{i=1}$) and spawning ($z_{i,t=1}$) horseshoe crabs at every survey occasion. The random variables w_i and $z_{i,t}$ are determined by the model (as shown above) and do not consist of real observations. We incorporated real observations of marked and unmarked horseshoe crabs counted within quadrats by using a binomial model for count data to estimate the proportion of the population with marks and total abundance, as suggested by Lyons et al. (unpublished report):

$$m_t \sim Binomial(C_t, \pi) \tag{6}$$

where the number of marked males counted (m_t) during survey occasion t is a binomial random variable of the total number of males counted (C_t) and the proportion of marked males in the population (π). The likelihood model of π is,

$$\hat{\pi} = {}^{m_t}/_{C_t} \qquad (7)$$

or the ratio of marked to unmarked males in the population. We kept the proportion of the population that was marked (π) constant for each season by assuming that the proportion does not change throughout the spawning season, but may change from year to year due to mortality and tagging effort. To determine Delaware Bay male population size for a season, we divided the sum of the number of marked (w_i) and spawning ($z_{i,t}$) males at each survey occasion by $\hat{\pi}$. To estimate the number of females in the Delaware Bay population for a season as a derived parameter with a posterior distribution, we divided the estimate of total male abundance by the 2.2 male-to-female sex ratio (Smith et al. 2006) within our model.

Analyses

Using our observed, non-augmented capture histories from 2003 and 2004, we ran a POPAN analysis for each year in Program MARK (MARK version 8.0, http://warnercnr.colostate.edu/~gwhite/mark/mark.htm, accessed 1 Sept 2014). Analyzing our data in MARK allowed us to confirm that it was structured properly before proceeding to our OpenBUGS (OpenBUGS version 3.2.3, http://www.openbugs.net/w/FrontPage, accessed 1 Dec 2014) analyses. It also provided estimates of marked males in Delaware Bay. The upper bounds of the 95% confidence intervals of these estimates served as an indicator of how many all-zero capture histories to add to our observed capture histories for proper data augmentation and CMSA parameter estimation (Kery and Schaub 2012).

To test accuracy and precision of our model, we simulated data with known parameter values (Table 1.1, Appendix B) and ran a Bayesian Markov chain Monte Carlo (MCMC) analysis in OpenBUGS. These simulated data mimicked how our real data were collected and structured, and consisted of 12 survey occasions and 3,500 capture histories, which we augmented out to 13,000 to match what we used for observed data from 2003 and 2004. Within this simulation, to mimic horseshoe crabs' high survival probability and maintain some control of what the model was estimating, we assumed that every horseshoe crab in this data set survived and set survival probability in the model to 1. We gave all other parameters uninformed, uniform or beta prior distributions in the OpenBUGS analysis of simulated data. We compared parameter estimates produced in this analysis to truth (Table 1.1) to assess model performance.

To estimate detection probability, proportion of population with marks, occasion-specific spawning probabilities, number of marked individuals, and total male and female abundance for the 2003 and 2004 spawning populations of Delaware Bay, we ran our hierarchical, state-space model using a Bayesian MCMC approach in OpenBUGS. We analyzed data from the 2003 and 2004 seasons separately. We gave prior probabilities for inclusion, survival, and detection uninformed, uniform distributions ranging from 0 to 1. We gave prior probabilities for spawning and proportion of population with marks flat, uninformed, beta distributions. We did this to avoid biasing model estimates and allow data to drive posterior estimation (Morris et al. 2015).

For the 2003, 2004, and simulated data analyses, we completed 110,000 realizations with 10,000 burn-ins, no thinning (Link and Eaton 2012), and 3 chains.

RESULTS

On average, 1,845 quadrats were counted throughout Delaware Bay for each survey occasion in 2003, and 1,985 quadrats were counted throughout the Bay for each survey occasion in 2004. In 2003, 56,239 males were counted within quadrats, and 63,418 males were counted within quadrats in 2004. In 2003, 48 marked males were encountered within quadrats and 122 marked males were encountered outside quadrats. In 2004, 63 marked males were counted within quadrats and 219 marked males were counted outside quadrats.

The 2003 MARK analysis estimated 5,130 (2,051 – 12,835; 95% CI) marked males in the Delaware Bay spawning population (Fig. 1.2). This estimate is low compared to the minimum number of marked individuals that were present in the Bay in that year (i.e., 12,505); however, the confidence interval of this estimate contains that minimum number. The analysis of 2004 data estimated that there were 4,096 (2,281 – 7,352; 95% CI) marked males in the population (Fig. 1.2). This estimate is also low as compared to the minimum number marked of 7,276; however, this estimate's confidence interval also contains that value. Because the highest value of the upper bound of the 95% confidence interval estimated in Program MARK between the two years was 12,835, we augmented each season's data set with enough all-zero capture histories to equal 13,000 capture histories total. We incorporated augmented data into the following hierarchical Bayesian analyses conducted in OpenBUGS.

Analysis of the simulated data set estimated that there were 3,848,000 (2,226,000 – 6,087,000; 95% CI) total males and 5,415 (3,268 – 8,159; 95% CI) marked males in the Delaware Bay population. These parameter estimates, along with the derived estimate of female abundance, were very close to their respective true values (Table 1.1). However, our model overestimated most spawning probabilities and underestimated detection probability. Although the estimate for proportion of the population with marks was close to the known value, our model overestimated this parameter and the known value was outside the estimated credible interval (Table 1.1).

Our analysis for 2003 estimated total male abundance in the Delaware Bay spawning population as 6,328,000 (2,044,000 – 10,320,000; 95% CI; Table 1.2). Male abundance decreased in 2004 to 3,293,000 (1,721,000 – 5,802,000; 95% CI). Derived estimates of female abundance decreased similarly from 2,876,000 (929,100 – 6,001,000; 95% CI) in 2003 to 1,497,000 (782,400 – 2,637,000; 95% CI) in 2004. These estimates and decreasing trends matched closely to the estimates from Hata and Hallerman's (2009) analysis of 2003 and 2004 trawl survey data (Fig. 1.4). Our estimates for the number of marked males in the population was lower in 2004 than in 2003 (Table 1.2), and for both years these estimates were lower than the minimum number of marked individuals in the Bay those years (i.e., 12,505 in 2003, 7,276 in 2004). Additionally, the credible intervals for the estimates for both years did not contain the minimum number marked. The proportion of marked males in the population was higher in 2004 than in 2003 (Table 1.2). The probability of detecting a spawning marked male during a survey in 2003 was 0.1664 (0.0054 – 0.6379; 95% CI) and increased to 0.3074 (0.0382 – 0.9204; 95% CI) in 2004.

DISCUSSION

The purpose of this study was to evaluate the efficacy of our mark-recapture, hierarchical modeling approach as compared to past estimation efforts that used trawl survey data (Hata and Hallerman 2009). Until 2012, analyses of trawl survey data had been used to inform horseshoe crab management and aid the decision-making process (McGowan et al. 2009). Funding for the expensive trawl survey has been discontinued, and the need for an alternative analysis approach is urgent (C. P. McGowan, personal communication). We used 2003 and 2004 data because the USGS conducted the best effort to date to tag horseshoe crabs in those years, therefore providing the greatest potential for high detection probabilities and more recapture data. Additionally, trawl survey data-derived abundance estimates existed for both years. Comparable results produced by our analyses of 2003 and 2004 spawning survey count and mark-recapture data may prove our approach's viability as an alternative. Efficacy of our approach is further supported by the accuracy of abundance estimates from the simulation study.

Despite producing estimates of the number of marked males in the Delaware Bay spawning population similar to those from the hierarchical Bayesian analyses (Fig. 1.2), using only MARK for analysis of mark-recapture data is not sufficient for our needs. The 2003 and 2004 data sets used in MARK included non-augmented capture histories, however that constitutes only a portion of data collected by surveyors. POPAN cannot incorporate marked-to-unmarked ratios of horseshoe crabs counted during spawning surveys, and is therefore limited in its estimation ability. Our hierarchical model had the capacity to use that information along with augmented capture histories, and, as a result, was able to produce estimates of the proportion of the population with marks and, therefore, total abundance (our primary parameter of interest) with credible interval distributions that directly estimate parameter uncertainty. The lack of information incorporated into MARK analyses may have been the cause of more imprecise estimates (i.e. large credible intervals) produced as compared to those from the hierarchical analyses (Fig. 1.2). However, MARK served as a guide in the data augmentation process and allowed us to choose the appropriate amount of all-zero capture histories without using "trial and error," thus simplifying our OpenBUGS analyses.

Our model has the following assumptions, as stated by Lyons et al. (unpublished report): 1) spawning, persistence, and detection probabilities are homogenous for marked and unmarked individuals; 2) tags are not lost or overlooked; 3) sampling is instantaneous; 4) no temporary emigration from the study area; and 5) independence of fates with respect to spawning, persistence, and detection probability for all individuals (Williams et al. 2002). These assumptions must be considered in regard to how spawning horseshoe crabs and surveyors behave, and any violation of them could bias or add uncertainty to estimates. In our application and development of this model, we estimated only male abundance because males have higher detection rates than females (Smith et al. 2006). However, young males tend to have fewer spawning bouts than older males (Smith et al. 2010), and older males are more susceptible to stranding (Penn and Brockmann 1995, Smith et al. 2010). These factors could cause differences in persistence and detection probabilities between ages and add bias to our estimates, but the magnitude of that bias is unknown (Pollock et al. 1990, Royle and Dorazio 2008). Concerning homogenous persistence and detection probabilities, studies have shown that tagging before or during the spawning season does not affect an individual's spawning behavior, and that no tag-induced mortality occurs (Brousseau et al. 2004, Smith et al. 2006, Mattei et al. 2011). Aside from behavioral differences between age groups, spawning and persistence probabilities of the entire Bay will not differ greatly between marked and unmarked males. Assumption 2 is occasionally violated because of tag loss and detection error (due to tags being overlooked; Nichols and Hines 1993, Schwarz and Seber 1999, Smith et al. 2006). Butler (2012) estimated tag loss to be 5.8% annually for males. However, within-season tag loss is unlikely given the short duration of the season, that many of the tags were applied prior to the start of the season, and that most tag loss typically occurs soon after initial application (Smith et al. 2006, Butler 2012). Although males do not bury themselves, tags may be overlooked when horseshoe crabs pile on top of each other during peak spawning (Smith et al. 2006). The amount of detection error that occurs is currently unknown, but because our data were collected under a single protocol and monitoring program, our rate of detection may be constant. If tags were lost or overlooked, abundance estimates would be negatively biased and less precise (Royle and Dorazio 2008, Williams et al. 2002). It is likely that assumption 3 is not violated because the spawning surveys occur simultaneously across Delaware Bay and individual sampling events are completed in a relatively short period (< 2 hours). For assumption 4, our superpopulation model can handle temporary emigration; therefore, it is not a concern (Dreitz et al. 2002). Because males do not affect spawning, persistence, or detection probabilities of other males (Hassler and Brockmann 2001), and because spawning surveys are spatially distributed (Smith et al. 2002), assumption 5 is satisfied.

The purpose of our simulation study was to test the accuracy and precision of our model against known values, and to generate confidence in our model’s estimation ability. Our model produced accurate and precise estimates of male and female abundance and number of marked males in the population as compared to known values in the simulation model (Table 1.1). However, its estimates of other parameters, while precise, were either negatively or positively biased. In the simulated data, we set the known value for detection probability to 0.05 to reflect recent research by Butler (2012), and our model greatly underestimated it (Table 1.1.). However, Butler's (2012) detection probability and ours have slightly different meanings; Butler's (2012) probability accounts mostly for horseshoe crabs recaptured during spawning surveys, but also accounts for recaptures reported from commercial fishermen, the biomedical industry, other research efforts, and the general public throughout a year. Our detection probability only accounts for recapturing marked and spawning horseshoe crabs during spawning surveys. Our detection probability should be higher than Butler's (2012) because our primary source of observation variability is accounted for apart from the estimate of detection probability and within the estimation of spawning probabilities. The cause of underestimation may be because with such low detection probabilities the simulated data were very sparse, similar to the observed data. With sparse data, the analysis may have had difficulty attributing uncertainty to various parameters, resulting in inaccuracy of estimated detection or spawning probability (Royle and Dorazio 2008, Kendall et al. 2009). However, the abundance estimates were relatively accurate; underestimated detection probability combined with overestimated spawning probabilities leads to adequate abundance estimates (Nichols et al. 1984, Pollock et al. 1990). Low detection probabilities also tend to cause an underestimation of the proportion of the population with marks. Our model overestimated this parameter, but only slightly (Table 1.1). The effect of this parameter on the abundance estimate was not likely great, but could have caused a negative bias (Nichols et al. 1984, Pollock et al. 1990). However, the primary focus of our research was to estimate abundance. Although the estimate for total male abundance was 348,000 greater than truth, the known value fell well within the 95% credible interval boundaries of that estimate (Table 1.1). Considering that our simulated data were very sparse and did not give the model much information, it preformed adequately. In other words, there is a tradeoff among parameters in our analysis; with a sparse data set the model incorrectly attributes variance to some parameters, but the analysis still potentially leads us to accurate estimates of abundance. However, this simulation study was rudimentary in that it only incorporated one data set. Therefore, our estimates could have been affected by a unique set of observation stochasticity within that data set. A more thorough analysis should simulate hundreds of data sets to determine average model bias, evaluate robustness of our model's estimates to variation, and generate more conclusive results.

