Refining capture-recapture recruitment estimation methods for Atlantic sturgeon

M. A. Baker[1], E. C. Ingram[2], D. L. Higginbotham[1], B. J. Irwin[3], A. G. Fox[1,*]

[1]Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA
[2]School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794, USA
[3]U.S. Geological Survey, Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

ABSTRACT: The Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* was once of great commercial importance in many coastal rivers of the eastern USA. Over the 19th and 20th centuries, most historical stocks of Atlantic sturgeon were depleted by human activities. Estimating recruitment for the remaining populations is challenging due to sampling constraints, limited age data, and natural variability. However, recruitment estimates could inform recovery efforts. The objectives of this study were to compare 2 modeling approaches to estimate recruitment of age-1 Atlantic sturgeon and provide an updated index of abundance across more than a decade of sampling in the Altamaha River, Georgia. First, we constructed capture histories of river-resident juveniles, using capture-mark-recapture data collected from 2008 to 2020, and assigned ages based on length–frequency analysis. Second, we compared more traditional Huggins closed population models and a recent nonlinear extension of Huggins models — vector generalized additive models (VGAMs) — to estimate abundance of age-1 fish. Both model types indicated similar yearly age-1 abundance estimates (Huggins: 163 in 2017 to 3839 in 2010; VGAM: 312 in 2020 to 4448 in 2010), but the VGAMs provided more direct interpretation for factors that might affect capture probability (e.g. sampling effort, temperature, fish length). This study indicates that the age-1 Altamaha River Atlantic sturgeon population has remained relatively stable over the past decade and provides a long-term baseline which will better enable managers to assess the effects of either future restoration actions or environmental disturbances on the population.

KEY WORDS: Population dynamics · Riverine fishes · Abundance · Anadromous

1. INTRODUCTION

The Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* is a long-lived anadromous species that inhabits waters along the Atlantic coast of North America. Its range extends from the George River in Labrador, Canada, to the St. Johns River in Florida, USA (Vladykov & Greeley 1963, Hilton et al. 2016). Historically, this range included almost 40 rivers; currently as few as 18 rivers are known or believed to contain spawning populations, although this estimate varies in the literature (ASSRT 2007, Hilton et al. 2016, ASMFC

2017, Waldman et al. 2019). Atlantic sturgeon spend most of their lives in the marine environment but migrate into the upper reaches of their natal rivers to spawn (Vladykov & Greeley 1963, Scott & Crossman 1973). Seasonality of spawning varies substantially across the range, with most southern populations (e.g. Altamaha River) spawning exclusively in the fall (Ingram & Peterson 2016, White et al. 2021) while others (e.g. Edisto River and Ogeechee River) appear to have genetically distinct spring and fall spawning events (White et al. 2021). After hatching, the larvae grow into river-resident juveniles and remain in the river

*Corresponding author: agfox@uga.edu

near the freshwater–saltwater interface for at least 2 yr (Kieffer & Kynard 1993, Bain 1997, Fox et al. 2018a, Fox & Peterson 2019). Following this period of growth and adaptation to higher salinities, river-resident juveniles become marine-migratory juveniles once they transition to coastal waters. These juveniles remain in the marine and estuarine environments until becoming sexually mature (Dovel & Berggren 1983, Bain 1997) although some individuals re-enter natal or non-natal rivers for periods of time (Waldman et al. 2013).

Atlantic sturgeon have experienced more than 150 yr of exploitation and overharvest, resulting in stock declines along the entire Atlantic coast (Colligan et al. 1998, ASSRT 2007). Even after the enactment of a coast-wide harvest moratorium in 1998, and despite efforts in the 1990s to work toward recovery, most stocks continued to decline (ASMFC 1998, Kahnle et al. 2005). In 2008, the species' range was conceptually divided into 5 distinct population segments (DPSs) based on genetic differences among regions (ASSRT 2007, Grunwald et al. 2008). In 2012, 4 of the DPSs (New York Bight, Chesapeake Bay, Carolina, and South Atlantic) were listed as endangered under the Endangered Species Act of 1973, and the Gulf of Maine DPS was listed as threatened (Federal Register 2012a,b, ASMFC 2016). Although commercial harvest has been halted in the US, anthropogenic influences such as incidental take as well as habitat loss and degradation are the main factors currently preventing Atlantic sturgeon stocks from recovering (Collins et al. 1996, 2000, Federal Register 2012a,b, Hilton et al. 2016).

