Comparing abundance estimates from closed population mark-recapture models of endangered adult Atlantic sturgeon

J. E. Kahn[1,2,*], C. Hager[3], J. C. Watterson[4], N. Mathies[3], K. J. Hartman[2]

[1]National Marine Fisheries Service, Office of Protected Resources, Silver Spring, Maryland 20910, USA
[2]Division of Forestry and Natural Resources, West Virginia University, Morgantown, West Virginia 26506-6125, USA
[3]Chesapeake Scientific, Williamsburg, Virginia 23185, USA
[4]U.S. Department of the Navy, Naval Facilities Engineering Command, Atlantic Norfolk, Virginia 23508, USA

ABSTRACT: Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* were listed as 5 distinct population segments under the US Endangered Species Act in 2012. At that time, only 2 abundance estimates of the Atlantic sturgeon population were available: one from commercial fisheries landings in the Hudson River ending in 1995 and one from mark-recapture research in the Altamaha River, Georgia, in 2004 and 2005. In 2013, we verified spawning in the York River, Virginia, system and initiated a multiple-year mark-recapture study focusing on spawning-run abundance. We used a Schumacher-Eschmeyer model and Program CAPTURE to produce estimates of annual spawning abundances from 2013 to 2018. The Schumacher-Eschmeyer estimates of spawning-run abundance with 95% confidence intervals from 2013 to 2018 were 75 (31–190), 157 (115–244), 184 (150–238), 222 (137–576), 212 (157–328), and 145 (89–381), respectively. Because Atlantic sturgeon do not spawn every year, the trends in estimates do not suggest a recovering or declining population, but rather variability in proportions of the adult population that return to spawn each year. The estimates produced in Program CAPTURE using M_0 (null), M_t (Chao M_t and Darroch), M_h (Chao M_h and Jackknife), and M_{th} (Chao M_{th}) models all produced similarly reliable estimates. The models that consider a behavioral response to initial capture (M_b, M_{bh}, and M_{tb}) failed to produce reliable estimates for these data, likely because as an endangered species, the dataset for Atlantic sturgeon was sparse. The Jackknife equation (model M_h) was the most precise every year with reliable accuracy and therefore is recommended.

KEY WORDS: Anadromous · Conservation · Endangered species · Fish · Mark-recapture · Monitoring · Native fish · Population ecology · Population modeling

1. INTRODUCTION

Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* are the largest anadromous fish along the Atlantic seaboard. Their reproductive populations were decimated between 1880 and 1905 (Smith 1985, Bushnoe et al. 2005, Dadswell 2006), likely extirpating populations in some rivers and leaving a small fraction of their historic abundance in others. Legal estuarine commercial fisheries continued to affect all remaining populations until being completely closed along the US east coast in 1998 (ASMFC 1998). Historically, Atlantic sturgeon reproduced in rivers between the St. Johns River in Florida to the St. Lawrence River in Canada. The Chesapeake Bay once supported as many as 6 reproductive populations (NMFS 2007), but reproduction has only been confirmed in 2 Chesapeake Bay systems since the commercial fisheries were closed (Balazik et al. 2012, Hager et al. 2014).

In 2012, the National Marine Fisheries Service (NMFS) listed the Gulf of Maine distinct population segment (DPS) as threatened, and the New York

*Corresponding author: jason.kahn@noaa.gov

Bight, Chesapeake Bay, Carolina, and South Atlantic DPSs as endangered under the US Endangered Species Act (NMFS 2012a,b). NMFS identified the lack of abundance information as a major concern when the species was listed. In 2012, adult Atlantic sturgeon abundance estimates existed for the Hudson and Altamaha River adult populations, likely the 2 healthiest in the USA. There are no abundance estimates available for any populations in the Chesapeake Bay. A limited amount of inference can be made for relative abundance of the James River population using effective population sizes (O'Leary et al. 2014, Waldman et al. 2018).

Atlantic sturgeon were confirmed reproducing in the Pamunkey River, a primary tributary to the York River, Virginia (Hager et al. 2014) in 2013 when sexually mature males and a spawned-out female still releasing eggs were captured. NMFS' status review (ASSRT 2007) concluded this population was historically harvested and may still be extant, but spawning adults had not been observed since 1973. Sampling in 2013 resulted in the capture and marking of 17 adult Atlantic sturgeon, 2 of which were recaptured. The 2013 spawning-run abundance was estimated between 17 and 168 individuals using a Schumacher-Eschmeyer model (Kahn et al. 2014).

Managers need more baseline information about the number of adult Atlantic sturgeon returning to each river system annually. Because Atlantic sturgeon routinely skip spawning, and males and females spawn at different frequencies (Smith 1985), an estimate of a single spawning run provides the most basic information useful to managers. Multiple consecutive spawning abundance estimates provide information on the ranges of variation for spawning runs and knowledge of whether spawning is occurring annually. However, annual spawning run estimates of iteroparous species that exhibit skipped spawning do not indicate population trends or overall population abundance without concurrent estimates of productivity. Ultimately, the best adult abundance information would estimate the total number of adults natal to a river. Annual spawning abundance estimates allow managers to make inferences about other, less well-understood populations through relative calculations, as well as providing more context to long-term population studies, emerging adult estimates, and juvenile abundance estimates to monitor population productivity and recovery (Peterson et al. 2008, Schueller & Peterson 2010, Bahr & Peterson 2016, Hale et al. 2016). Ultimately, with the knowledge

of population statuses in multiple river systems along the coast, NMFS will better understand which activities and which life stages are limiting Atlantic sturgeon recovery.

The objectives of this study were to conduct mark-recapture analyses to (1) estimate the size of annual spawning runs within the York River system using a variety of closed mark-recapture models, (2) compare the confidence intervals around those estimates, (3) assess the possible sources of bias in the estimates, and (4) assess the estimates in terms of survival and recovery of this endangered species. In addition, given the number of recaptured sturgeon in this study, we were also able to assess tag retention. These objectives will produce the first series of sequential year estimates of annual spawning-run abundance in over a decade along the Atlantic coast and the first ever within the Chesapeake Bay.