In our analysis of 2003 and 2004 data, the probability of detecting a marked male spawning on a beach during a survey increased from 0.1664 in 2003 to 0.3074 in 2004 (Table 1.2). The cause of this increase could be due to more recapture data collected in 2004 than in 2003. High detection probabilities are unrealistic for our species due to the large number of horseshoe crabs in the population, the limited area surveyed during a survey occasion (i.e., ~22 beaches), and limited tag visibility at night when horseshoe crab densities are high (Smith et al. 2006). Smith et al. (2006) and Butler (2012) used similar data to ours and estimated low detection probabilities (<5%), however, their methods of estimation and detection probability definitions differed from ours.

Alternatively, studies by Swan (2005) and Smith et al. (2010) calculated detection probabilities greater than ours, but their recapture protocols differed from what we used, therefore, we cannot compare our estimates to theirs. Our high detection probabilities for both seasons could be due the high visibility of tags at night during surveys or horseshoe crabs being tagged recently before or within a year of being recaptured (Brousseau et al. 2004, Swan 2005, Smith et al. 2006, 2010). Additionally, these detection probabilities may be high because data include marked males found in- and outside of quadrats at any time during a survey, and the hierarchical nature of our model first determines if an individual is spawning, then calculates the probability of detecting that individual. Because our detection probability is the probability of recapturing a highly visible, marked individual anywhere on a beach during a spawning survey (that occurs during peak spawning, Smith et al. 2002), the high estimates produced for 2003 and 2004 may be realistic. Regardless, the posterior distribution of the detection probability parameter for both years shows wide variation, and we conclude that our model had difficulty estimating that parameter (Fig 1.3). These distributions do reach peaks below 0.15, but there is uncertainty about the actual probability of detecting a marked male, particularly in 2004. Given the nature of the wide posterior distribution for detection probability, it may be more advisable to use the median estimate of this parameter because the median is not influenced by extremely high or low values in the distribution. The median estimate for 2003 was 0.0847, and for 2004 was 0.2125. These estimates, while still higher than <5% (Smith et al. 2006, Butler 2012), may more accurately represent the probability of observing a marked and spawning male during a survey.

Our model estimated fewer marked horseshoe crabs in 2004 than in 2003 (Table 1.2, Fig. 1.2). This could be due to increased precision of the estimate for 2004, or that many individuals migrated away from Delaware Bay and did not return to spawn in 2004 (King et al. 2005, Swan 2005). Precision of this parameter estimate increased in 2004 despite fewer surveys conducted that year (i.e., 12 instead of 15 the previous year). However, 140 more quadrats were sampled per survey occasion and 112 more marked individuals were encountered that season than in 2003. These factors may have contributed to the increase in estimate precision (Williams et al. 2002, MacKenzie et al. 2002). For both years, the estimates for number of marked males were lower than the known minimum number of marked individuals in Delaware Bay, and the estimates' credible intervals did not contain the known minimums. Tag loss, tag-induced mortality, and an effect of tagging on an individual's spawning behavior are not likely (Brousseau et al. 2004, Smith et al. 2006, Mattei et al. 2011, Butler 2012), and, therefore, do not contribute to the lower estimates we observed. Although the simulation study indicates that this parameter is potentially estimated accurately (Table 1.1), observation-related error may have led to the underestimation of marked individuals for 2003 and 2004. Although potentially biased high as shown in the simulation study, the proportion of the population with marks was greater in 2004 (Table 1.2). A higher proportion along with more recapture data could have increased precision of number of marked individuals and abundance parameter estimates (Nichols et al. 1984, Pollock et al. 1990).

Male and female abundance estimates decreased in number and increased in precision in 2004 as compared to 2003 (Table 1.2, Fig. 1.4). The decrease in abundance estimates could have been because both detection probability and the proportion of the population marked increased that year (Nichols et al. 1984, Pollock et al. 1990). However, Hata and Hallerman's (2009) trawl survey data estimates of male and female abundance also decreased in 2004 (Fig. 1.4), which indicates the possibility of a population-level decline within Delaware Bay or other factors that prevented horseshoe crabs from spawning or entering the Bay that year. The increase in precision of the abundance estimates observed in 2004 may be due to a larger number of recapture data collected during that season, therefore giving the model more data to work with.

A study by Smith et al. (2006) was similar to ours in that they analyzed Delaware Bay mark-recapture data from 2003, but differed in analysis approach and amount of data used. They used a maximum likelihood estimation approach on data from one spring tide period (3 survey days) in late May of 2003. They did this to satisfy the population closure assumption of their analysis, but as a result, their abundance estimates were imprecise as compared to ours and those of Hata and Hallerman (2009). The difference in these estimates may be because they used less data; detection probabilities estimated from a small data set are likely more imprecise and underestimated, thus leading to positively biased abundance estimates (Nichols et al. 1984, Pollock et al. 1990).

Thus far, there has been no effort made to analyze an entire season's worth of Delaware Bay mark-recapture data to produce estimates of horseshoe crab abundance. We accomplished that using a hierarchical, state-space model of a modified CMSA superpopulation approach and our analysis generated similar estimates to those of past trawl survey data analyses. For 2003, our mean estimates of Delaware Bay adult male and female abundance matched very closely to those of Hata and Hallerman (2009) despite being less precise (Fig. 1.4). For 2004, our mean estimates were lower but more precise than Hata and Hallerman's (2009). For both years and sexes, our credible intervals overlap with Hata and Hallerman's (2009), suggesting that our model produced comparable results, although "truth" is still unknown.

In these analyses, we used uninformative priors with uniform distributions for survival and detection parameters. We did this because we were only trying to assess how useful our approach was for analyzing mark-recapture data and estimating abundance. However, if we wanted to improve estimate precision and accuracy, constricting the prior distribution of survival from 0.25 to 0.95 (Carmichael et al. 2003) and detection from 0 to 0.1 (Butler 2012; D. R. Smith, personal communication) may be a useful approach without compromising estimate accuracy (Morris et al. 2015). Future analyses in a Bayesian framework might consider using informed priors to improve results.

To further increase estimate precision, it may be useful to incorporate occasion-, site-, or individual-specific covariates (Williams et al. 2002, Royle and Dorazio 2008). Hierarchical, state-space models can easily incorporate covariates (Schwarz and Arnason 1996, Royle and Dorazio 2008, Kery and Schaub 2012), and using covariates in these models may improve parameter estimates (Moore and Barlow 2011). We did not incorporate covariates in our analyses to focus on testing the efficacy of our approach, and with such sparse recapture data, estimating covariate relationships may be unfruitful given the uncertainty inherent in the data. However, incorporating covariates, such as age, beach, quadrats surveyed, wave height, water temperature, barometric pressure, and lunar phase, could produce informative and interesting results. Furthermore, results may be improved if covariates are included on parameters, such as detection probability or spawning probability, that had previously been inaccurately estimated or contributed to assumption violations (Royle and Dorazio 2008, Kery and Schaub 2012).

Effective and consistent monitoring is an essential component of wildlife management, especially for exploited populations like that of horseshoe crabs (Williams et al. 2002). In an adaptive management context, monitoring provides information to managers that helps improve understanding of a population, elucidates sources of uncertainty in a system, evaluates management performance, and aids the decision-making process (Lyons et al. 2008). To ensure usefulness of this information, data must be collected and analyzed in a way that reduces uncertainty in the status of a system or population being managed (Kendall et al. 2009). Additionally, data collection and analyses must be economically and logistically feasible for them to be of any use to management. Trawl surveys provided useful information to horseshoe crab managers, but were too expensive to perpetually operate and were discontinued. Spawning surveys had not been able to provide information analogous to that of trawl surveys, but are comparatively inexpensive and utilize the help of volunteers. Our analysis approach provides managers with an alternative that takes advantage of annual spawning survey and mark-recapture data collection efforts, and produces useful estimates for management. This approach could improve with future work and development.

Hierarchical, state-space models such as ours are very flexible and have a wide range of applications (Kery and Schaub 2012), especially for horseshoe crabs. For instance, our model could be altered to assess multiple states (e.g., years, ages, sexes, geographical locations; Calvert et al. 2009), annual exploitation rates (Michielsens et al. 2006), and movement (Patterson et al. 2008) using horseshoe crab mark-recapture data.

However, it may be more important to first explore the effects of increasing tagging or recapture effort on estimate precision. The more precise abundance estimates of 2004 were most likely due to a larger recapture data set for that year, and imply that estimates may improve with denser data. Work by Lyons et al. (unpublished data) and Lahoz-Monfort et al. (2013) suggests that increasing the proportion of the population that is marked or amount of surveys conducted in a season may lead to better recapture data and, therefore, more precise and informative estimates. This exploration is important because improvements in monitoring can increase the quality of information provided to managers (Williams et al. 1996).

LITERATURE CITED

Anderson, L. I., and C. N. Shuster, Jr. 2003. Throughout geologic time: where have they lived? Pages 189-224 *in* Shuster Jr., C.N. et al., editors. The American horseshoe crab. Harvard University Press, Cambridge, Massachusetts, USA.

Atlantic States Marine Fisheries Commission (ASMFC). 1998. Interstate fishery management plan for horseshoe crab. Fishery management report no. 32. ASMFC, Washington, D.C., USA.

_____. 2012. Addendum VII to the interstate fishery management plan for the horseshoe crab for public comment: adaptive resource management framework. ASMFC, Washington, D.C., USA.

Baker, A. J., P. M. Gonzalez, T. Piersma, L. J. Niles, I. de Lima Serrano do Nascimento, P. W. Atkinson, N. A. Clark, C. D. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refueling rates and late arrival in Delaware Bay. Proceedings of the Royal Society of London, Series B: Biological Sciences 271:875-882.

Berkson, J., and C. N. Shuster. 1999. The horseshoe crab: the battle for a true multiple-use resource. Fisheries 24:6-10.

Botton, M. L., R. E. Loveland, and T. R. Jacobsen. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of horseshoe crab (*Limulus polyphemus*) eggs. Auk 111:605-616.

Brousseau, L. J., M. Sclafani, D. R. Smith, and D. B. Carter. 2004. Acoustic-tracking and radio-tracking of horseshoe crabs to assess spawning behavior and subtidal habitat use in Delaware Bay. North American Journal of Fisheries Management 24:1376-1384.

Butler, C. A. 2012. Estimation of survival of the Atlantic horseshoe crab, *Limulus polyphemus*, by analysis of mark-recapture tag loss. Thesis, Auburn University, Auburn, Alabama, USA.

Calvert, A. M., S. J. Bonner, I. D. Jonsen, J. M. Flemming, S. J. Walde, and P. D. Taylor. 2009. A hierarchical Bayesian approach to multi-state mark-recapture: simulations and applications. Journal of Applied Ecology 46:610-620.

Carmichael, R. H., D. Rutecki, and I. Valiela. 2003. Abundance and population structure of the Atlantic horseshoe crab *Limulus polyphemus* in Pleasant Bay, Cape Cod. Marine Ecology Progress Series 246:225-239.

Crosbie, S. F., and B. F. Manly. 1985. A new approach for parsimonious modelling of capture-mark-recapture experiments. Biometrics 41:385-398.

Dreitz, V. J., J. D. Nichols, J. E. Hines, R. E. Bennetts, W. M. Kitchens, and D. L. Deangelis. 2002. The use of resighting data to estimate the rate of population growth of the snail kite in Florida. Journal of Applied Statistics 29:609-623.

Hall, W. R., Jr. 1992. The horseshoe crab - a reminder of Delaware's past. University of Delaware, Sea Grant Marine Advisory Service, Newark, Delaware, USA.

Hassler, C., and H. J. Brockmann. 2001. Evidence for use of chemical cues by male horseshoe crabs when locating nesting females (*Limulus polyphemus*). Journal of Chemical Ecology 27:2319-2335.

Hata, D., and J. Berkson. 2003. Abundance of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay area. Fishery Bulletin 101:933-938.

Hata, D., and J. Berkson. 2004. Factors affecting horseshoe crab *Limulus polyphemus* trawl survey design. Transactions of the American Fisheries Society 133:292-299.