Quantifying the abundance of a sturgeon population, as with many wild fish populations, is a difficult task. Beginning with the development of the Lincoln-Petersen index (Petersen 1896, Lincoln 1930), biologists have attempted to use capture-mark-recapture studies to quantify the number of individuals in a population. These methods were expanded to include multiple recapture events in both open (Cormack 1964, Jolly 1965, Seber 1965) and closed populations (Schnabel 1938, Darroch 1958), which allowed for estimation of additional population level parameters such as survival and mortality rates, recruitment, and population growth. In 1989, Richard Huggins proposed a collection of closed capture models which incorporates individual covariates (e.g. age, size) when dealing with heterogeneous capture probabilities (Huggins 1989). Eight variations of the Huggins models were originally proposed (Otis et al. 1978, Huggins 1991, Williams et al. 2002). Further development of the models incorporating a vector

generalized additive model approach (VGAM) has allowed for the inclusion of multiple environmental covariates while using a reduced parameterization (Yee 2015, Yee et al. 2015).

To better understand the population dynamics of Atlantic sturgeon, previous studies using different methods have targeted several life history stages with varying degrees of success in estimating abundance (Peterson et al. 2008, Waldman et al. 2013). Given the logistical complexity of sampling adult sturgeon in the marine environment, as well as the inability to determine in the field an individual's river of origin, the practice of instead sampling juvenile age-1 sturgeon has been used successfully as a method of assessing population-level trends (Pine et al. 2001, Secor et al. 2002, Schueller & Peterson 2010). In this way, age-1 abundance is a measure of recruitment (Peterson et al. 2000). Because age-1 juveniles reside in their natal estuary at the same time, entire cohorts can be effectively sampled (Fox & Peterson 2019). In recent years, several studies have estimated juvenile Atlantic sturgeon abundance through various closed capture models in South Atlantic DPS rivers (Fig. 1), including the Savannah (Bahr & Peterson 2016; Huggins
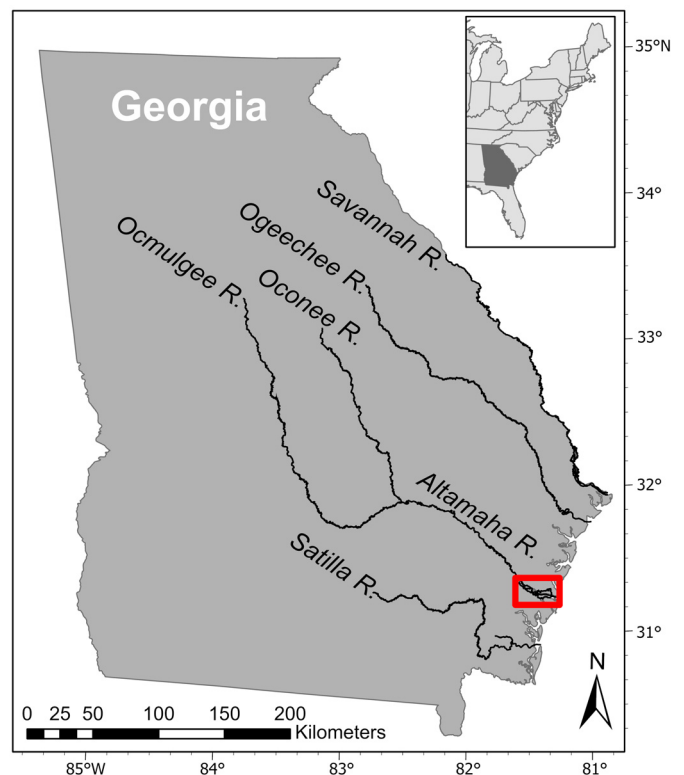