2. MATERIALS AND METHODS

2.1. Location and sampling

The York River is located along the western edge of the Chesapeake Bay on the US east coast, north of the James River and south of the Rappahannock River (Fig. 1). It is a 55 km long river from the mouth to the confluence of its 2 main tributaries, the Pamunkey and Mattaponi Rivers, in West Point. It ranges from
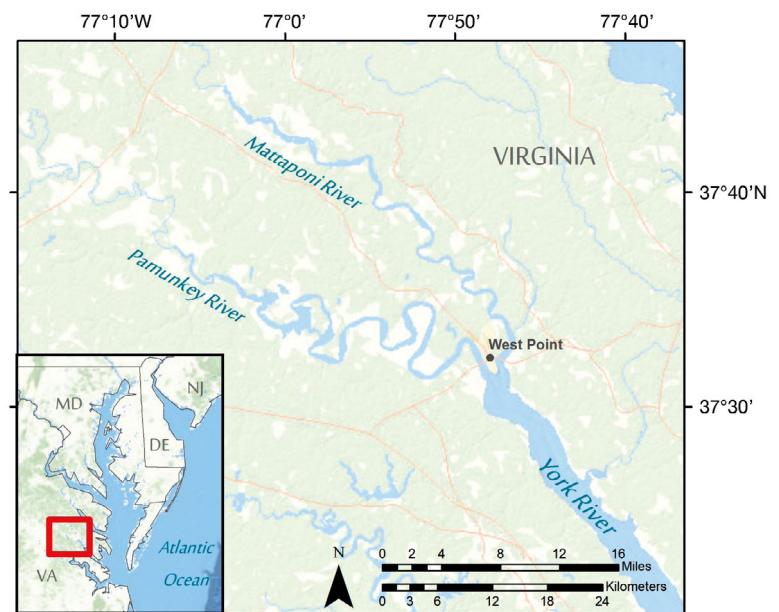

Fig. 1. Chesapeake Bay (lower inset), with the area of the red box enlarged to identify York River and its 2 main tributaries, the Pamunkey and Mattaponi Rivers

oligohaline at its most upstream to polyhaline at its mouth just east of Gloucester, Virginia. The Pamunkey River, 150 km long, and the Mattaponi River, 166 km long, are both freshwater for most of their lengths. Despite being longer, the Mattaponi River has only 50 to 60% of the flow in the Pamunkey River.

Adult Atlantic sturgeon were sampled using 22.86 to 35.56 cm stretch mesh gill nets between 2013 and 2018. Nets were set for adults in the spring from April to June for a minimum of 10 d each year between 2014 and 2016 and in the summer/fall from July to October for a minimum of 13 d each year. We assumed spring and fall spawning would be separate events and therefore we analyzed them separately. Sampling for each season was considered a primary sampling period (Table 1), such that sampling from August to October 2014 was a primary sampling period, from November to July was considered open, and then a new primary sampling period began in August 2015. Nets were custom-made to stretch from bank to bank and tall enough for the lead line to be on the bottom and float line to be at or just below the surface depending on flow, which if high enough would push the top of the net no more than 30 cm underwater. Between 3 and 5 nets were fished in this manner, in sequence, within 1 km of the river. This series of nets was analyzed as a single sampling period. During each sampling day, multiple mesh sizes were used to target both the largest and smallest adults as well as all sizes in between.

Adults were sampled in the Pamunkey River between river kilometer (rkm) 48 and 88 during fall 2013 and in the Mattaponi River between rkm 37 and 70. During the falls of 2014 to 2018, adults were sampled in the Pamunkey River at rkm 74 based on telemetry observations within the system during the 2013 spawning season. This location was confirmed each subsequent year, showing that all spawning adults aggregate around this location, with periodic movements upstream and downstream continuously throughout the year, allowing for capture and recapture opportunities throughout each spawning season.

This is the lowest spawning location, so all adults are available for capture throughout the spawning season, whereas sampling further upstream could miss some adults and sampling downstream would reduce the capture opportunities, as fish would only be available for capture twice in those locations (Hager 2016). A static sampling location gave a more consistent number of captures and recaptures than a random sampling design and was safer for this endangered species because we avoided unknown snags in new stretches of river each day. Because the nets stretched from bank to bank and surface to substrate, water depths in the sampled locations in the Pamunkey River ranged from 0 to 6.7 m and from 0 to 11.7 m in the Mattaponi River. During the spring in the Pamunkey River, nets were set at rkm 74 in 2014 and from rkm 15 to the mouth in 2015 and 2016. Initially we sampled further upstream near the Pamunkey River late summer/fall spawning grounds, but moved downstream closer to the salt wedge in subsequent springs to sample in habitats that other researchers (Dovel & Berggren 1983, Smith 1985) had suggested for spring spawning. Each spring, nets were fished in the Mattaponi River up to 15 km upstream of the mouth. Immediately below these locations, both rivers would transition to oligohaline habitat, which is not believed to be suitable for Atlantic sturgeon spawning (Van Eenennaam et al. 1996). All nets were fished during daylight hours. Soak times were limited to between 30 min and 2 h between checks to comply with federal permit requirements established by NMFS (Kahn & Mohead 2010). Fishing did not occur when temperatures were above 29°C or dissolved oxygen was below 4.5 ppm.

When Atlantic sturgeon were captured, they were all tagged with a passive integrated transponder (PIT) tag and a T-bar tag, and had a 1 cm^2 piece of fin removed for genetic analysis. The tissue sample was preserved in 95% ethanol. The sex of 81.25% of captured fish was confirmed by palpating the abdomen, causing the release of sperm or eggs, or during surgical inspection.