Hata, D., and E. Hallerman. 2009. Report to the Atlantic States Marine Fisheries Commission Horseshoe Crab Technical Committee. Virginia Polytechnic Institute and State University, Horseshoe Crab Research Center, Blacksburg, Virginia, USA.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both dead and immigration-stochastic model. Biometrika 52:225-247.

Kendall, W. L., S. J. Converse, P. F. Doherty, Jr., M. B. Naughton, A. Anders, J. E. Hines, and E. Flint. 2009. Sampling design considerations for demographic studies: a case of colonial seabirds. Ecological Applications 19:55-68.

Kery, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts, USA.

King, T. L., M. S. Eackles, A. P. Spidle, and H. J. Brockmann. 2005. Regional differentiation and sex-biased dispersal among populations of the horseshoe crab *Limulus polyphemus*. Transactions of the American Fisheries Society 134:441-465.

Lahoz-Monfort, J. J., M. P. Harris, B. J. T. Morgan, S. N. Freeman, and S. Wanless. 2013. Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. Journal of Applied Ecology 51:534-543.

Link, W. A., and M. J. Eaton. 2012. On thinning of chains in MCMC. Methods in Ecology and Evolution 3:112-115.

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. The Journal of Wildlife Management 72:1683-1692.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Manion, M. M., R. A. West, and R. E. Unsworth. 2000. Economic assessment of the Atlantic Coast horseshoe crab fishery. Division of Economics, U. S. Fish and Wildlife Service, Arlington, Virginia, USA.

Mattei, J. H., M. A. Beekey, H. R. Potter, C. S. Bond, A. R. Woronik, J. A. Roberts, and K. A. Smith. 2011. Estimation of short-term tag-induced mortality in horseshoe crabs *Limulus polyphemus*. Transactions of the American Fisheries Society 140:954-958.

McGowan, C. P., J. E. Hines, J. D. Nichols, J. E. Lyons, D. R. Smith, K. S. Kalasz, L. J. Niles, A. D. Dey, N. A. Clark, P. W. Atkinson, C. D. Minton, and W. Kendall. 2011*a*. Demographic consequences of migratory stopover: linking red knot survival to horseshoe crab spawning abundance. Ecosphere 2(6):1-22.

McGowan, C., D. Smith, J. Sweka, J. Martin, J. Nichols, R. Wong, J. Lyons, L. Niles, K. Kalasz, and J. Brust. 2009. A framework for adaptive management of horseshoe crab harvest in the Delaware Bay constrained by red knot conservation. Stock assessment report no. 09-02 (supplement B) of the Atlantic States Marine Fisheries Commission. Washington, DC, USA.

McGowan, C. P., D. R. Smith, J. A. Sweka, J. Martin, J. D. Nichols, R. Wong, J. E. Lyons, L. J. Niles, K. Kalasz, J. Brust, M. Davis, and B. Spear. 2011*b*. Multispecies modeling for adaptive management of horseshoe crabs and red knots in the Delaware Bay. Natural Resource Modeling 24:117-156.

Michielsens, C. G., M. K. McAllister, S. Kuikka, T. Pakarinen, L. Karlsson, A. Romakkaniemi, I. Pera, and S. Mantyniemi. 2006. A Bayesian state-space mark-recapture model to estimate exploitation rates in mixed-stock fisheries. Canadian Journal of Fisheries and Aquatic Sciences 63:321-334.

Mizrahi, D. S., and K. A. Peters. 2009. Relationships between sandpipers and horseshoe crabs in Delaware Bay. Pages 65-87 *in* J. T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Moore, J. E., and J. Barlow. 2011. Bayesian state-space model of fin whale abundance trends from a 1991-2008 time series of line-transect surveys in the California Current. Journal of Applied Ecology 48:1195-1205.

Morris, W. K., P. A. Vesk, M. A. McCarthy, S. Bunyavejchewin, and P. J. Baker. 2015. The neglected tool in the Bayesian ecologist's shed: a case study testing informative priors' effect on model accuracy. Ecology and Evolution 5:102-108.

Nichols, J. D., J. E. Hines, and K. H. Pollock. 1984. Effects of permanent trap response in capture probability on Jolly-Seber capture-recapture model estimates. Journal of Wildlife Management 48:289-294.

Nichols, J., and J. Hines. 1993. Survival rate estimation in the presence of tag loss using joint analysis of capture-recapture and resighting data. Pages 229-243 *in* J. D. Lebreton, and P. M. North, editors. Marked individuals in the study of bird populations. Birkhauser, Basel, Switzerland.

Niles, L. J., J. Bart, H. P. Sitters, A. D. Dey, K. E. Clark, P. W. Atkinson, A. J. Baker, K. A. Bennett, K. S. Kalasz, N. A. Clark, J. Clark, S. Gillings, A. S. Gates, P. M. Gonzalez, D. E. Hernandez, C. D. T. Minton, R. I. G. Morrison, R. R. Porter, R. K. Ross, and C. R. Veitch. 2009. Effects of horseshoe crab harvest in Delaware Bay on red knots: are harvest restrictions working? Bioscience 59:153-164.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. Trends in Ecology and Evolution 23:87-94.

Penn, D., and H. J. Brockmann. 1995. Age-biased stranding and righting in male horseshoe crabs, *Limulus polyphemus*. Animal Behaviour 49:1531-1539.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical-inference for capture-recapture experiments. Wildlife Monographs 107:1-97.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115.

Royle, J., and R. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. First edition. Academic Press, London, United Kingdom.

Royle, J. A., and R. M. Dorazio. 2012. Parameter-expanded data augmentation for Bayesian analysis of capture-recapture models. Journal of Ornithology 152:S521-S537.

Royle, J. A., and M. Kery. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813-1823.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860-873.

Schwarz, C.J., and G.A. Seber. 1999. Estimating animal abundance: review III. Statistical Science 14:427-456.

Seber, G. A. 1965. A note on the multiple recapture census. Biometrika 52:249-259.

Shuster Jr, C. N. 1982. A pictorial review of the natural history and ecology of the horseshoe crab *Limulus polyphemus,* with reference to other *Limulidae*. Progress in Clinical and Biological Research 81:1.

Shuster, C. N., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L), in Delaware Bay. Estuaries 8:363-372.

Smith, D. R., L. J. Brousseau, M. T. Mandt, and M. J. Millard. 2010. Age and sex specific timing, frequency, and spatial distribution of horseshoe crab spawning in Delaware Bay: insights from a large-scale radio telemetry array. Current Zoology 56:563-574.

Smith, D. R., C. P. McGowan, J. P. Daily, J. D. Nichols, J. A. Sweka, and J. E. Lyons. 2013. Evaluating a multispecies adaptive management framework: must uncertainty impede effective decision-making? Journal of Applied Ecology 50:1431-1440.

Smith, D. R., and S. F. Michels. 2006. Seeing the elephant. Fisheries 31:485-491.

Smith, D. R., M. J. Millard, and R. H. Carmichael. 2009. Comparative status and assessment of *Limulus polyphemus* with emphasis on the New England and Delaware Bay populations. Pages 361-386 *in* J. T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Smith, D. R., M. J. Millard, and S. Eyler. 2006. Abundance of adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay estimated from a bay-wide mark-recapture study. Fishery Bulletin 104:456-464.

Smith, D. R., P. S. Pooler, B. L. Swan, S. F. Michels, W. R. Hall, P. J. Himchak, and M. J. Millard. 2002. Spatial and temporal distribution of horseshoe crab (*Limulus polyphemus*) spawning in Delaware Bay: implications for monitoring. Estuaries 25:115-125.

Smith, D. R., and T. J. Robinson. 2015. Horseshoe crab spawning activity in Delaware Bay, USA, after harvest reduction: a mixed-model analysis. Estuaries and Coasts: 1-10.

Swan, B. L. 2005. Migrations of adult horseshoe crabs, *Limulus polyphemus*, in the Middle Atlantic Bight: a 17-year tagging study. Estuaries 28:28-40.

Walls, E. A., J. Berkson, and S. A. Smith. 2002. The horseshoe crab, *Limulus polyphemus*: 200 million years of existence, 100 years of study. Reviews in Fisheries Science 10:39-73.

Williams, B. K., F. A. Johnson, and K. Wilkins. 1996. Uncertainty and the adaptive management of waterfowl. Journal of Wildlife Management 60:223-232.

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

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2007. Adaptive management: the U.S. Department of the Interior technical guide. Adaptive Management Working Group, Washington, D.C., USA.

Zimmerman, J., S. Michels, D. Smith, and S. Bennett. 2013. Horseshoe Crap Spawning Activity in Delaware Bay: 1999-2012. Report to the Atlantic States Marine Fisheries Commission's Horseshoe Crab Technical Committee. Atlantic States Marine Fisheries Commission, Washington, DC, USA.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

FIGURES AND TABLES

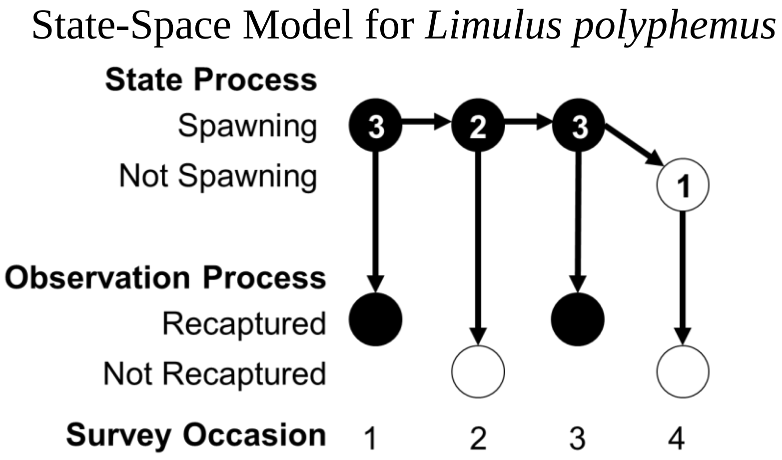

Figure 1.1. A state-space model that describes Atlantic horseshoe crab (*Limulus polyphemus*) capture history data with a model for the unobservable or partially observable state process (conditional on ecological or individual variation), and a model for the observation process (conditional on detection error and the state process). Assuming that all horseshoe crabs arrive before the spawning season, the states for an individual at each survey occasion are: (1) in the study area (Delaware Bay) but not spawning (open circle); (2) in the study area, spawning (closed circle), but not recaptured (open circle); and (3) in the study area, spawning (closed circle), and recaptured (closed circle). The capture history for this individual for a season was 1010.

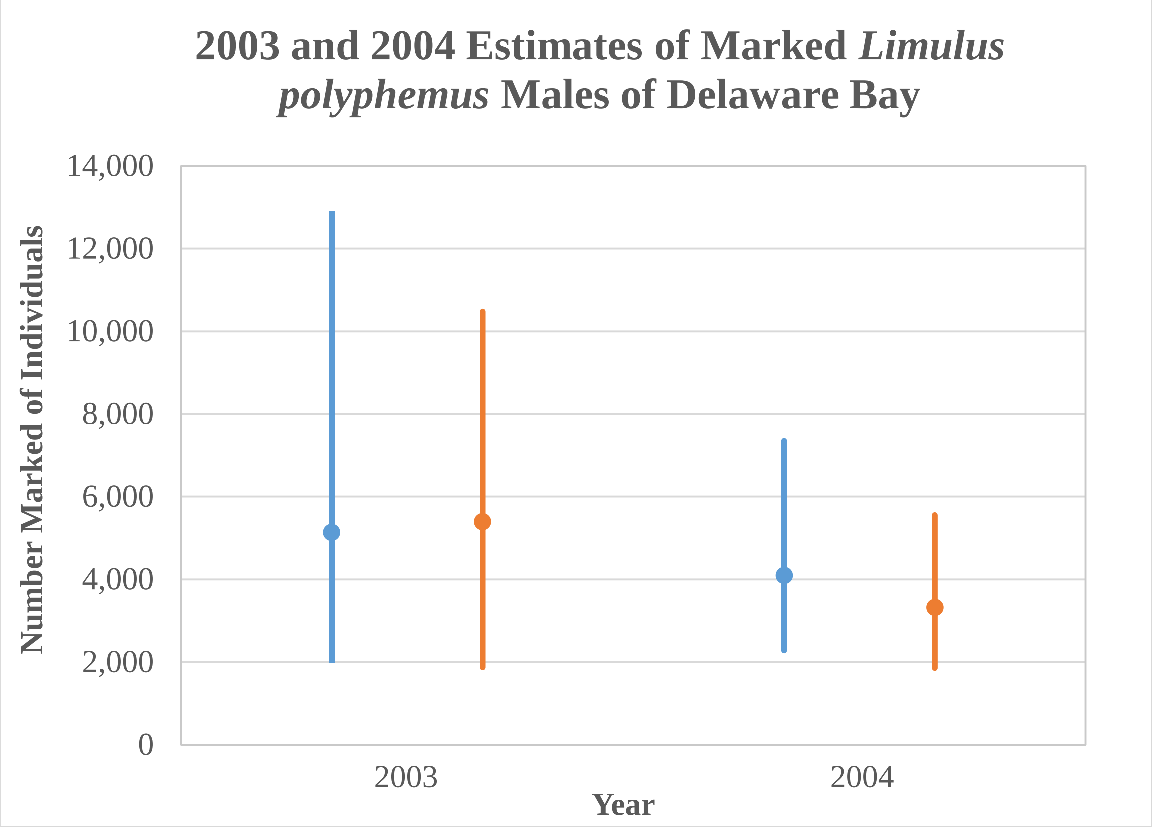

Figure 1.2. Estimates of marked Atlantic horseshoe crab (*Limulus polyphemus*) males of the 2003 and 2004 Delaware Bay spawning populations from two different mark-recapture analysis approaches preformed in Program MARK (blue) and OpenBUGS (orange). The round dots represent a mean estimate. Lines show the extent of the 95% confidence/credible intervals for that mean estimate.