Fig. 1. Coastal rivers in Georgia, USA, where Atlantic sturgeon maintain spawning populations. Altamaha River estuary study site shown in red box

models), Ogeechee (Farrae et al. 2009; Huggins models), and Satilla (Fritts et al. 2016; Huggins multi-state models). The Altamaha River in Georgia is thought to contain one of the healthiest populations of Atlantic sturgeon in the South Atlantic DPS (ASSRT 2007, Peterson et al. 2008); this population is also the southernmost population that spawns consistently (Schueller & Peterson 2010, Fritts et al. 2016, Fox et al. 2018b). However, the most recent recruitment estimate was conducted in 2007 (Schueller & Peterson 2010) — before Atlantic sturgeon were listed as endangered. The current status of the Altamaha River population (in terms of annual recruitment and consistency of recruitment) is relatively unknown. Long-term sets of recruitment data can provide insight into population trends of a struggling species. For example, consistent year to year recruitment, especially in increasing numbers, might indicate a recovering population. In contrast, inconsistent annual recruitment, especially at low numbers of individuals, might indicate a fragile population that is not moving toward recovery. Given the lack of knowledge related to long term recruitment trends in this river, the primary objective of this study was to provide a long-term set of estimates of Atlantic sturgeon recruitment (i.e. age-1 juvenile abundance) in the Altamaha River for 2008–2020. Our secondary objectives were 2-fold: we sought to compare the utility of a recent modeling advancement to the estimation methods used in previous studies and to determine the environmental effects of water temperature and dissolved oxygen on capture probability in these recruitment models.

2. MATERIALS AND METHODS

2.1. Site description

The Altamaha River, one of the largest drainage basins east of the Mississippi River (36 000 km^2), is formed by the confluence of the Oconee and Ocmulgee rivers and flows southeast through Georgia for approximately 207 river kilometers (rkm) before emptying into the Atlantic Ocean near the town of Darien, GA (Fig. 1). The tidally influenced portion of the river extends upwards of 54 rkm from the mouth, and the fresh–saltwater interface typically occurs between rkm 35 and 50 during normal flows (Rogers & Weber 1995, Sheldon & Alber 2002). Although both of the main tributaries of the Altamaha River are dammed above the fall line, nearly the full extent of historically available habitat remains accessible to Atlantic sturgeon.

2.2. Sturgeon sampling

Capture of sturgeon occurred during the summer months (May–August) of 2008–2020 and was focused between rkm 10 and 35 (Peterson et al. 2008, Schueller & Peterson 2010, Peterson & Bednarski 2013, Ingram & Peterson 2016, Fox & Peterson 2019). Sampling was conducted approximately 8–10 times per week at randomly selected discrete sites. Thirty-eight sampling sites were selected based on fishability and were often separated by shallow, unfishable reaches. We deployed anchored monofilament gill and trammel nets perpendicular to the current for approximately 30–90 min at slack tides (for full description of sampling procedures, see Schueller & Peterson 2010). The same combination of nets (2 gill nets and 1 trammel net) was used at all sampling sites, and captures were combined across nets within a single sampling event. After all nets had been retrieved, we measured the fork length (FL) of each captured individual and scanned it for a passive integrated transponder (PIT) tag. If a tag was not detected, we inserted a 12.5 mm PIT tag subcutaneously under the fourth dorsal scute. All fish were allowed time to recover before being released. On each sampling occasion, we recorded surface and bottom measurements of water temperature (°C), dissolved oxygen (DO; mg l^{-1}), and DO saturation (%). Methods for capture and handling of Atlantic sturgeon were performed in accordance with relevant state and federal guidelines and were authorized under National Marine Fisheries Service Permits (nos. 16482, 17861, and 23096) and Georgia Department of Natural Resources Scientific Collection Permits.