Table 1. Sampling design. Each of the 6 sampling years are primary periods composed of open and closed portions. All mark-recapture sampling days within each closed season are secondary periods, while open periods are times of *Acipenser oxyrinchus oxyrinchus* migration to and from spawning locations. Ellipsis: a representation of the consistently structured primary and secondary sampling periods of 2015 to 2017

Primary period (yr)	2013				2014			...	2018		
Secondary period (d)	1	2	3		1	2	3	...	1	2	3
Status	Closed			Open	Closed			Open	Closed		

The PIT tag was the primary mark for this study. T-bar tags were used to quickly identify recaptured fish within a season, at which point they could be scanned for a PIT tag in the boat and released without being held streamside. In the event a PIT tag was not found in a T-bar-identified fish, it was given a new PIT tag and rescanned to ensure detection. As a tertiary mark, we identified all unmarked fish genetically and were able to confirm the rare fish that was recaptured without either tag. No fish lost both tags within the spawning season they were marked in.

2.2. Adult spawning abundance estimates

The assumptions of closed population estimates are (1) the population remains constant over the sampling period (closed), (2) the animals act independently, (3) all animals are equally likely to be captured during each sample, (4) marking does not affect catchability, (5) marks are recorded correctly, and (6) all marks are retained (Ricker 1975, Krebs 1989, Lindberg & Rexstad 2002, Chao & Huggins 2005). A violation of these assumptions can cause the abundance estimate to be biased (Ricker 1975). Additionally, reliability of estimates improves greatly as the number of marks and recaptures in the dataset increase (Robson & Regier 1964, Roff 1973, Chao & Huggins 2005).

We were careful not to violate any of the assumptions of closed population models. Telemetry data collected during the study period revealed that the spawning population was completely closed from September 5 to 26 in all years, with most fish available for capture during the entire sampling period (Hager 2016). Because sturgeon move to the spawning area gradually before spawning and leave gradually after spawning, there were periods of in-migration before September 5 and out-migration after September 26. While the population was completely closed for at least a 3 wk period each year, corresponding to the most intensive sampling, adult sturgeon spent similar amounts of time in the sampling area each year, even though some may arrive earlier and others leave later. Therefore, the probability of capturing any sturgeon during the entire spawning season was roughly equal. The potential bias introduced from differing residency is under-estimating spawning abundance because we are more likely to capture and recapture fish with longer spawning durations. Because most fish were available during most of the sampling season, the amount of bias in this study is limited and likely no different than some fish being present in sampling reaches more often than others by chance. Because many fish were captured in multiple years of this project (Kahn et al. unpubl. data) and recapture rates approach levels that would produce unbiased estimates if no assumptions were violated (Robson & Regier 1964, Roff 1973), we believe the impact of migratory periods is minimal.

Sturgeon movement within a river appears independent, though males may follow females in anticipation of spawning. This behavior would not affect the probability of capturing and recapturing the same individuals because males do not follow the same female all season.

All adult sturgeon were equally likely to be captured during each primary sampling period, though probability of capture varied during each secondary period as adult sturgeon move within the spawning grounds throughout the spawning period (Table 1). For this project, nets were set in the location of greatest likelihood of encounter (rkm 74) for all adults. Following capture and release, fish required a period of 2 tide changes (roughly 12 h) to have a similar likelihood of being recaptured at any later point during the spawning season (Fig. 2). Therefore, each secondary sampling period was a day of sampling between dawn and dusk.

There was no evidence of aborted spawning runs or delayed mortality from implanting tags during this study. Furthermore, observation of adult movement before and after capture did not appear to change as
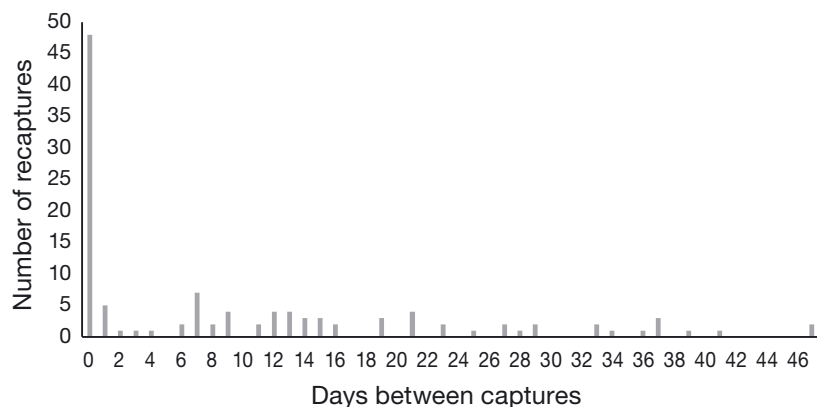

Fig. 2. Days between capture and recapture of *Acipenser oxyrinchus oxyrinchus* within each primary sampling period, where 0 days represents fish not considered recaptures because they were captured multiple times on the same day, while Days 1 through 47 suggest an equal recapture probability during the closed portion of the spawning run

a result of the capture event, as fish generally continued moving in the same trajectory (Hager 2016). Recaptures were not counted if they occurred on the same sampling day and only within-year recaptures were assessed by this study.

All fish were marked with 2 separate tags and a DNA tissue sample. The marks were recorded in multiple locations and cross-referenced against each other. However, as is described later (Section 3.1), not all marks were retained during the course of this study, but each fish's DNA did not change and therefore each individual could be tracked through time.

2.3. Schumacher-Eschmeyer model

The Schumacher-Eschmeyer formula for multiple census (Ricker 1975) is:

$$\widehat{N} = \frac{\sum_{d=1}^{m} C_d M_d^2}{\sum_{d=1}^{m} R_d M_d} \tag{1}$$

where $\widehat{N}$ is the estimate of adult abundance during a particular spawning season; C_d is the total number of fish captured in a day within that season, both previously marked and previously uncaught; M_d is the number of marked fish available at the beginning of each sampling day within that season; and R_d is the number of recaptures during a sampling day within that season. Subscript d refers to each sampling day, separated by at least 2 tidal cycles during a single closed season, where $d = 1, \ldots, m$, and m represents the total number of sampling days during which fish were captured in each season.