Posterior Density of Detection Probability Estimates for the 2003 and 2004 Delaware Bay *Limulus polyphemus* Populations

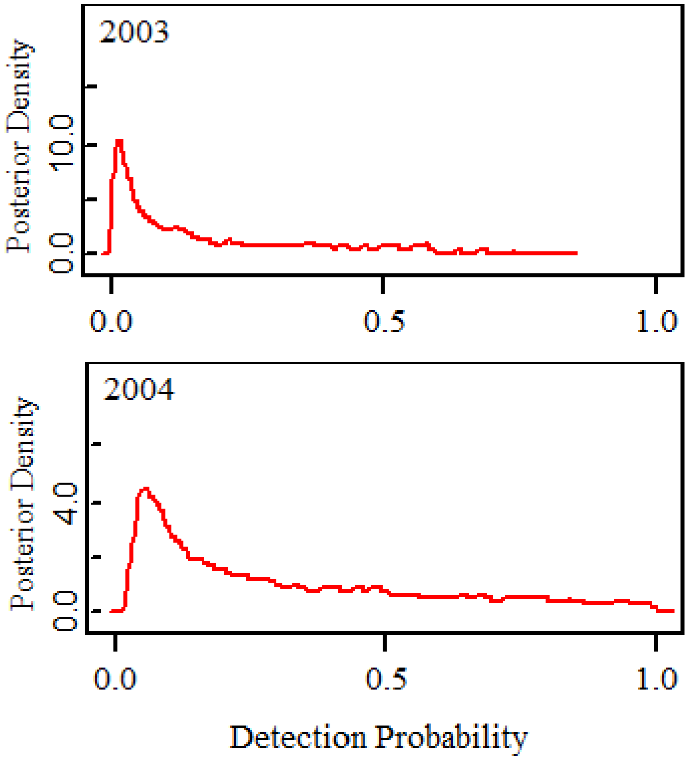

Figure 1.3. Posterior density of detection probability estimates produced by hierarchical Bayesian analyses of the 2003 and 2004 Delaware Bay Atlantic horseshoe crab (*Limulus polyphemus*) male spawning populations in OpenBUGS. The uniform prior distribution of detection probability, *p*, was restricted from 0 to 1.

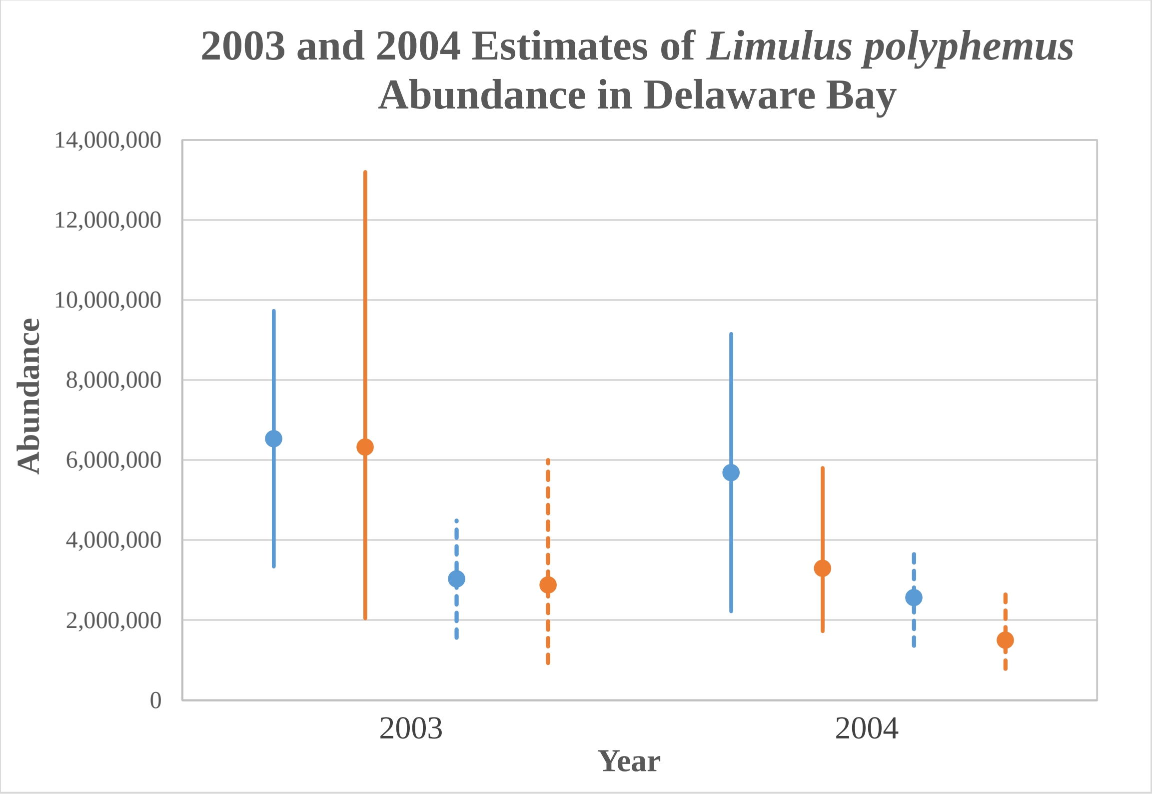

Figure 1.4. Abundance estimates of male (solid lines) and female (dashed lines) Atlantic horseshoe crabs (*Limulus polyphemus*) of the 2003 and 2004 Delaware Bay spawning populations produced in the spawning survey data analyses of this study (orange), and the trawl data analyses of D. Hata and E. Hallerman (unpublished data; blue). The round dots represent a mean estimate. Lines show the extent of the 95% credible intervals for that mean estimate.

Table 1.1. A comparison of known values, or truth, and the mean and 95% credible interval (CI) estimates of various parameters produced in a hierarchical Bayesian analysis of hypothetical Delaware Bay Atlantic horseshoe crab (*Limulus polyphemus*) spawning population and mark-recapture data.

	Truth	Model Estimates	
Parameter	Value	Mean	95% CI
Total Males[a]	3,500,000	3,848,000	2,226,000 – 6,087,000
Total Females[a]	1,590,909	1,749,000	1,012,000 – 2,767,000
Marked Males[a]	3,500	5,415	3,268 – 8,159
Proportion Marked[b]	0.001	0.0014	0.0012 – 0.0017
Detection Probability[c]	0.05	0.0166	0.0096 – 0.0277
Spawning Probability[d]			
Occasion 1	0.02	0.0711	0.0254 – 0.1440
Occasion 2	0.02	0.0359	0.0071 – 0.0880
Occasion 3	0.1	0.2406	0.1362 – 0.3754

Occasion 4	0.1	0.2999	0.1785 – 0.4527
Occasion 5	0.2	0.4803	0.3104 – 0.6833
Occasion 6	0.4	0.8845	0.6655 – 0.9957
Occasion 7	0.4	0.6585	0.4423 – 0.8991
Occasion 8	0.5	0.8665	0.6390 – 0.9944
Occasion 9	0.3	0.7154	0.4881 – 0.9483
Occasion 10	0.2	0.4205	0.2667 – 0.6070
Occasion 11	0.1	0.2160	0.1199 – 0.3432
Occasion 12	0.05	0.0720	0.0255 – 0.1441

[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[d] Probability of a male spawning at every survey occasion.

Table 1.2. Mean and 95% credible interval (CI) estimates for various parameters of the 2003 and 2004 Delaware Bay Atlantic horseshoe crab (*Limulus polyphemus*) spawning populations produced by a hierarchical Bayesian analysis in OpenBUGS.

	2003		2004	
Parameter	Mean	95% CI	Mean	95% CI
Total Males[a]	6,328,000	2,044,000 – 13,200,000	3,293,000	1,721,000 – 5,802,000
Total Females[a]	2,876,000	929,100 – 6,001,000	1,497,000	782,400 – 2,637,000
Marked Males[a]	5,399	1,871 – 10,480	3,322	1,854 – 5,551
Proportion Marked[b]	0.0008709	0.000644 – 0.001129	0.001024	0.0007918 – 0.001288
Detection Probability[c]	0.1664	0.0054 – 0.6379	0.3074	0.0382 – 0.9204
Spawning Probability[d]				
Occasion 1	0.0304	0.0007148 – 0.1278	0.0730	0.0286 – 0.1416
Occasion 2	0.0279	0.0006942 – 0.1048	0.0823	0.0336 – 0.1552
Occasion 3	0.0283	0.0006894 – 0.1056	0.1546	0.0804 – 0.2553
Occasion 4	0.1117	0.0298 – 0.2506	0.6881	0.4640 – 0.9291
Occasion 5	0.0280	0.0006959 – 0.1050	0.6078	0.4034 – 0.8456

Occasion 6	0.0839	0.0169 – 0.2073	0.9182	0.7190 – 0.9978
Occasion 7	0.3078	0.1455 – 0.5399	0.0310	0.0063 – 0.0769
Occasion 8	0.7278	0.4584 – 0.9747	0.1856	0.1013 – 0.2975
Occasion 9	0.8155	0.5536 – 0.9907	0.0206	0.0024 – 0.0587
Occasion 10	0.8746	0.6446 – 0.9954	0.0515	0.0161 – 0.1092
Occasion 11	0.8746	0.6435 – 0.9955	0.0824	0.0335 – 0.1555
Occasion 12	0.2236	0.0918 – 0.4199	0.1235	0.0597 – 0.2131
Occasion 13[e]	0.1398	0.0439 – 0.2955		
Occasion 14[e]	0.2800	0.1278 – 0.5009		
Occasion 15[e]	0.3077	0.1447 – 0.5393		

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[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[d] Probability of a male spawning at every survey occasion.

[e] 2003 season only

Chapter 2: Evaluating the Effects of Increasing Tagging and Recapture Effort on Estimate Precision and Accuracy

ABSTRACT

Effective and consistent monitoring is an essential component of wildlife management, especially for exploited populations. In the United States, the quality of information provided to managers of Atlantic horseshoe crabs (*Limulus polyphemus*), an exploited species, could improve with an increase in monitoring effort. In this chapter, we used a simulated data set to evaluate the effects of increasing tagging and recapture effort on precision and relative bias of estimates of a newly developed mark-recapture model within a Bayesian framework. We assessed the effects on model estimates when proportion of the population with marks was 0.001, 0.003, and 0.006. We also assessed effects on estimates when 12, 18, and 24 survey occasions occurred within a spawning season. Increasing the proportion of the population with marks from 0.001 to 0.003 resulted in a 47% decrease in the coefficient of variation, but a 68% increase in relative bias. Increasing the proportion from 0.001 to 0.006 produced a 68% decrease in the coefficient of variation, but a 57% increase in relative bias. Adding 6 additional surveys to total 18 occasions for the season produced a 42% decrease in the coefficient of variation, but a 69% increase in relative bias. Doubling the sampling effort to total 24 survey occasions for the seasons resulted in a 60% decrease in the coefficient of variation, but a 69% increase in relative bias. Although an increase in estimate precision

with increasing effort was achieved, future work is needed to increase estimate accuracy and improve the quality of information provided to horseshoe crab managers.