2.3. Data analysis

2.3.1. Age-1 capture histories

Length–frequency histograms were constructed to assign ages to each fish captured (age-1 were 250–500 mm FL; Figs. 2 & S1a–d in the Supplement at www.int-res.com/articles/suppl/n051p203_supp.pdf). The ages indicated by the modes were validated by previous aging studies that used pectoral fin spines from a sample of juveniles (Schueller & Peterson 2010, Bahr & Peterson 2016). After assigning an age to each individual (using the length at first capture), yearly capture histories were constructed where a 1 represented that an individual was captured on a particular sampling occasion (a set of nets fished at a site on a given day) and an 0 represented that an individual was not captured on a sampling occasion.
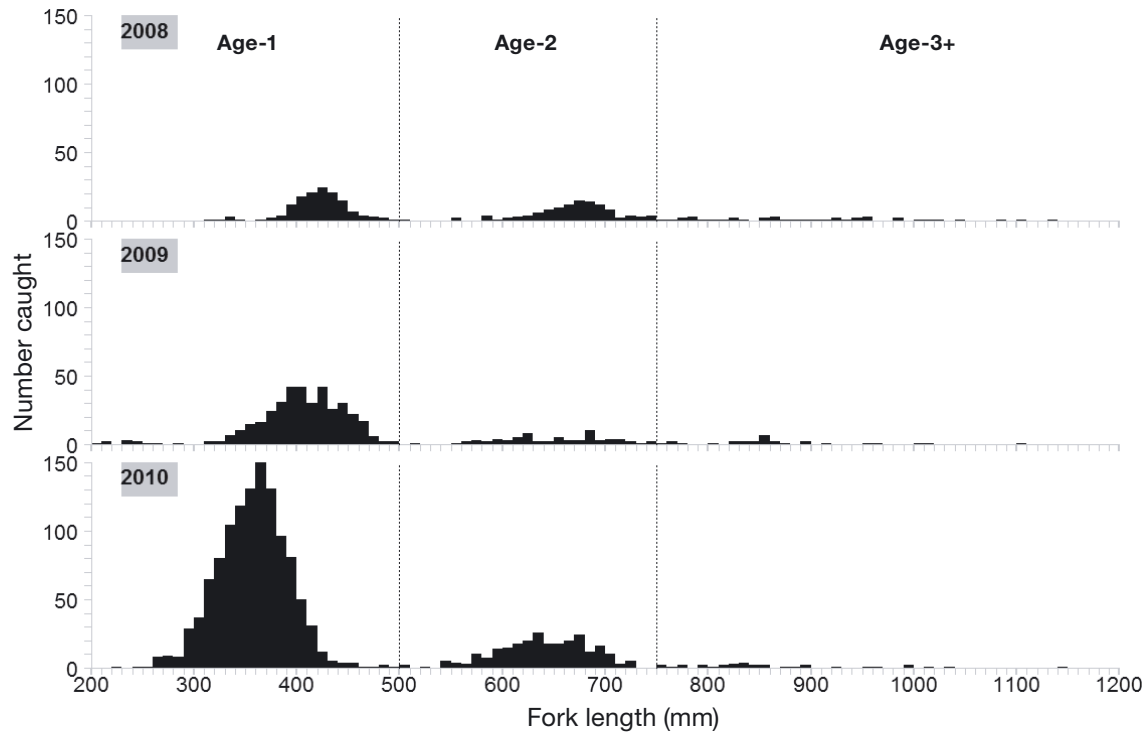
Fig. 2. Selected examples of length–frequency histograms and age assignments for Atlantic sturgeon captured in the Altamaha River, GA, USA, 2008–2010. Ages were determined based on length distributions as described in Schueller & Peterson (2010). Histograms for all years of this study period can be found in Fig. S1

From these multi-occasion capture histories, we used 2 types of conditional likelihood models to estimate yearly age-1 abundance for each sampling year separately.

2.3.2. Huggins closed capture models

We estimated yearly abundances of age-1 Atlantic sturgeon ($\hat{N}$) using Huggins closed capture conditional models within the 'RMark' package of Program R (Version 3.4.2; Huggins 1989, 1991, Laake 2013, R Core Team 2017, Fox & Peterson 2019). These models can vary in form and corresponding assumptions, which we briefly review in relation to sampling of juvenile Atlantic sturgeon in Text S1 in the Supplement at www.int-res.com/articles/suppl/n051p203_supp.pdf. We included 7 traditional Huggins models, which allow for differing sources of variation within capture probability (p_c) and recapture probability (p_r) (Table 1). We fit these models to each year of age-1 capture data and included a generic time-varying model where capture probability was allowed to vary across each sampling occasion, a behavioral model to account for a change in capture probability after the initial capture, a hetero-

geneity model to account for the length of the individual, and combinations of these.