The formula for the 95% confidence interval (CI) (Ricker 1975) is $1/\widehat{N} \pm t_{(0.975, m-1)} \times SE$, where SE is the estimated standard error and t refers to a standard t-table with $m-1$ degrees of freedom. Estimated standard error is calculated as the square root of the variance of $1/\widehat{N}$. The variance (V) of $1/\widehat{N}$ is:

$$V\left(1/\widehat{N}\right) = \frac{s^2}{\left(\sum_{d=1}^{m} C_d M_d^2\right)} \tag{2}$$

where s^2 is the standard deviation of the regression coefficient and m is the number of days Atlantic sturgeon were captured (Ricker 1975), calculated as follows:

$$s^2 = \frac{\left(\sum_{d=1}^{m} \frac{R_d^2}{C_d}\right) - \left[\frac{\left(\sum_{d=1}^{m} R_d M_d\right)^2}{\left(\sum_{d=1}^{m} C_d M_d^2\right)}\right]}{m-1} \tag{3}$$

We propose a sensitivity analysis for this equation because closure is not complete in this dataset and the

effects of emigration and immigration can bias the results either positively or negatively (Otis et al. 1978). Kendall (1999) identified 3 scenarios when capture probability would remain unbiased even when closure is not complete: (1) movement into and out of the sampling area is completely random, (2) the entire population is closed at first and then there is intermittent emigration from the area, and (3) immigration is intermittent before becoming closed. In the case of the last 2 scenarios, Kendall (1999) suggested pooling the periods of migration and isolating the sample when the population is completely closed to produce 2 sample periods with unbiased capture probabilities. Kendall (1999) then suggests using a Lincoln-Petersen estimator to assess the 2 samples. That scenario can be applied and modified here to pool in-migration captures and isolating the first day of population closure to have equal capture probabilities during those periods. Likewise, the last day of complete closure can be isolated, with all out-migration captures being pooled to produce equal capture probabilities. Consistent with closed population estimate assumptions, during the period of complete closure, each animal is equally likely to be captured on each sampling occasion. Therefore, we analyzed our data using the traditional Schumacher-Eschmeyer equation and also the above modified approach to Kendall's (1999) unbiased capture probability solution.

2.4. Program CAPTURE

We used the Program MARK (version 8.2; White et al. 1978, Rexstad & Burnham 1991, White & Burnham 1999) to produce closed population abundance estimates corresponding to each spawning run. The data was input as primary and secondary sampling periods (Table 1). The capture probability for each fish in a primary period is the same as the capture probability for that fish in at least one secondary period. Once the primary and secondary capture data was entered into Program MARK, we used 10 of Program CAPTURE's 11 equations to estimate spawning-run abundance for each year. These equations rely on 7 different models: M_0, M_t, M_h, M_b, M_{bh}, M_{th}, and M_{tb}. The calculations of the various equations used to derive abundance estimates using these models are described in greater detail by Pollock (1982).

The null equation uses model M_0, which assumes all individuals in the population have an equal probability of being captured and therefore estimates constant capture probability over all sample occasions. When capture probabilities are not constant,

the estimates will be biased by whether the probability of capture increases or decreases.

The Darroch and Chao M_t models rely on model M_t, which estimates variable capture probabilities through time. For both models, the probability of capture is different on each sampling occasion, but the Chao M_t equation performs better when capture probabilities are low (Rexstad & Burnham 1991). Capture probabilities were lower in 2016 and 2018 than other years.

The Jackknife and Chao M_h equations rely on the M_h model, which assumes heterogeneous capture probabilities that vary by individual. Because individual behavior does vary, these estimators should be less biased if no assumptions are violated.

The Zippin equation uses the M_b model, which assumes capture probability changes as a behavioral response to the initial capture. Therefore, this model calculates an initial capture probability and also a different probability of being recaptured. This model would be most reliable if sturgeon exhibited an avoidance of the sampling area caused by the initial capture, but because the river is linear and blocked by nets, unless the sturgeon aborted its spawning run, it could not avoid the sampling area.

The Generalized Removal and Pollock and Otto equations use the model M_{bh} and assume that capture probability varies by individual and in response to initial capture, conceivably resulting in 2 capture probabilities for every individual in the population. The Chao M_{th} equation uses the M_{th} model, which calculates capture probability as a variable of time by individual. The Burnham equation uses the M_{tb} model, which calculates capture probability as a variable of time and behavioral response to initial capture. The primary limitation of any of these models or equations is that they may fail to provide estimates if data is sparse, which may be the case when working with Atlantic sturgeon annual spawning runs where adults exhibit skipped spawning. The data analyzed each year are a fraction of the adult portion of an endangered population (White et al. 1978, Rexstad & Burnham 1991).

3. RESULTS

3.1. General capture information

During the fall sampling seasons of 2013 to 2018, a total of 240 individual Atlantic sturgeon were marked (Tables S1–S6 in the Supplement at www. int-res.com/articles/suppl/n039p063_supp.pdf). Of those 240 Atlantic sturgeon, 50 were confirmed female, 145 were male, and 45 were sexually unidentified. Female Atlantic sturgeon ranged in size from 1588 to 2301 mm fork length (FL). Male Atlantic sturgeon ranged in size from 1330 to 1934 mm FL. Sexually unidentified fish ranged in size from 1250 to 2020 mm FL (Fig. 3). From 2016 to 2018, all suspected females were tagged and verified female during surgery, which significantly reduced the length of sexually unidentified fish, while also slightly reducing the length of females compared with previous years (Fig. 3). During the last 3 yr, no males were accidentally tagged when sex was technically unknown before the surgery.

We measured T-bar and PIT tag retention between 2013 and 2018. Within a season, sturgeon were recaptured 74 times and between seasons were recaptured 110 times. In some instances, T-bar tags were not deployed because we ran out during sampling, affecting the apparent number of recaptures. T-bar tag retention within a sampling season was 95.7% (67/70), though after at least a year at sea, that retention fell to 40.7% (44/108). PIT tag retention within a sampling season was 100% during all 6 yr. During 2013 and 2014, we used the Biomark® MK-7 applicator, and between-year retention has been 88.4% (61/69). After upgrading to the Biomark® MK-10 applicator in 2015, between-year retention is 97.6% (40/41). We used the genetic fin clips to verify that 7 fish (7/110, 6.4%) had lost both tags between capture and recapture events between years. Additionally, 2 fish lost a PIT tag but retained the T-bar tag.