INTRODUCTION

Effective and consistent monitoring is an essential component of wildlife management, especially for exploited populations (Williams et al. 2002). In an adaptive management context, monitoring provides information to managers that helps improve understanding of a population, elucidates sources of uncertainty in a system, evaluates management performance, and aids the decision-making process (Lyons et al. 2008). Additionally, managers attempting to reach desired levels of abundance or harvest for a species can analyze data collected from monitoring efforts to determine the status of a population and adjust management accordingly (Williams et al. 2002, Lyons et al. 2008). However, most species are impossible to monitor without error, which introduces uncertainty into estimates and may make decision-making difficult for managers (MacKenzie et al. 2002, Royle and Kery 2007, Royle and Dorazio 2008, Kendall et al. 2009). Reducing uncertainty of parameter estimates increases the certainty surrounding the state of a population and increases the quality of information provided to managers (Williams et al. 1996, Kendall et al. 2009). Increasing the quantity of data is one way to increase the quality of information (Zippin 1958, Williams et al. 2002, Royle and Dorazio 2008), therefore, priority should potentially be placed on improving monitoring effort by increasing the amount of data collected (Dreitz et al. 2002, MacKenzie et al. 2002). As an example, management and monitoring of Atlantic horseshoe crabs, *Limulus polyphemus* (hereafter horseshoe crab), in Delaware Bay, USA could improve with an increase in data collection effort.

Horseshoe crabs have a unique physiology and reproductive strategy that make them an important ecological and economic multiple-use resource (Berkson and Shuster 1999, Smith et al. 2009). Each spring, the heavy spawning activity of millions of male and female horseshoe crabs draws migratory shorebirds to Delaware Bay beaches for two to three weeks, where they regain mass from the widely abundant, energy-rich horseshoe crabs eggs available there (Niles et al. 2009, Mizrahi and Peters 2009). Additionally, the biomedical industry extracts blood from hundreds of thousands of horseshoe crabs annually to create Limulus Ameobocyte Lysate (LAL), which is used in testing for bacterial contamination in pharmaceutical and medical products (Hall 1992, ASMFC 1998). Lastly, commercial whelk (*Busycon spp.*) and American eel (*Anguilla rostrada*) fisheries catch hundreds of thousands of horseshoe crabs each year along certain portions of the Atlantic Coast for bait (ASMFC 1998). Management of horseshoe crabs is important to satisfy the needs of all user groups while ensuring their role in the ecosystem for the long-run (ASMFC 1998). The Atlantic States Marine Fisheries Commission created a management plan for horseshoe crabs in 1998 to accomplish this, and adopted an adaptive management plan in 2012 that addressed the concern over migratory shorebirds' potential reliance on horseshoe crab eggs for survival (McGowan et al. 2009, ASMFC 2012). The objectives for adaptive management of horseshoe crabs included adjusting harvest policies and management actions according to all competing stakeholder objectives, best available scientific data, and ecological uncertainty surrounding horseshoe crabs and shorebirds (Williams et al. 2002, 2007; McGowan et al. 2009, 2011; Smith et al. 2013).

Monitoring is essential for this adaptive management plan and provides information that aids the decision-making process. Prior to 2013, analyses of offshore trawl survey data had been the primary source of information for managers (Hata and Berkson 2004, McGowan et al. 2009). However, these surveys were expensive to operate and funding was discontinued (C. P. McGowan, U.S. Geological Survey, personal communication). Recently, a new analysis approach was developed that takes advantage of annual, volunteer-based spawning survey and mark-recapture data collection efforts (Smith and Michels 2006), and produces results that are comparable to those of trawl surveys (see Chapter 1). However, the quality of estimates produced by this approach might improve with the use of larger data sets. Larger amounts of horseshoe crab data could be accomplished by increasing the proportion of the population that is marked, or by increasing the amount of surveys conducted within the spawning season.

In this chapter, we used a simulated data set that mimics the annual spawning survey and mark-recapture data collected on horseshoe crabs to evaluate the effects of increasing tagging and recapture effort on precision and relative bias of estimates produced by the hierarchical, state-space model we developed in Chapter 1. We used a simulation study to check that our estimates from the OpenBUGS analysis correctly estimated known values, and analyzed data that reflect higher levels of monitoring effort not currently conducted on horseshoe crabs (Kery and Schaub 2012).

METHODS

A full description of the hierarchical, state-space superpopulation model we developed is provided in Chapter 1 of this thesis. Our model is a modified version of Jolly-Seber (Jolly 1965, Seber 1965) mark-recapture models developed by Crosbie and Manly (1985) and Schwarz and Arnason (1996), and allows for an open population. Our model is similar to one recently applied to red knot abundance estimation by J.E. Lyons et al. (U.S. Fish and Wildlife Service, unpublished report). However, it differs in that our state-space model partitions variance in survey-to-survey encounters of horseshoe crabs into a population-level, temporally-dependent spawning probability state process, and a constant detection and survival probability observation process conditional on the state process.

In addition to other parameters, our model calculated the total number of marked males in Delaware Bay for a season by summing together the number of marked and spawning horseshoe crabs (as determined by the model) from every survey occasion. We incorporated "real" observations of marked and unmarked horseshoe crabs counted within quadrats by summing the first 25% of each column in the capture history data set to obtain a count of the number of tagged crabs observed in the quadrats. We simulated the total number counted at each survey occasion by multiplying the total population size by the spawning probability for that occasion and some proportion of the available habitat surveyed; for these simulations we used 0.9%. Our analysis used a binomial model for count data to estimate the proportion of the population with marks and total abundance, as suggested by Lyons et al. (unpublished report):

$$m_t \sim Binomial(C_t, \pi) \tag{1}$$

where the number of marked males counted (m_t) during survey occasion t is a binomial random variable of the total number of males counted (C_t) and the proportion of marked males in the population (π). The likelihood model of π is,

$$\hat{\pi} = {}^{m_t}/_{C_t} \tag{2}$$

or the ratio of marked-to-unmarked males in the population. We kept the proportion of the population that was marked (π) constant for each season by assuming that the proportion does not change throughout the spawning season, but may change from year to year due to mortality and tagging effort. Our model calculated the total Delaware Bay male population size (superpopulation) for a season by dividing the sum of the number of marked and spawning males at each survey occasion by $\hat{\pi}$. To estimate Delaware Bay female abundance for a season as a derived parameter with a posterior distribution, we divided male abundance by a male-to-female sex ratio of 2.2 (Smith et al. 2006) within our model.

To evaluate the effects of increasing tagging and recapture effort, we developed a simulation model (Appendix B) to simulate data similar to those collected in and analyzed for 2003 and 2004 (from Chapter 1). The simulation generated capture histories for known numbers of tagged individuals, with known population size, detection probability, and spawning probabilities. As in a previous analysis (see Chapter 1), we simulated 3,500 marked individuals from a population of 3,500,000 males (e.g., 0.001 proportion of the animals were marked), collected from 12 survey occasions for this simulation study to represent the most basic level of tagging and recapture effort (Table 2.1). We augmented the 3,500 capture histories out to 13,000 to match the data augmentation process we used in Chapter 1. Parameter-expanded data augmentation (PX-

DA) is the process of adding an arbitrary but fixed amount of all-zero capture histories to recapture data to account for marked individuals that were never recaptured, and analyzing the augmented data set with a reparameterized mark-recapture model (Royle and Dorazio 2008, 2012). Augmented capture histories help account for imperfect detection and heterogeneity among individuals, therefore, estimates would be less precise in the absence data augmentation (Royle and Dorazio 2008). Additionally, for this simulation study we increased the proportion of the population that is marked from 0.001 to 0.003 and 0.006, holding the total population size constant at 3,500,000. Within these 0.003- and 0.006-proportion marked tagging effort scenarios, data were collected on 12 survey occasions, and contained 10,500 marked individuals and 20,500 capture histories (including data augmentation) for 0.003, and 21,000 marked individuals and 31,000 capture histories (including data augmentation) for 0.006 (Tables 2.2 and 2.3).

We also increased the number of survey occasions within a season from 12 to 18 and 24, keeping the total population size constant at 3,500,000. For these 18- and 24-survey occasion scenarios, we kept the proportion of the population with marks at 0.001, resulting in 13,000 capture histories (with data augmentation), and 3,500 marked individuals (Tables 2.4 and 2.5). For all tagging and recapture effort scenarios, we set detection probability at 0.05 to reflect recent mark-recapture analyses, although those analyses used somewhat different data than our study (Butler 2012). Additionally, we set survival probability to 1 in the simulation model to mimic horseshoe crabs' high survival and maintain some control over what the model was estimating.

For each effort scenario, we ran a Bayesian Markov chain Monte Carlo analysis of our hierarchical, state-space model using simulated data for that scenario, and completed 50,000 realizations with 5,000 burn-ins, no thinning (Link and Eaton 2012), and 3 chains in OpenBUGS (OpenBUGS version 3.2.3, http://www.openbugs.net/w/FrontPage, accessed 1 Dec 2014). We gave all parameters uninformed prior distributions from uniform or beta distributions, as appropriate.

We calculated the relative bias of abundance estimates produced in these analyses by,

$$Bias = \left({}^{(\widehat{N} - N)}\!\big/_{N} \right) \times 100 \tag{3}$$

where $\widehat{N}$ is the mean abundance estimate and N is the known abundance value. We used the coefficient of variation (CV) from each effort scenario to compare precision of abundance estimates.

RESULTS

The analysis of simulated data containing 12 occasions and 0.001 proportion of the population marked estimated that there were 3,848,000 (2,226,000 – 6,087,000; 95% CI) males in our simulated horseshoe crab population (Table 2.1). The relative bias of this estimate was 9.9% and the CV was 26.6%. The estimate of the number of marked males in the population was 5,415 (3,268 – 8,159; 95% CI). The credible intervals of the mean estimates of those parameters, as well as the interval for the female abundance estimate, contained the known value (Table 2.1). In this scenario, our model overestimated the proportion of the population with marks and most spawning probabilities, and underestimated detection probability. Estimates for those parameters did not contain truth in their credible intervals (Table 2.1).

The analysis of data from the 0.003-proportion marked scenario estimated 2,424,000 (1,831,000 – 3,164,000; 95% CI) males in the population (Table 2.2), with a negative relative bias of 30.7% and CV of 14.2%. The credible interval of estimated male abundance, as well as the credible interval for the estimate of female abundance, did not contain the known value. The analysis estimated that there were 10,080 (7,865 – 12,840; 95% CI) marked males in the population when the proportion marked was 0.003, and the credible intervals for that mean estimate did contain truth (10,500; Table 2.2). Increasing the proportion of the population marked from 0.001 to 0.003 resulted in a 47% decrease in the coefficient of variation, but a 68% increase in relative bias.

The analysis of 0.006-proportion marked tagging effort data estimated 2,688,000 (2,249,000 – 3,105,000; 95% CI) males in the simulated population (Table 2.3), with a negative relative bias of 23.2% and CV of 8.2%. As in the 0.003-proportion marked scenario, the credible intervals of that parameter estimate and the estimate of female population size did not contain truth. The estimate of marked males was 21,390 (18,290 – 24,040; 95% CI) and its credible interval contained the known value (21,000; Table 2.3). Increasing the proportion of the population with marks from 0.001 to 0.006 produced a 68% decrease in the coefficient of variation, but a 57% increase in relative bias.

In both tagging effort scenarios, our model overestimated the proportion of the population that was marked and most spawning probabilities, and underestimated the probability of detection (Tables 2.2 and 2.3). All of those estimates' credible intervals did not contain known values from the simulation model.

Analysis of the recapture effort scenario with 18 survey occasions estimated 2,370,000 (1,757,000 – 3,182,000; 95% CI) males in the simulated population (Table

2.4), with a negative relative bias of 32.3% and CV of 15.3%. Female abundance was also underestimated, and the credible intervals for estimates of male and female abundance did not contain truth. The estimate for the number of marked horseshoe crabs in the population was 3,270 (2,547 – 4,251: 95% CI) for 18 survey occasions, and its credible interval did encompass the known value (3,500; Table 2.4). Analysis of the 24-survey occasions scenario estimated that there were 2,387,000 (1,928,000 – 2,917,000; 95% CI) males in the simulated population (Table 2.5), with a negative relative bias of 31.8% and 10.6% CV. Female abundance was similarly underestimated. The credible intervals for male and female abundance estimates did not contain each estimates' respective known value. The number of marked males in the population was 3,627 (3,056 – 4,272; 95% CI), and the credible interval for that estimate contained truth (3,500; Table 2.5). For both recapture effort scenarios, our model overestimated the proportion of the population that was marked and underestimated detection probability (Tables 2.4 and 2.5). Both of these estimates did not contain truth in their credible intervals. Our model also overestimated most spawning probabilities, but the credible intervals for spawning probability at occasions 1, 2, 4 and 18 contained truth when the data contained 18 survey occasions. Additionally, only occasions 1 and 4 in the 24-survey effort scenario had spawning probability credible interval estimates that contained truth.

Adding 6 additional surveys to total 18 occasions for the season produced a 42% decrease in the coefficient of variation and a 69% increase in relative bias. Doubling the sampling effort to total 24 survey occasions for the seasons resulted in a 60% decrease in the coefficient of variation and a 69% increase in relative bias.