2.3.3. Vector generalized additive models

A second modeling approach used VGAMs to incorporate time-varying effects while estimating a single slope parameter for each effect (Yee 2015, Yee et al. 2015). These models have an advantage over the original Huggins models because they do not require a separate capture probability parameter for each sampling occasion and are therefore less subject to over-fitting in the event of small sample sizes. We considered 7 VGAMs that included environmental factors at the time of capture (bottom temperature and DO) as well as the effort (net hours) during each sampling occasion to model differing capture probabilities (Table 2). Consequently, unlike previous studies where sampling occasion was defined as a weekly interval (Schueller & Peterson 2010, Peterson & Bednarski 2013, Bahr & Peterson 2016), all models within this study (both Huggins and VGAM) defined sampling occasion to be a set of nets (2 gill nets and 1 trammel net) fished at 1 site on a particular day. As a result,

Table 1. Candidate models (M) and corresponding parameter and variable definitions for the traditional Huggins capture-mark-recapture model set. Models differ in their restrictions on capture probability (p_c) and recapture probability (p_r). FL: fork length

Symbol	Description
M_0	Constant capture probability; constant recapture probability (model parameters: N, p)
M_b	Capture probability constant; recapture probability differs from capture probability because of behavioral change (model parameters: N, p_c, p_r)
M_t	Capture probability varies across K-number of sampling events (model parameters: N, p_j, $j = 1, …, K$)
M_h	Capture probability varies based on individual heterogeneity (FL) (model parameters: N, p_h)
M_{tb}	Capture probability varies across K-number of sampling events; recapture probability differs from capture probability because of behavioral change (model parameters: N, p_{cj}, p_{rj}, $j = 1, …, K$)
M_{th}	Capture probability varies across K-number of sample events and by individual heterogeneity (parameters: N, p_j, p_h, $j = 1, …, K$)
M_{tbh}	Capture probability varies across K-number of sampling events and by individual heterogeneity; recapture probability differs from capture probability because of behavioral change (model parameters: N, p_{cj}, p_{rj}, p_h, $j = 1, …, K$)

where:

N	population size
K	number of sampling events, from $j = 1, …, K$
p	overall capture probability
p_c	probability of first capture in a behavioral response model
p_r	probability of recapture in a behavioral response model
p_j	probability of capture during sampling event j where $1 \leq j \leq K$
p_h	slope parameter for capture probability in a heterogeneity model
p_{cj}	probability of first capture during sampling event j where $1 \leq j \leq K$
p_{rj}	probability of recapture during sampling event j where $1 \leq j \leq K$

Table 2. Candidate models (M) and corresponding parameter and variable definitions for the vector generalized additive models (VGAM) set

Symbol	Description
M_e	Capture probability varies based on effort across sampling events (model parameters: N, p_e)
M_f	Capture probability varies based on water temperature (bottom) across sampling events (model parameters: N, p_f)
M_d	Capture probability varies based on dissolved oxygen content across sampling events (model parameters: N, p_d)
M_{eh}	Capture probability varies based on effort across sampling events and by individual heterogeneity (model parameters: N, p_e, p_h)
M_{fh}	Capture probability varies based on temperature (bottom) across sampling events and by individual heterogeneity (model parameters: N, p_f, p_h)
M_{dh}	Capture probability varies based on dissolved oxygen across sampling events and by individual heterogeneity (model parameters: N, p_d, p_h)
M_{efh}	Capture probability varies based on effort and temperature (bottom) across sampling events and by individual heterogeneity (model parameters: N, p_e, p_f, p_h)

where:

N	population size
p_e	slope parameter for capture probability associated with effort
p_f	slope parameter for capture probability associated with temperature
p_d	slope parameter for capture probability associated with dissolved oxygen
p_h	slope parameter for capture probability in a heterogeneity model

each day was assigned as its own sampling occasion, and when multiple sites were fished in a single day, those were each assigned as unique sampling occasions. Although we recognize that site location was likely of biological relevance, the VGAM package is not yet capable of including categorical time-varying effects, so site was not used to model capture probability. Several single variable models were included as well as models that

investigated the additive effects of these multiple predictors. Multicollinearity was evaluated using a correlation matrix for all predictor variables, and when 2 variables were determined to be highly correlated ($|r| \geq 0.7$), the variable presumed to be more biologically meaningful was retained (Booth et al. 1994, Dormann et al. 2013). Because the VGAM package is also not set up to provide age-specific abundance estimates, only years with sufficient age-1 capture data could be used.