Because adult Atlantic sturgeon are present in the upper portions of the Pamunkey River during the late summer spawning period, we attempted sampling in the same locations during the spring months of 2014,
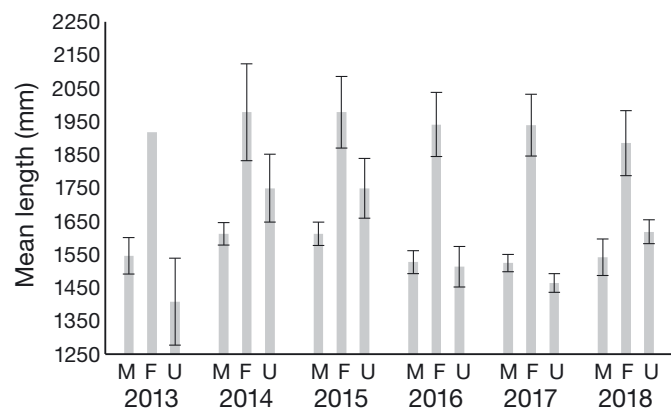

Fig. 3. Mean lengths of individual Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* captured during each primary sampling period from 2013 to 2018, grouped by sex (M: male; F: female; U: unknown). Error bars: 95% CI

but after catching zero adult Atlantic sturgeon, we moved down to the freshwater saltwater interface for 2015 and 2016 to ensure spring fish were not spawning lower in the river. We also sampled the lower Mattaponi River during all 3 yr. In the spring, no adults were ever caught, and while nets were set from bank to bank covering from the surface to substrate, 3 in sequence, no nets ever moved to indicate a large fish may have bumped them but not been captured. There was no indication of a spring run and therefore, no spring sampling was conducted after 2016.

3.2. Schumacher-Eschmeyer model

Only Atlantic sturgeon of spawning size in spawning habitat of the Pamunkey River were caught during a summer/fall spawning run, and therefore the mark-recapture abundance estimates are of the adult portion of the population. Because Atlantic sturgeon are iteroparous but exhibit skipped spawning, each spawning run represents a fraction of the total adult population natal to the river. Traditional Schumacher-Eschmeyer abundance estimates as well as a modification of the equation that pools sampling periods during migratory periods are presented in Tables 2 & 3. In all cases, when pooling migratory periods, the point estimate of abundance was less than if we considered each sampling day independently.

Robson & Regier (1964) noted that the power of confidence intervals depends on the proportion of marked and unmarked fish in the population. The number of marked fish relative to the estimated abundance, as well as the proportion of recaptures relative to the total number of fish captured each year, are also presented in Table 2. The higher the proportion of the estimate that is marked, the more reliable the estimate.

Only 7 Atlantic sturgeon were captured in the Mattaponi River, 6 during 2016. Two of the 6 fish had been previously captured in the Pamunkey River. Two of the fish were gravid females, the other 4 were males expressing milt. No abundance estimate could be calculated during any year in the Mattaponi River. Mid-spawn or post-spawn sturgeon still releasing eggs have yet to be identified in the Mattaponi River. Despite the small sample size, the spawning-run sex ratio of Atlantic sturgeon in the Mattaponi River appears to be similar to the ratio observed in the Pamunkey River.

3.3. Program CAPTURE

We assessed all 6 years of mark-recapture data in Program MARK using the equations in Program CAPTURE. All models provided reliable estimates, except those that attempted to estimate abundance assuming a behavioral response to initial capture. The M_0 (Null), M_t (Chao M_t and Darroch), M_h (Chao M_h and Jackknife), and M_{th} (Chao M_{th}) models provided estimates similar to one another during all 5 seasons (Fig. 4). The M_b (Zippin), M_{bh} (Generalized Removal and Pollock and Otto), and M_{tb} (Burnham) models provided estimates that were intuitively inaccurate because there was no evidence that transmitted fish exhibited a trap response and the estimates produced by these models were simply the number of fish marked in each year. The estimates of all models are produced in Table 3 and shown in Fig. 4, but only the 6 equations that produced reliable estimates are mentioned further in the results.

The 2013 range of reliable mean abundance estimates was between 44 and 73 individuals, with 95% CIs as low as 24 and as high as 273 (Table 3). In 2014, the mean estimates ranged from 133 to 157, with a range of 95% CIs between 93 and 264. In 2015, the

Table 2. Annual capture information showing various endpoints of mark-recapture study of *Acipenser oxyrinchus oxyrinchus*, identifying proportion of population marked, mean abundance and 95% CIs of the Schumacher-Eschmeyer model from 2013 to 2018

Year	No. marked	No. recaptured	Proportion of marked fish that were recaptured (%)	Proportion of marked fish relative to estimated abundance (%)	Mean abundance	95% CI
2013	17	2	12	25	75	31−190
2014	63	15	24	41	157	115−244
2015	80	21	26	46	184	150−238
2016	60	8	13	26	222	137−576
2017	84	21	25	43	212	157−328
2018	44	7	16	29	145	89−381

Fig. 4. Estimated abundance provided by each model between 2013 and 2018, showing general agreement of the discussed models, disagreement of the behavioral response models, and number of *Acipenser oxyrinchus oxyrinchus* individuals marked each year. Solid black lines: Schumacher-Eschmeyer, M_0 (Null), M_t (Chao M_t, Darroch), M_h (Chao M_h, Jackknife), and M_{th} (Chao M_{th}) models; light grey lines: M_b (Zippin), M_{bh} (Generalized Removal, Pollock and Otto), and M_{tb} (Burnham) models; dashed line: number of adults marked during each primary sampling occasion

mean estimates ranged from 152 to 190, with 95% CIs between a low of 117 and a high of 277. The 2016 sampling season produced a range of mean estimates from 219 to 284, with 95% CIs ranging from 129 to 625. The 2017 estimated abundance ranged from 181 to 215, with 95% CIs ranging from 134 to 343. The 2018 estimates ranged from 154 to 200, with 95% CIs as low as 86 and as high as 464. The 95% CIs of these estimates overlap and the point estimates each fit within the narrowest confidence intervals produced by the Jackknife equation (Fig. 5).