DISCUSSION

The purpose of this simulation study was evaluate the effects of increasing tagging and recapture effort on estimate precision and relative bias produced by the mark-recapture model we developed. In theory, increasing effort may reduce bias and variance in estimates, and, therefore, increase the quality of information provided to horseshoe crab managers and aid the decision-making process (Williams et al. 1996, 2002; Royle and Dorazio 2008; Kendall et al. 2009). We could have investigated the effects of very high levels of effort on the estimates, however we focused on evaluating effects of reasonable increases in effort that managers could implement with limited resources.

In this study, when effort increased, precision increased but relative bias increased as well (Figs. 2.1 and 2.2). Regarding the abundance estimates, we expected relative bias to decrease with more recapture data (Pollock et al. 1990, Williams et al. 2002). The increase in relative bias we observed may have been because the abundance estimate is derived from several different parameters. The estimate for number of marked males in all scenarios was very accurate, but we divided it by the positively biased proportion of the population with marks to determine male abundance. That bias coupled with increasing estimate precision resulted in the negative relative bias and failure of credible intervals to contain truth that we observed for abundance estimates. However, this simulation study was rudimentary in that it only incorporated one data set. Therefore, our estimates were most likely affected by a unique set of observation stochasticity within that data set, and our conclusions are limited. A more thorough analysis should simulate hundreds of data sets to determine average model bias and generate more conclusive results.

In every scenario, our model underestimated detection probability, and overestimated most spawning probabilities and proportion of the population with marks. We created sparse data sets for each scenario to mimic low detection probabilities experienced during spawning surveys, but with such sparse data, our model may have had difficulty attributing uncertainty to various parameters in the model, resulting in inaccuracy of detection probabilities, proportions of the population with marks, and spawning probabilities (Royle and Dorazio 2008, Kendall et al. 2009). Consequently, estimates of total abundance in each scenario were biased low (Figs. 2.1 and 2.2; Pollock et al. 1990, Williams et al. 2002, Royle and Dorazio 2008, Kendall et al. 2009). Additionally, state-space models do not provide unbiased estimates of abundance because counts of horseshoe crabs are always smaller than the true population size (Kery and Schaub 2012). Regardless, analyses of various data sets with different sources of variation may produce different results. Running multiple data sets would help us determine the degree to which our model over-, under-, or correctly estimates certain parameters.

Furthermore, our simulated data and the empirical data collection may not have met the assumptions of our model, which possibly led us to the results we observed. Specifically, for this simulation study, counts of marked individuals were generated by summing the first 25% of capture histories, not determined independently from the mark-recapture data collection (Appendix B). This process mimicked the actual data collection in the field. However, in theory, the capture histories and marked-to-unmarked data are supposed to represent two independent data streams (Lyons et al., unpublished report). We also did not include environmental, behavioral, or observational variation (which would be expected in real data sets) into the count data created for this simulation study. Future development of this model and simulation should consider these complexities.

The tagging and recapture effort scenarios used for this simulation study were set to reflect potentially achievable effort levels by managers willing to improve data quality. Ten years ago, there were about 60,000 marked individuals (male and female) in the Delaware Bay population (D. R. Smith, U.S. Geological Survey, personal communication). That may not have been the exact amount present in 2003, but given that number, 0.003 would be the proportion of the population marked based on Smith et al.'s (2006) total abundance estimate of 19,980,000 (12,780,000 – 28,240,000; 90% CI). Additionally, 0.006 would be the proportion based on D. Hata and E. Hallerman's (Virginia Polytechnic Institute and State University, unpublished data) total abundance estimate of 9,560,000 (4,900,000 –14,220,000; 95% CI) for 2003. The proportion of the population with marks is variable depending on the estimate produced, but 0.003 and 0.006 levels are achievable, and, as this simulation study showed, increasing the amount of tagging effort brings more precise, but inaccurate, estimates of abundance (Fig. 2.1). Surveys are currently limited to only 12 or 15 occasions within a spawning season, take place 2 days before, the day of, and 2 days after new or full moons (spring tides) in May and June, and coincide with peak spawning activity (Shuster and Botton 1985; Smith et al. 2002, 2010). As shown in this study, increasing the amount of survey occasions to 18 or 24 increases precision (Fig. 2.2), and is possible because volunteers who participate in data collection have great interest in the research (Smith and Michels 2006).

Simulation studies similar to ours have been conducted in the past. Lyons et al. (unpublished report) developed a simulation study to evaluate, among other things, the effects increasing the number of scan samples per day and proportion of the population that was marked on bias and precision of estimates for the proportion marked. They found that bias was about zero for all scenarios, but precision of estimates for the proportion marked increased when the number of scan samples per day increased. Additionally, they concluded that if tagging efforts continue, thus increasing the proportion of the population that is marked over time, the precision of estimates generated from data collected on the population would increase as well. A simulation study by Lahoz-Monfort et al. (2013) differed from ours in that they removed data (as opposed to adding) from an existing mark-recapture data set within a frequentist framework, and evaluated the effects of decreasing tagging and resighting (recapture) effort only on the estimate of survival. They found that estimate precision decreased and bias increased with a decrease in tagging and resighting effort and, therefore, an increase in data sparseness. Calvert et al. (2009) concluded similarly to Lahoz-Monfort et al. (2013), and found that bias and precision of all parameter estimates produced by their hierarchical model within a Bayesian framework decreased with improved data quality. These studies come to similar conclusions as we did in regard to estimate precision, however our analyses resulted in decreased accuracy, which indicates potential problems with our simulated data or analytical model. Future work is needed to improve accuracy of estimates.

The ultimate goal of this study was to analyze data that reflect higher but feasible levels of monitoring effort not currently conducted on horseshoe crabs, and provide valuable information to horseshoe crab managers for designing an improved monitoring plan. While the results of this chapter were not completely satisfying, they did produce some useful insights regarding the utility of the Bayesian analytic framework for estimating horseshoe crab abundance. Future development of this model may be necessary, especially with respect to detection and spawning probabilities and running more simulated data sets, but if the inaccuracy we observed is consistent for all data analyzed, adjustments can be made to estimates that may capture truth more effectively.

If a manager used our model in its current form to design a monitoring plan, increasing the proportion of the population that is marked by tagging more individuals could yield more precise estimates of abundance. To accomplish this, we would suggest adding more tags to the population annually, either before the spawning season starts or throughout the year. Managers could also increase estimate precision by increasing the amount of surveys conducted in a season by scheduling more surveys between those that currently take place during spring tides, such as during neap tide periods when substantial spawning is believed to occur (Smith and Robinson 2015). Given that a tagging effort of 0.003 and conducting 18 surveys brought sufficient estimate precision (around 15% CV; Brown 1948), there is no need for additional tagging or survey effort beyond those levels. Tagging animals for mark-recapture studies can be very time consuming and costly (Royle 2004), therefore, increasing the number of surveys may be a more feasible option for horseshoe crab managers.

LITERATURE CITED

Atlantic States Marine Fisheries Commission (ASMFC). 1998. Interstate fishery management plan for horseshoe crab. Fishery management report no. 32. ASMFC, Washington, D.C., USA.

_____. 2012. Addendum VII to the interstate fishery management plan for the horseshoe crab for public comment: adaptive resource management framework. ASMFC, Washington, D.C., USA.

Berkson, J., and C. N. Shuster. 1999. The horseshoe crab: the battle for a true multiple-use resource. Fisheries 24:6-10.

Butler, C. A. 2012. Estimation of survival of the Atlantic horseshoe crab, *Limulus polyphemus*, by analysis of mark-recapture tag loss. Thesis, Auburn University, Auburn, Alabama, USA.

Brown, C. E. 1948. Coefficient of variation. Pages 155-157 *in* Applied multivariate statistics in geohydrology and related sciences. Springer Science & Business Media, New York, USA.

Calvert, A. M., S. J. Bonner, I. D. Jonsen, J. M. Flemming, S. J. Walde, and P. D. Taylor. 2009. A hierarchical Bayesian approach to multi-state mark-recapture: simulations and applications. Journal of Applied Ecology 46:610-620.

Crosbie, S. F., and B. F. Manly. 1985. A new approach for parsimonious modelling of capture-mark-recapture experiments. Biometrics 41:385-398.

Dreitz, V. J., J. D. Nichols, J. E. Hines, R. E. Bennetts, W. M. Kitchens, and D. L. Deangelis. 2002. The use of resighting data to estimate the rate of population growth of the snail kite in Florida. Journal of Applied Statistics 29:609-623.

Hall, W. R., Jr. 1992. The horseshoe crab - a reminder of Delaware's past. University of Delaware, Sea Grant Marine Advisory Service, Newark, Delaware, USA.

Hata, D., and J. Berkson. 2004. Factors affecting horseshoe crab *Limulus polyphemus* trawl survey design. Transactions of the American Fisheries Society 133:292-299.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both dead and immigration-stochastic model. Biometrika 52:225-247.

Kendall, W. L., S. J. Converse, P. F. Doherty, Jr., M. B. Naughton, A. Anders, J. E. Hines, and E. Flint. 2009. Sampling design considerations for demographic studies: a case of colonial seabirds. Ecological Applications 19:55-68.

Kery, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, Massachusetts, USA.

Lahoz-Monfort, J. J., M. P. Harris, B. J. T. Morgan, S. N. Freeman, and S. Wanless. 2013. Exploring the consequences of reducing survey effort for detecting individual and temporal variability in survival. Journal of Applied Ecology 51:534-543.

Link, W. A., and M. J. Eaton. 2012. On thinning of chains in MCMC. Methods in Ecology and Evolution 3:112-115.

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. The Journal of Wildlife Management 72:1683-1692.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

McGowan, C., D. Smith, J. Sweka, J. Martin, J. Nichols, R. Wong, J. Lyons, L. Niles, K. Kalasz, and J. Brust. 2009. A framework for adaptive management of horseshoe crab harvest in the Delaware Bay constrained by red knot conservation. Stock assessment report no. 09-02 (supplement B) of the Atlantic States Marine Fisheries Commission. Washington, DC, USA.

McGowan, C. P., D. R. Smith, J. A. Sweka, J. Martin, J. D. Nichols, R. Wong, J. E. Lyons, L. J. Niles, K. Kalasz, J. Brust, M. Davis, and B. Spear. 2011. Multispecies modeling for adaptive management of horseshoe crabs and red knots in the Delaware Bay. Natural Resource Modeling 24:117-156.

Mizrahi, D. S., and K. A. Peters. 2009. Relationships between sandpipers and horseshoe crabs in Delaware Bay. Pages 65-87 *in* J. T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Niles, L. J., J. Bart, H. P. Sitters, A. D. Dey, K. E. Clark, P. W. Atkinson, A. J. Baker, K. A. Bennett, K. S. Kalasz, N. A. Clark, J. Clark, S. Gillings, A. S. Gates, P. M. Gonzalez, D. E. Hernandez, C. D. T. Minton, R. I. G. Morrison, R. R. Porter, R. K. Ross, and C. R. Veitch. 2009. Effects of horseshoe crab harvest in Delaware Bay on red knots: are harvest restrictions working? Bioscience 59:153-164.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical-inference for capture-recapture experiments. Wildlife Monographs 107:1-97.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115.

Royle, J., and R. Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. First edition. Academic Press, London, United Kingdom.

Royle, J. A., and R. M. Dorazio. 2012. Parameter-expanded data augmentation for Bayesian analysis of capture-recapture models. Journal of Ornithology 152:S521-S537.

Royle, J. A., and M. Kery. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813-1823.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860-873.

Seber, G. A. 1965. A note on the multiple recapture census. Biometrika 52:249-259.

Shuster, C. N., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L), in Delaware Bay. Estuaries 8:363-372.

Smith, D. R., L. J. Brousseau, M. T. Mandt, and M. J. Millard. 2010. Age and sex specific timing, frequency, and spatial distribution of horseshoe crab spawning in Delaware Bay: insights from a large-scale radio telemetry array. Current Zoology 56:563-574.

Smith, D. R., C. P. McGowan, J. P. Daily, J. D. Nichols, J. A. Sweka, and J. E. Lyons. 2013. Evaluating a multispecies adaptive management framework: must uncertainty impede effective decision-making? Journal of Applied Ecology 50:1431-1440.

Smith, D. R., and S. F. Michels. 2006. Seeing the elephant. Fisheries 31:485-491.

Smith, D. R., M. J. Millard, and R. H. Carmichael. 2009. Comparative status and assessment of *Limulus polyphemus* with emphasis on the New England and Delaware Bay populations. Pages 361-386 *in* J. T. Tanacredi et al., editors. Biology and conservation of horseshoe crabs. Springer Science & Business Media, New York, USA.

Smith, D. R., M. J. Millard, and S. Eyler. 2006. Abundance of adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay estimated from a bay-wide mark-recapture study. Fishery Bulletin 104:456-464.