2.3.4. Candidate model set

In total, 14 models were considered between the 2 approaches which sometimes allowed for various covariates to influence capture and recapture pro-

bability (Tables 1 & 2) for each of the 12 yr of the age-1 capture histories. Akaike′s information criterion (AIC) was used to select the most plausible model of each type from the candidate set for each year (Akaike 1973). Following the Burnham & Anderson (2002) recommendations regarding the n/K ratio, corrected AIC (AIC_c) was computed to account for small sample size. Models which failed to converge, either because of too many missing data values or overfitting, were removed from consideration. We present the top model of each type selected from this candidate set for each year as well as the associated age-1 abundance and 95% confidence intervals (see Table 4). We also plotted the annual abundance estimates from the top Huggins and top VGAM each year to further compare the 2 approaches (see Fig. 3). Confidence intervals for the yearly abundance estimates were derived from the model standard errors (Burnham & Anderson 2002). Due to low sampling effort and sample size, no model was produced for the year 2013.

3. RESULTS

3.1. Sampling results

In all years, we were able to capture age-1 Atlantic sturgeon in the Altamaha River. However, limited sampling resources in 2013 meant that we were only able to set nets during 1 sampling occasion, for a total of just 2.1 net hours. We did not recapture any sturgeon that year. Therefore, 2013 data are excluded from our analyses. Over the 12 yr of data collection (2008–2020), 3175 individual nets were set in the Altamaha River, for a total of 2710 net hours of sampling time (Table 3). Annual sampling effort varied from 43.5 to nearly 390 net hours. We set a mean of 242 nets yr^{-1}(SD = 128). Within each study year, the number of sampling occasions varied from 12 to 152, with a mean of 77. We captured a total of 6890 Atlantic sturgeon; fish lengths varied from 181 to 2030 mm FL. Sturgeon catch included 2896 unique age-1 individuals; age-1 catch varied by year from a minimum of 12 to a maximum of 1181 (mean = 241; SD = 319) with no consistent trend in annual catches. Of those, 273 age-1 fish were recaptured during the same summer in which they were tagged, resulting in an overall within-summer age-1 recapture rate of 9.24% (SD = 0.08). Annual recapture rates varied from a minimum of 0.00 in 2014 to a maximum of 0.25 in 2017.

3.2. Abundance model results

3.2.1. Huggins closed capture models

The conventional Huggins models converged (and were able to be used to estimate age-1 abundance) in all sampling years. The time-varying model (M_t) was most commonly selected as the top model, although FL was also found to be useful in some years. Behavior was never used in the top model to predict capture probability (Table 4). The overall range of age-1 abundance estimates for the Huggins models was a low of 163 individuals (95% CI; 123–226) in 2017 to a high of 3839 individuals (95% CI; 3263–4550) in 2010 (Table 4, Fig. 3).

3.2.2. Vector generalized additive models

The VGAMs converged and were used to estimate age-1 abundance in 8 of the 12 yr of sampling. Effort was the most common covariate found in the top VGAMs, although FL and temperature also appeared in some years (all of which were positively related to capture probability). Neither behavior nor DO were useful covariates for predicting capture probability. The age-1 abundance estimates produced from these models

Table 3. Yearly sampling effort and catch results for age-1 (250 mm ≤ fork length ≤ 500 mm) Atlantic sturgeon in the Altamaha River, GA, USA, from 2008 to 2020. Sampling occasion was defined as a set of nets fished at a particular site on a given day. Total captures include all ages. All capture counts represent individual fish