4. DISCUSSION

Adult Atlantic sturgeon can transiently visit rivers with no intention of spawning. They can also be in an estuary or oligohaline reaches of one river, only to leave and be on the spawning grounds of another river within a few days. That makes confirmation of Atlantic sturgeon spawning difficult, and different researchers identify different evidence of spawning as conclusive, suggestive, or possible. The NMFS (2007) identified 20 known spawning populations, relying on eggs, larvae, or juvenile fish presence. Hilton et al. (2016) listed 27 rivers currently known to support spawning, without specifying any criteria for their conclusions. Two of the 27 rivers are the Pamunkey and Mattaponi Rivers studied here, which are actually just tributaries to the York River and share a spawning population. The Atlantic States Marine Fisheries Commission (ASMFC 2017) identified criteria for identifying spawning in various rivers, ranging from certain to unknown or suspected/historical. We endorse establishing categories with clear criteria as a more scientific approach.

The first category identified by the ASMFC (2017) is 'confirmed', ranging from eggs to young of year smaller than 30 cm total length. The second category, 'highly likely', is defined as 'large adults physically

Table 3. Point estimates (Est.) and 95% CIs of *Acipenser oxyrinchus oxyrinchus* mean abundance using the Schumacher-Eschmeyer, M_0, M_t, M_h, M_b, M_{th}, M_{bh}, and M_{tb} models run in Program CAPTURE for 2013–2018. NA: not available; no abundance estimate produced by the model for that spawning season

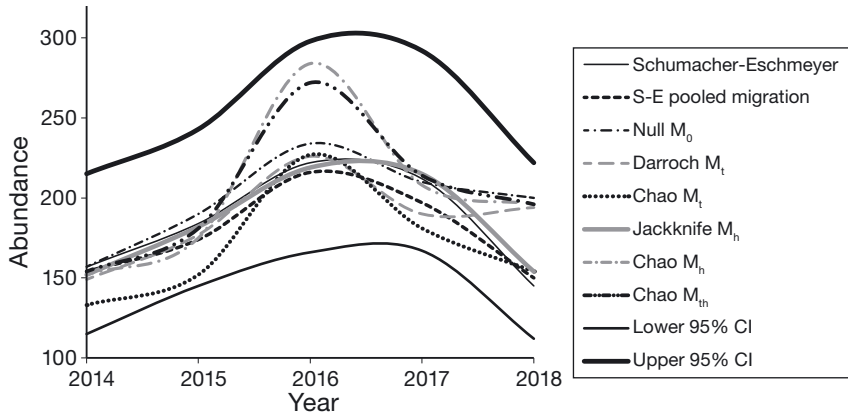| Model variations	2013 Est.	CI	2014 Est.	CI	2015 Est.	CI	2016 Est.	CI	2017 Est.	CI	2018 Est.	CI
Schumacher-Eschmeyer with pooled migration	68	32–449	154	112–249	174	134–250	216	123–888	197	150–288	144	82–615
Schumacher-Eschmeyer	75	31–190	157	115–244	184	150–238	222	137–576	212	157–328	145	89–381
M_0 (Null)	68	30–226	157	109–253	190	141–277	234	139–446	210	155–308	200	104–449
M_t (Darroch)	57	28–175	149	105–236	177	134–255	226	135–426	190	143–274	194	103–429
M_t (Chao)	44	24–124	133	93–219	152	117–224	227	129–467	181	134–275	154	86–334
M_h (Jackknife)	52	35–85	152	115–215	182	145–243	219	166–298	215	167–292	154	112–222
M_h (Chao)	73	30–266	152	102–264	175	128–267	284	149–625	208	147–329	196	99–464
M_b (Zippin)	19	18–34	69	63–92	118	93–196	NA	NA	104	92–141	74	51–185
M_{bh} (Generalized Removal)	19	18–34	60	60–60	118	93–197	0	93–197	104	92–141	85	50–361
M_{bh} (Pollock and Otto)	35	23–72	60	60–60	190	141–281	180	126–280	292	211–427	104	71–178
M_{th} (Chao)	73	30–273	154	107–248	181	136–263	272	144–595	214	150–343	196	103–438
M_{tb} (Burnham)	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Fig. 5. Point estimates of the 8 equations (2 Schumacher-Eschmeyer [S-E] estimates and M_0, M_t, M_h, and M_{th} models) producing the most consistently similar annual *Acipenser oxyrinchus oxyrinchus* abundance estimates from the 2014 to 2018 primary sampling periods, bounded by the more precise Jackknife 95% CIs

Table 4. Proposed levels of certainty for identifying *Acipenser oxyrinchus oxyrinchus* spawning, and the criteria for their justification. FL: fork length

Category	Criteria
Confirmed	(1) Recently spawned-out female still releasing nonviable eggs in freshwater in the presence of milting males; (2) spawning female (actively releasing viable eggs in freshwater in the presence of milting males; (3) presence of eggs to 180 d post-hatch fish
Near certain	(1) Juveniles under 400 mm FL in freshwater or low-salinity areas; (2) gravid female in upstream freshwater (at least 15 km upstream of the freshwater/saltwater interface)
Possible	(1) Milting male in upstream freshwater
Uncertain	(1) Capture of adult in any condition in lower freshwater (near salinity interface); (2) telemetry detection of adult female in unknown reproductive stage in freshwater
Probably meaningless	(1) Telemetry detection of adult male in unknown sexual condition in upstream or lower freshwater

duce 100 pounds (45 kg) or more of eggs. Therefore, we would argue that a female releasing eggs in freshwater is conclusive proof of spawning in that location. The same is not true for males releasing milt in freshwater, as there is minimal bioenergetic cost to sperm production, and research has shown that up to 5% of male Atlantic sturgeon captured in the marine environment, where reproduction would not occur, were spermiating (Van Eenennaam & Doroshov 1998). Sperm production may have more to do with a physiological response to abiotic conditions such as temperature or photoperiod or a response to biotic conditions such as female hormones or other males in the area releasing gametes. Using the categories and criteria we suggest in Table 4, Atlantic sturgeon spawning is confirmed in the Pamunkey River (Hager et al. 2014), and nearly certain in the Mattaponi River.