Smith, D. R., P. S. Pooler, B. L. Swan, S. F. Michels, W. R. Hall, P. J. Himchak, and M. J. Millard. 2002. Spatial and temporal distribution of horseshoe crab (*Limulus polyphemus*) spawning in Delaware Bay: implications for monitoring. Estuaries 25:115-125.

Smith, D. R., and T. J. Robinson. 2015. Horseshoe crab spawning activity in Delaware Bay, USA, after harvest reduction: a mixed-model analysis. Estuaries and Coasts: 1-10.

Williams, B. K., F. A. Johnson, and K. Wilkins. 1996. Uncertainty and the adaptive management of waterfowl. Journal of Wildlife Management 60:223-232.

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

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2007. Adaptive management: the U.S. Department of the Interior technical guide. Adaptive Management Working Group, Washington, D.C., USA.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

FIGURES AND TABLES

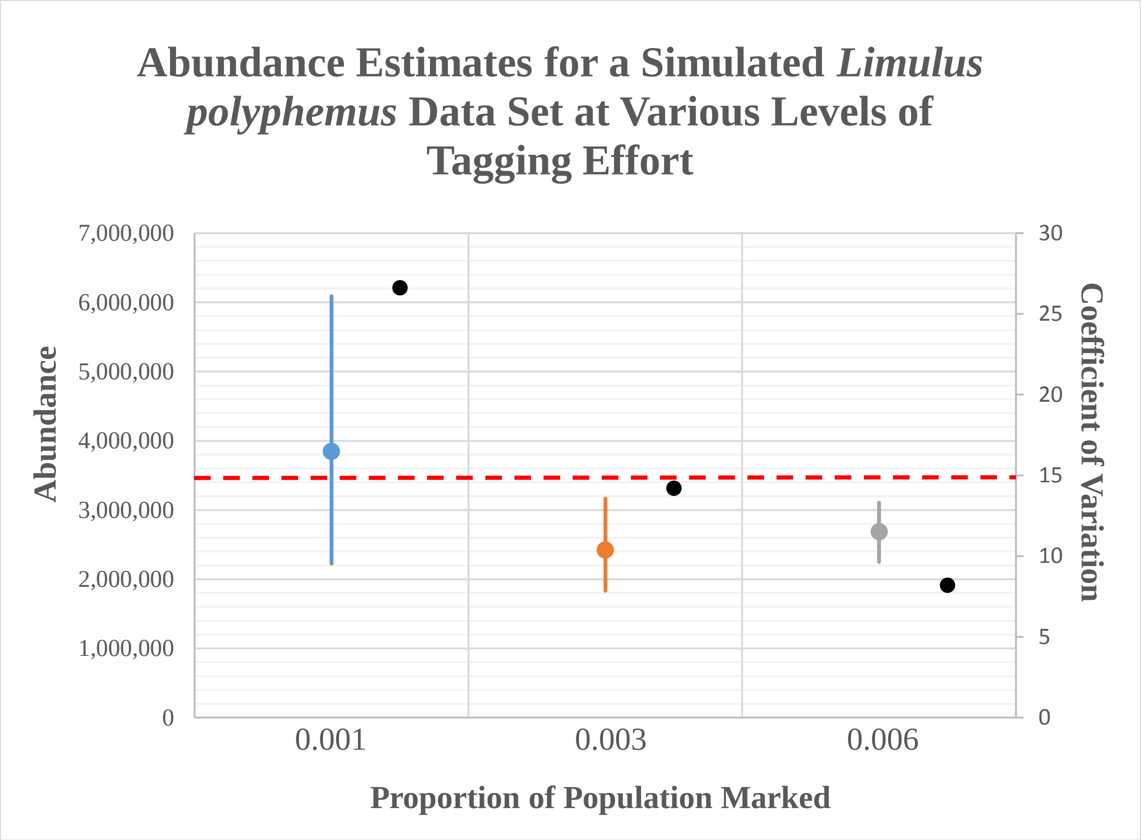

Figure 2.1. Abundance estimates and coefficients of variation at various levels of tagging effort from a hierarchical Bayesian analysis on a simulated data set of male Atlantic horseshoe crabs (*Limulus polyphemus*). A colored round dot represents a mean estimate (left y-axis) for the level of tagging effort listed on the x-axis, and the line extending from a mean estimate shows the range of its 95% credible interval. A black dot is the coefficient of variation (right y-axis) for the mean estimate of that tagging effort scenario. The red dotted line shows the known value (3,500,000) for abundance estimates. This red dotted line also is the 15% coefficient of variation threshold indicative of sufficient estimate precision.

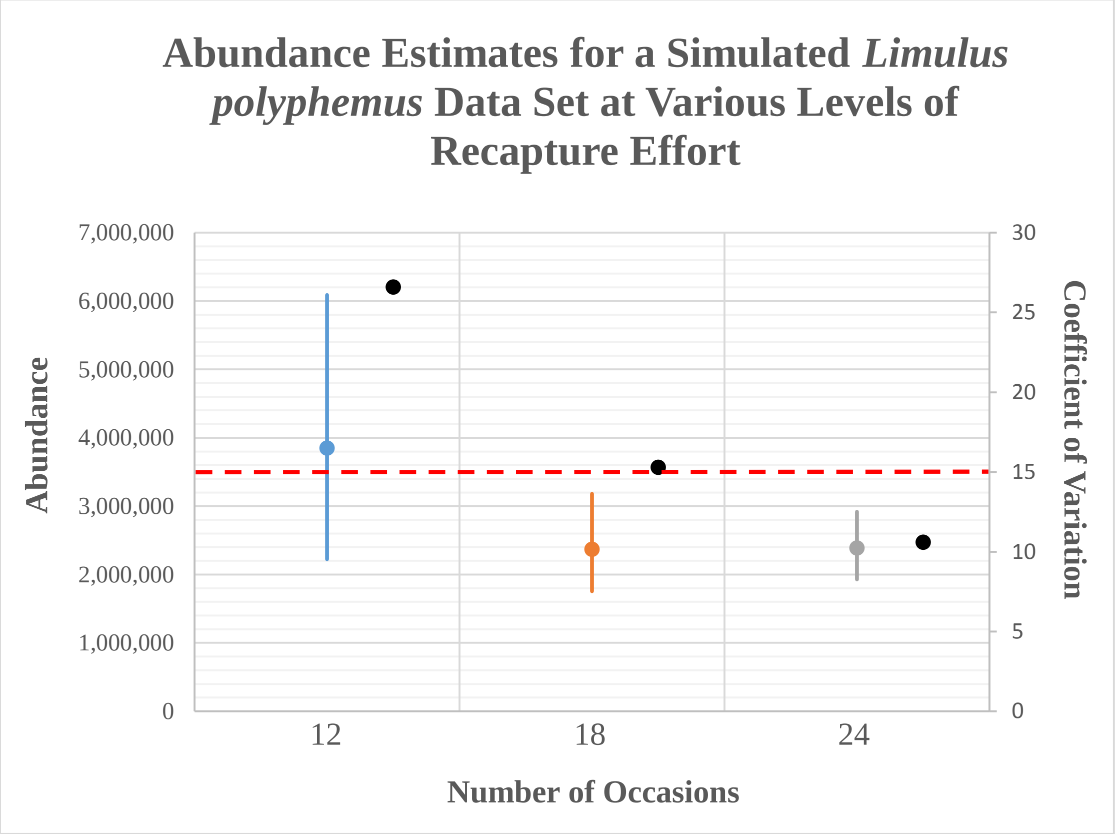

Figure 2.2. Abundance estimates and coefficients of variation at various levels of recapture effort from a hierarchical Bayesian analysis on a simulated data set of male Atlantic horseshoe crabs (*Limulus polyphemus*). A colored round dot represents a mean estimate (left y-axis) for the level of recapture effort listed on the x-axis, and the line extending from a mean estimate shows the range of its 95% credible interval. A black dot is the coefficient of variation (right y-axis) for the mean estimate of that tagging effort scenario. The red dotted line shows the known value (3,500,000) for abundance estimates. This red dotted line also is the 15% coefficient of variation threshold indicative of sufficient estimate precision.

Table 2.1. A comparison of known values, or truth, and the mean and 95% credible interval (CI) estimates of various parameters produced from a hierarchical Bayesian analysis of a simulated Atlantic horseshoe crab (*Limulus polyphemus*) population, of which the proportion with tags is 0.001 and number of survey occasions is 12.

	Truth	Model Estimates	
Parameter	Value	Mean	95% CI
Total Males[a]	3,500,000	3,848,000	2,226,000 – 6,087,000
Total Females[a]	1,590,909	1,749,000	1,012,000 – 2,767,000
Marked Males[a]	3,500	5,415	3,268 – 8,159
Proportion Marked[b]	0.001	0.0014	0.0012 – 0.0017
Detection Probability[c]	0.05	0.0166	0.0096 – 0.0277
Spawning Probabilities[d]			
Occasion 1	0.02	0.0711	0.0254 – 0.1440
Occasion 2	0.02	0.0359	0.0071 – 0.0880
Occasion 3	0.1	0.2406	0.1362 – 0.3754
Occasion 4	0.1	0.2999	0.1785 – 0.4527

Occasion 5	0.2	0.4803	0.3104 – 0.6833
Occasion 6	0.4	0.8845	0.6655 – 0.9957
Occasion 7	0.4	0.6585	0.4423 – 0.8991
Occasion 8	0.5	0.8665	0.6390 – 0.9944
Occasion 9	0.3	0.7154	0.4881 – 0.9483
Occasion 10	0.2	0.4205	0.2667 – 0.6070
Occasion 11	0.1	0.2160	0.1199 – 0.3432
Occasion 12	0.05	0.0720	0.0255 – 0.1441

---

[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[d] Probability of a male spawning at every survey occasion.

Table 2.2. A comparison of known values, or truth, and the mean and 95% credible interval (CI) estimates of various parameters produced from a hierarchical Bayesian analysis of a simulated Atlantic horseshoe crab (*Limulus polyphemus*) population, of which the proportion with tags is 0.003.

	Truth	Model Estimates	
Parameter	Value	Mean	95% CI
Total Males[a]	3,500,000	2,424,000	1,831,000 – 3,164,000
Total Females[a]	1,590,909	1,102,000	832,400 – 1,438,000
Marked Males[a]	10,500	10,080	7,865 – 12,840
Proportion Marked[b]	0.003	0.0042	0.0037 – 0.0047
Detection Probability[c]	0.05	0.0279	0.0198 – 0.0395
Spawning Probability[d]			
Occasion 1	0.02	0.0332	0.0144 – 0.0607
Occasion 2	0.02	0.0513	0.0264 – 0.0844
Occasion 3	0.1	0.2128	0.1456 – 0.2861
Occasion 4	0.1	0.2278	0.1572 – 0.3050

Occasion 5	0.2	0.3454	0.2462 – 0.4468
Occasion 6	0.4	0.7526	0.5574 – 0.9289
Occasion 7	0.4	0.7375	0.5464 – 0.9114
Occasion 8	0.5	0.9157	0.7149 – 0.9977
Occasion 9	0.3	0.5913	0.4345 – 0.7389
Occasion 10	0.2	0.3490	0.2478 – 0.4503
Occasion 11	0.1	0.1725	0.1146 – 0.2367
Occasion 12	0.05	0.0990	0.0597 – 0.1456

---

[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[e] Probability of a male spawning at every survey occasion.

Table 2.3. A comparison of known values, or truth, and the mean and 95% credible interval (CI) estimates of various parameters produced from a hierarchical Bayesian analysis of a simulated Atlantic horseshoe crab (*Limulus polyphemus*) population, of which the proportion with tags is 0.006.

	Truth	Model Estimates	
Parameter	Value	Mean	95% CI
Total Males[a]	3,500,000	2,688,000	2,249,000 – 3,105,000
Total Females[a]	1,590,909	1,222,000	1,022,000 – 1,411,000
Marked Males[a]	21,000	21,390	18,290 – 24,040
Proportion Marked[b]	0.006	0.0080	0.0073 – 0.0086
Detection Probability[c]	0.05	0.0265	0.0214 – 0.0353
Spawning Probability[d]			
Occasion 1	0.02	0.0395	0.0233 – 0.0598
Occasion 2	0.02	0.0520	0.0324 – 0.0753
Occasion 3	0.1	0.1885	0.1350 – 0.2396
Occasion 4	0.1	0.1831	0.1308 – 0.2328

Occasion 5	0.2	0.3805	0.2798 – 0.4647
Occasion 6	0.4	0.7701	0.5706 – 0.9171
Occasion 7	0.4	0.7791	0.5813 – 0.9274
Occasion 8	0.5	0.9140	0.6975 – 0.9977
Occasion 9	0.3	0.5150	0.3813 – 0.6211
Occasion 10	0.2	0.4149	0.3054 – 0.5050
Occasion 11	0.1	0.2065	0.1481 – 0.2612
Occasion 12	0.05	0.0989	0.0669 – 0.1326

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[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[d] Probability of a male spawning at every survey occasion.