The 6 sequential years of spawning-run abundance estimates presented here are the first sequential spawning-run abundance estimates for Atlantic sturgeon in a decade and the first for the Chesapeake Bay DPS. We were unable to estimate the spawning abundance in the Mattaponi River. We can make a proportional estimate if we assume similar capture probabilities and acknowledge wide potential error from low captures. First, using telemetry detections (Hager 2016), 90% of telemetered fish returned to the Pamunkey River from 2014 to 2018, regardless of where they were first telemetered. Less convincing but with similar results is an analysis of our 2016 catch data where we captured 6 fish in the Mattaponi River and 60 in the Pamunkey River with roughly equal sampling effort. The proportion of previously marked fish in 2016 was also consistent between both rivers (2 out of 6 compared with 23 out of 60). There does not appear to be any fidelity between the 2 rivers in subsequent years, but within a season, adults do not move back and forth between the rivers. Therefore, the number of adult Atlantic sturgeon using the Mattaponi River hypothetically for spawning each year

observed expressing gametes in freshwater tidal reaches of the tributary; discrete genetic composition associated with adults or early life stages within a tributary'. Unfortunately, the 'confirmed' definition would not necessarily correctly identify spawning in either the Pamunkey or Mattaponi Rivers, because during parts of the year, the confluence of the 2 tributaries is entirely freshwater or of low enough salinity to allow young-of-year fish to move between systems. Furthermore, females spend several years sacrificing growth in favor of egg production to pro-

appears to be about one-tenth or less of the abundance in the Pamunkey River.

This research confirms late summer/fall spawning of a natal population of Atlantic sturgeon in the York River, just like other southeastern systems of the USA (Balazik et al. 2012, Flowers & Hightower 2015, Smith et al. 2015, Ingram & Peterson 2016). There is no evidence of spring spawning in either tributary to the York River. Balazik & Musick (2015) hypothesized that spring and fall spawning 'likely occurs in various degrees along most, if not all, of the Atlantic sturgeon's range'. However, the latter researchers only collected 4 adult Atlantic sturgeon from 1 river without even producing a spawned-out or ovulating female in the spring in that river. There may be anecdotal reasons to suspect a spring Atlantic sturgeon spawn in the James River (Balazik & Musick 2015), but there is yet to be conclusive evidence in that system, and there is no evidence to support that assumption in the York River. It is possible a spring run was extirpated and never re-established, or it is possible that it is so small as to have not been detected during the 3 yr we spent looking, or it is possible there never was and still is not a spring run.

In an effort to determine whether a spring Atlantic sturgeon spawning run in the York River occurred historically, we reviewed the historic fishing records and diaries from colonial settlers. Captain John Smith (Smith 1624, Kupperman 1988) kept a diary in the 1600s, stating that Atlantic sturgeon were present in the James River from February to May but not in the Pamunkey River until the heat of the summer. Because Jamestown is near the saltwater interface, it is likely he was referring to estuarine or lower freshwater reaches of the James River, but the Pamunkey River is almost entirely freshwater, suggesting spawning. His diary also suggests the Pamunkey River was the primary spawning river in the York River system 400 yr ago. Commercial fisheries targeted estuarine areas, and landings were recorded by county, not capture location, and are thus an unreliable indicator of spawn timing. Therefore, there is not any indication that there was ever a spring run that was extirpated or that one continues to persist at low levels today.

The fall Atlantic sturgeon spawning run in the Pamunkey River was large enough to conduct a mark-recapture study. Closed population estimates are straightforward and represent the number of individuals present during a particular period with no changes to the abundance, in this case, annual spawning runs. Increases or decreases in spawning-run abundance between years do not necessarily reflect increases or decreases in the total population

because the same proportion of the adult population does not return to the spawning grounds each year (Smith 1985, J. Kahn unpubl. data).

The M_0 (Null), M_t (Chao M_t, Darroch), M_h (Chao M_h, Jackknife), and M_{th} (Chao M_{th}) models were very similar to one another, as were the 2 Schumacher-Eschmeyer models during most years (Fig. 5). Despite the fact that the equations for models M_0, M_t, M_h, and M_{th} all provided roughly comparable estimates with overlapping confidence intervals, the Jackknife (model M_h) equation provides the tightest confidence intervals, within which all other reliable point estimates fall. Grimm et al. (2014) also found the heterogeneity models, specifically the Jackknife equation in Program CAPTURE, to be the most accurate abundance estimators when sampling a known population. The null and Schumacher-Eschmeyer equations both assume equal capture probability throughout the study and both produce abundance estimates that mirror one another, but the null equation estimate is always slightly higher. The Chao M_t equation was consistently a little lower than the other estimates every year, suggesting that if there is a time effect, then abundance is relatively lower. The Chao M_h and Chao M_{th} models both have higher estimates during years when capture probabilities for all fish were generally lower due to environmental conditions. However, the heterogeneity model seems to adjust the capture probabilities of un-recaptured fish downward, increasing the annual abundance estimates in those years, while during years with high captures and recaptures, the abundance estimates are in agreement with the other models. The Jackknife calculation is also a heterogeneous model, but does not seem to adjust the abundance estimates higher during years with universally lower capture probabilities, and as a result is the most precise during each year of this study.

As was noted by Robson & Regier (1964), the number of captured individuals must exceed the number of uncaptured individuals for a mark-recapture study to be unbiased, suggesting the 2015 and 2017 estimates were very close to unbiased, while bias was less than 5% for other years (Table 2). When bias was present, the abundance estimates were likely underestimates of true abundance. Because the point estimates of each abundance estimate fits within the confidence intervals of the Jackknife equation, all of these equations and their confidence intervals likely provide a decent approximation of the true abundance of each spawning run (Fig. 5).

The 3 models (M_b, M_{bh}, and M_{tb}) that consider a behavioral response (Rexstad & Burnham 1991) to

initial capture failed to provide reliable estimates for this study. Interestingly, the M_b (Zippin) and M_{bh} (Generalized Removal) models provided very similar estimates each year. When recapture rates were lower in 2013, 2014, 2016, and 2018, the abundance estimates were roughly equivalent to the number of individuals marked during those years, even though the assumption of a behavioral response to the initial capture is one possible explanation for the relatively limited recaptures. Strangely, during the 2 years with the highest number of recaptures, the abundance estimates were still lower than the other model estimates, including the Schumacher-Eschmeyer, even though a model assuming lower recapture probability should increase the abundance estimate relative to the models that do not consider behavioral response to initial capture. The other M_{bh} model (Pollock and Otto) provided unreliable estimates in 2013 and 2014, but as more data were entered, the estimates from 2015 to 2018 have at least partial overlap with the confidence intervals of the other models. Because many of these models struggle when data is sparse (White et al. 1978), it could be that there is insufficient data in our dataset to rely on behavioral response models.

Apart from Kahn et al. (2014), 3 estimates of adult Atlantic sturgeon abundance are available (Kahnle et al. 2007, Peterson et al. 2008, Dadswell et al. 2017). Stokesbury et al. (2014) and Flowers & Hightower (2015) produced abundance estimates of mixed-stock aggregations of sturgeon but these are not comparable to estimates of populations natal to an individual river. Because Atlantic sturgeon are an iteroparous anadromous species that exhibit sexually variable spawning, we are unable to extrapolate multiple spawning-run abundances to a total abundance estimate without obtaining more information for robust models (Kendall et al. 2019). Kahnle et al. (2007) and Dadswell et al. (2017) both attempt to estimate the total number of spawning adults in the population, rather than just the number of fish spawning each year in those systems. The estimates produced in the present paper and those produced by Kahnle et al. (2007) and Dadswell et al. (2017) are not comparable. Peterson et al. (2008) produced annual spawning abundance estimates in the Altamaha River of 324 (95% CI: 143–667) and 386 (95% CI: 216–787) in 2004 and 2005, respectively. Ingram & Peterson (2016), using telemetry, showed the adults marked and recaptured in the spring did not spawn until the fall as part of a 2-step migration. If migratory behavior is similar every year in the Altamaha, that would suggest the abundance estimates produced for those

2 years represent only approximately 37% of the annual fall spawning-run abundance. This suggests that the Altamaha River during those years may have had a spawning-run abundance in the ballpark of 876 (95% CI: 386–1803) and 1043 (95% CI: 584–2127). Comparing the York River estimates to these extrapolated values, it appears approximately 4 to 8 times more Atlantic sturgeon spawn annually in the Altamaha River.

Comparing the only consecutive years of abundance estimates on the Atlantic coast is difficult because of differences in river size and adult migratory behavior. However, average annual spawning abundances in the Altamaha and York Rivers are approximately 960 and 162, respectively. The density of spawning adults within the Altamaha and York Rivers is 5.9 and 1.0 adults km^{-1} of available spawning habitat, respectively. The average discharge of the Altamaha River is approximately 383 m^3 s^{-1}, while the York River discharge is approximately 31 m^3 s^{-1}. The Altamaha River therefore has 12.35 times more flow than the York River, but only 6.23 times as many adult Atlantic sturgeon spawning on average. The linear length of spawning area in each river reflects the differences in abundance more closely than volume, which makes sense for an animal that distributes benthically and not throughout the water column. It is also possible the number of spawning adults of a long-lived, anadromous species will show no or a very loose connection to the length or volume of the natal river. Another important fact is that these populations are both listed as endangered under the US Endangered Species Act, and as they recover to carrying capacity, comparisons of their abundances and relative densities will be more meaningful.

The James and York River Atlantic sturgeon populations are the only 2 confirmed spawning populations in the Chesapeake Bay. The Chesapeake Bay DPS is considered endangered, meaning it is likely to be extirpated in the foreseeable future. The annual spawning runs in the Pamunkey River are the smallest documented spawning runs, not just in the Chesapeake Bay, but along the entire coast. Extirpation is rarely caused by a single event but rather by a combination of anthropogenic and natural factors, chance events, and biological attributes (Lande 1988, Angermeier 1995, Kerr & Currie 1995, Jonsson et al. 1999, Fagan 2002, Frankham 2005). The first step towards an extirpation event is a population crash; in the case of the York River Atlantic sturgeon population, this was due to overfishing (Hildebrand & Schroeder 1928). The Endangered Species Act provides the tools to protect this population from suc-

cumbing to anthropogenic risks, but because the population is currently so small, stochastic events pose a significant threat. On the other hand, iteroparity with skipped spawning may provide a biological buffer to protect the species from chance events. For the good of this population, the Chesapeake Bay DPS, and the Atlantic sturgeon species, increasing natural productivity or reproductive success combined with efforts to reduce threats should improve the intrinsic rate of population growth (Gross et al. 2002).

In recent years, non-invasive means of estimating population abundances, such as side-scan sonar enumeration (Flowers & Hightower 2013, 2015, Mora et al. 2015) or environmental DNA (eDNA) calculations (Lacoursiere-Roussel et al. 2016), have described methods to make enumeration of closed populations simpler. These methods have enormous potential, particularly for enumerating endangered species without risking injury to individuals (Flowers & Hightower 2015). Both techniques could and should be validated with mark-recapture studies, most easily completed by sampling small spawning populations like in the Pamunkey River. As noted in Section 2.3, as individuals are in-migrating or out-migrating, the closure assumption can be violated in the short term and can only be met when the sampling period encompasses the entire closed period and the calculation is modified to address in-migration and out-migration. If non-invasive methods are used when there is incomplete closure, the spawning abundance could be under-estimated, and in larger systems where adults are spread out over large areas, there is the chance of double-counting individuals, not detecting individuals that are passed, or of errors being introduced by extrapolating data from samples taken from limited portions of the spawning area. However, if the goal is estimating the total abundance of adult sturgeon in a population, an experimental design that can account for unequal probability of capture, temporary emigration, birth, and death will be needed.

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