Table 2.4. A comparison of known values, or truth, and the mean and 95% credible interval (CI) estimates of various parameters produced from a hierarchical Bayesian analysis of a simulated Atlantic horseshoe crab (*Limulus polyphemus*) population with 18 survey occasions.

	Truth	Model Estimates	
Parameter	Value	Mean	95% CI
Total Males[a]	3,500,000	2,370,000	1,757,000 – 3,182,000
Total Females[a]	1,590,909	1,077,000	798,600 – 1,446,000
Marked Males[a]	3,500	3,270	2,547 – 4,251
Proportion Marked[b]	0.001	0.0014	0.0012 – 0.0016
Detection Probability[c]	0.05	0.0271	0.0192 – 0.0370
Spawning Probability[d]			
Occasion 1	0.02	0.0459	0.0126 – 0.1000
Occasion 2	0.02	0.0231	0.0027 – 0.0655
Occasion 3	0.1	0.2659	0.1614 – 0.3996

Occasion 4	0.1	0.1040	0.0462 – 0.1861
Occasion 5	0.1	0.2896	0.1779 – 0.4312
Occasion 6	0.1	0.1849	0.1015 – 0.2956
Occasion 7	0.2	0.4165	0.2753 – 0.5869
Occasion 8	0.4	0.7364	0.5294 – 0.9522
Occasion 9	0.4	0.8536	0.6461 – 0.9918
Occasion 10	0.4	0.8305	0.6204 – 0.9887
Occasion 11	0.4	0.7360	0.5282 – 0.9514
Occasion 12	0.5	0.9292	0.7725 – 0.9977
Occasion 13	0.3	0.5783	0.4000 – 0.7865
Occasion 14	0.25	0.5553	0.3840 – 0.7593
Occasion 15	0.25	0.4508	0.3023 – 0.6284
Occasion 16	0.2	0.4512	0.3017 – 0.6319
Occasion 17	0.1	0.2542	0.1527 – 0.3844
Occasion 18	0.05	0.1041	0.0459 – 0.1871

---

[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[d] Probability of a male spawning at every survey occasion.

Table 2.5. A comparison of known values, or truth, and the mean and 95% credible interval (CI) estimates of various parameters produced from a hierarchical Bayesian analysis of a simulated Atlantic horseshoe crab (*Limulus polyphemus*) population with 24 survey occasions.

	Truth	Model Estimates	
Parameter	Value	Mean	95% CI
Total Males[a]	3,500,000	2,387,000	1,928,000 – 2,917,000
Total Females[a]	1,590,909	1,085,000	876,500 – 1,326,000
Marked Males[a]	3,500	3,627	3,056 – 4,272
Proportion Marked[b]	0.001	0.0015	0.0013 – 0.0017
Detection Probability[c]	0.05	0.0238	0.0190 – 0.0300
Spawning Probability[d]			
Occasion 1	0.02	0.0351	0.0071 – 0.0891
Occasion 2	0.02	0.0821	0.0323 – 0.1553
Occasion 3	0.1	0.2696	0.1673 – 0.3999
Occasion 4	0.1	0.1644	0.0880 – 0.2663

Occasion 5	0.1	0.2463	0.1482 – 0.3660
Occasion 6	0.1	0.2345	0.1387 – 0.3528
Occasion 7	0.2	0.1877	0.1052 – 0.2949
Occasion 8	0.4	0.2696	0.1667 – 0.3990
Occasion 9	0.4	0.4102	0.2761 – 0.5726
Occasion 10	0.4	0.8083	0.6125 – 0.9802
Occasion 11	0.4	0.8422	0.6505 – 0.9890
Occasion 12	0.5	0.8168	0.6221 – 0.9830
Occasion 13	0.3	0.8339	0.6396 – 0.9873
Occasion 14	0.25	0.8839	0.7053 – 0.9948
Occasion 15	0.25	0.7978	0.6028 – 0.9778
Occasion 16	0.2	0.9293	0.7865 – 0.9977
Occasion 17	0.1	0.5632	0.3996 – 0.7551
Occasion 18	0.05	0.5291	0.3711 – 0.7178
Occasion 19	0.05	0.6445	0.4673 – 0.8515
Occasion 20	0.05	0.5156	0.3607 – 0.6979

Occasion 21	0.05	0.4816	0.3333 – 0.6573
Occasion 22	0.05	0.4346	0.2955 – 0.6027
Occasion 23	0.05	0.2347	0.1409 – 0.3542
Occasion 24	0.05	0.1411	0.0713 – 0.2346

[a] Estimate of the population in Delaware Bay for that season.

[b] Proportion of the male segment of the population that is marked for that season.

[c] Probability of detecting a marked male on a spawning beach during a survey occasion for that season.

[d] Probability of a male spawning at every survey occasion.

APPENDIX A. 2003 CODE

```
model {

  # Priors and constraints
  psi ~ dunif(0,1)                           #inclusion probability with uniform prior distribution
  mean.phi ~ dunif(0,1)                      #survival probability with uniform prior distribution
  psight ~ dunif(0,1)                        #detection probability with uniform prior distribution

  for (i in 1:M) {
    for (t in 1:(n.occasions-1)) {            #survival probability
      phi[i,t] <- mean.phi
    }
    for (t in 1:n.occasions) {               #detection probability
      p[i,t] <- psight
    }}

for(t in 1:n.occasions){
   pspawn[t] ~ dbeta(1,1)                    #uniform prior for spawning probability, must spawn to be observed
}

  # Likelihood
  for (i in 1:M) {
    w[i] ~ dbern(psi)                        #parameter-expanded data augmentation parameter (1=marked and available for sampling,
                                             ##0=otherwise)
  for(t in 1:n.occasions) {
      # State process
      z[i,t] ~ dbern(pspawn[t])               #1=individual is present in study area at time t, 0=individual not yet spawning
                                              ##or has already departed at time t
      # Observation process
      mu[i,t] <- z[i,t] * p[i,t] * w[i] * mean.phi    #probability of detecting an alive, marked, and spawning individual at each survey occasion
      Acaphist[i,t] ~ dbern(mu[i,t])                  #1=yes, you recaptured a marked individual during this survey occasion, 0=no, you did not
}}

  # Calculate derived population parameters
  for (i in 1:M) {
    for (t in 1:n.occasions) {
```

```
   u[i,t] <- z[i,t]*w[i]                #1=an individual is part of the population and present in study area at time t, 0=otherwise
  }}

 for (i in 1:M) {
  Nind[i] <- sum(u[i,1:n.occasions])    #number of marked individuals spawning and part of population for all survey occasions
  Nalive[i] <- 1 - equals(Nind[i],0)    #equals(x,z); if x=z then 1; if x ≠ z then 0; So 1-1=0 (dead) and 1-0=1 (alive); converts Nind to 0s and 1s
 }

 Nsuperflag <- sum(Nalive[])            #number marked in Delaware Bay spawning population for season
 Nsuperstop <- sum(Nalive[])/pflag      #total males in Delaware Bay spawning population for season
 Nsuperfemale<-Nsuperstop/2.2           #total females in Delaware Bay spawning population for season

 # Binomial model for scan samples
 # Priors
 pflag ~ dbeta(1,1)                     #proportion of the population marked with uniform prior distribution
 # Likelihood
 for (t in 1:n.occasions){
  m[t] ~ dbin(pflag, K[t])              #m=number marked individuals, K=total number counted (from data below)
 }}


#data       # (M=number of capture histories, n.occasions=number of survey occasions, K=total crabs counted at each survey occasions,
            ##m=number of marked individuals counted at each survey occasion, Acaphist=capture histories generated for a season)
list(
M=13000,n.occasions=15,K=c(131,225,153,3615,92,74,6820,5117,10088,6256,11122,2014,1565,3938,5029),
m=c(0,0,0,1,0,1,3,8,14,7,6,1,1,2,4),Acaphist=structure(
.Data=c(
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0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,…
[repeated until 13,000 capture
histories generated]
…0,0,0,0,0,0,0,0,0,0,0,0,0,0,0),
.Dim=c(13000,15))
)
```

APPENDIX B. SIMULATION CODE

```
#Simulating data for 0.003 marked-to-unmarked ratio evaluation
##Note: code is similar for 0.006 and 18/24 occasions, except for changes to rmean, N.occ, sp, n.tag.spwn, N.aug, or m

N.occ=12                                    #number of occasions
rmean= 0.003                                #proportion of horseshoe crabs tagged
dp=0.05                                     #known detection probability for simulation
Pc = 0.009                                  #proportion of available spawning habitat that is counted


#Simulate ratio/count data

TotPop=3500000                              #total population size
rsd= 0.01*rmean                             #standard deviation of the ratio
aratio=rmean*((rmean*(1-rmean)/rsd)-1)      #beta distribution shape parameters
bratio=(1-rmean)*((rmean*(1-rmean)/rsd)-1)
ratio=rbeta(N.occ,aratio,bratio)            #draw ratio values from a beta distribution

#Simulate capture histories
#Known spawning probabilities
sp1=0.02
sp2=0.02
sp3=0.1
sp4=0.1
sp5=0.2
sp6=0.4
sp7=0.4
sp8=0.5
sp9=0.3
```

```
sp10=0.2
sp11=0.1
sp12=0.05

#Combine all spawning probabilities into a single vector
sp=c(sp1,sp2,sp3,sp4,sp5,sp6,sp7,sp8,sp9,sp10,sp11,sp12)

T=round((TotPop*sp)*Pc)                          #number of crabs counted at each survey occasion

T                                                #check data
ratio                                            #check ratios

N.tag=TotPop*rmean                               #number of tagged horseshoe crabs

#Occasion-specific spawning data, different spawning probabilities on each occasion, creates 12 columns of 1s and 0s to represent
   ##whether and when an individual spawns on each occasion
n.tag.spwn1=matrix(rbinom(N.tag*N.occ,1,sp1),N.tag,1)
n.tag.spwn2=matrix(rbinom(N.tag*N.occ,1,sp2),N.tag,1)
n.tag.spwn3=matrix(rbinom(N.tag*N.occ,1,sp3),N.tag,1)
n.tag.spwn4=matrix(rbinom(N.tag*N.occ,1,sp4),N.tag,1)
n.tag.spwn5=matrix(rbinom(N.tag*N.occ,1,sp5),N.tag,1)
n.tag.spwn6=matrix(rbinom(N.tag*N.occ,1,sp6),N.tag,1)
n.tag.spwn7=matrix(rbinom(N.tag*N.occ,1,sp7),N.tag,1)
n.tag.spwn8=matrix(rbinom(N.tag*N.occ,1,sp8),N.tag,1)
n.tag.spwn9=matrix(rbinom(N.tag*N.occ,1,sp9),N.tag,1)
n.tag.spwn10=matrix(rbinom(N.tag*N.occ,1,sp10),N.tag,1)
n.tag.spwn11=matrix(rbinom(N.tag*N.occ,1,sp11),N.tag,1)
n.tag.spwn12=matrix(rbinom(N.tag*N.occ,1,sp12),N.tag,1)

#Combine each occasion into a single array
n.tag.spwn =cbind(n.tag.spwn1,n.tag.spwn2,n.tag.spwn3,n.tag.spwn4,n.tag.spwn5, n.tag.spwn6,n.tag.spwn7,n.tag.spwn8,
```

```
   n.tag.spwn9,n.tag.spwn10,n.tag.spwn11,n.tag.spwn12)

#Apply detection probability to spawning data, generate a second array of 1s and 0s with binomial probability, and multiply by the
   ##spawning data
n.tag.spwn.obs=matrix(rbinom(N.tag*N.occ,1,dp),N.tag,N.occ)*n.tag.spwn

#Check data
head(n.tag.spwn)
head(n.tag.spwn.obs)


N.aug<-10000                             #the number of all-zero encounter histories to add
aug=matrix(0,N.aug,N.occ)                #create matrix of all-zero capture histories length N.aug and width N.occ
Acaphist <- rbind(n.tag.spwn.obs,aug)    #add all-zero capture histories to observed capture histories
K=T                                      #set K(OpenBUGS notation) equal to total crabs counted
N.tag                                    #check number of tagged horseshoe crabs
N.tag*.25                                #multiply number of tagged by 25% to find number tagged found in quadrats
m=apply(Acaphist[1:2625,],2,sum)         #number of tagged crabs observed within  plots


length(Acaphist[,1])                     #check total number of capture histories
m                                        #check number of tagged crabs observed within plots at each occasion
K                                        #check total crabs counted at each occasion
```