Year	Sampling period	Occasions	Effort (net hours)	Total captures	Age-1 juveniles Marked	Recaptured
2008	April 1–August 29	70	182.9	332	140	15
2009	May 12–August 4	82	222.0	512	378	22
2010	May 10–July 29	146	353.5	1622	1181	105
2011	April 6–August 5	152	389.7	1934	262	34
2012	April 9–August 1	55	372.4	316	12	1
2013	August 30	1	2.1	1	1	0
2014	May 7–June 27	24	84.8	118	56	0
2015	May 6–August 8	12	43.5	76	27	0
2016	May 4–August 1	34	111.8	286	156	5
2017	April 18–July 28	99	240.5	400	24	6
2018	May 1–July 27	77	192.9	410	233	36
2019	May 6–August 2	72	232.8	500	317	25
2020	May 18–August 7	95	283.7	384	110	24

Table 4. Top models of each type used to estimate age-1 Atlantic sturgeon abundance in the Altamaha River, GA, USA, from 2008 to 2020. Each type of model, either Huggins (H) or VGAM (V), allows for different sources of variability in capture probability (p_c) and recapture probability (p_r) through individual specific and occasion specific covariates including sampling occasion, occasion specific sampling effort, occasion specific temperature (bottom), and fork length (see Tables 1 & 2 for model decriptions). Akaike weights (W) and number of parameters (K) are given for each model (only top models for each year are shown). Resulting age-1 abundance estimates and 95% confidence intervals are provided

| Year	Type	Model	W	K	Age-1 abundance	95% CI
2008	H	M_t	0.55	70	673	447–1063
2008	V	M_e	0.50	2	695	369–1022
2009	H	M_t	0.86	82	2162	1528–3122
2009	V	M_e	0.82	2	2221	1293–3149
2010	H	M_t	0.65	146	3839	3263–4550
2010	V	M_e	0.74	2	4448	3532–5366
2011	H	M_t	0.67	152	3169	2831–3567
2011	V	M_{efh}	1.00	4	1134	760–1508
2012[a]	H	M_t	0.52	55	214	119–399
2014[a]	H	M_t	0.70	24	1138	327–3274
2015[a]	H	M_t	0.67	12	333	128–969
2016	H	M_t	0.84	34	3061	1536–6275
2016	V	M_e	0.80	2	2845	111–5578
2017[a]	H	M_t	0.80	98	163	123–226
2018	H	M_{th}	0.57	78	841	682–1064
2018	V	M_{eh}	0.59	3	858	616–1100
2019	H	M_t	0.85	72	1926	1437–2628
2019	V	M_e	0.81	2	1914	1235–2592
2020	H	M_{th}	0.59	96	340	254–479
2020	V	M_e	0.58	2	312	206–417

[a]Only Huggins models were considered for this year
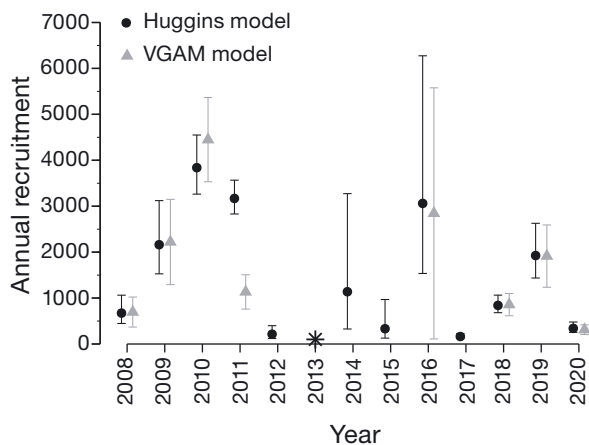
Fig. 3. Age-1 abundance estimates (± 95% confidence intervals) of Atlantic sturgeon in the Altamaha River, GA, USA, from 2008 to 2020. Yearly point estimates from top annual Huggins models and vector generalized additive models (VGAMs) are shown with 95% confidence intervals. Model estimates for VGAMs were not available for 2012, 2014, 2015, and 2017 because they failed to converge. *No data are plotted for 2013 due to insufficient sampling

ranged from a low of 312 individuals (95% CI; 206–417) in 2020 to a high of 4448 individuals (95% CI; 3532–5366) in 2010 (Table 4).

3.2.3. Model comparison

The criterion-based approach used to evaluate our population abundance models indicated that the top models varied across sampling year. Notably, the behavioral effect did not appear in the top model for any years and did not receive ≥0.25 Akaike weight, indicating that our assumption of no difference in capture probability between marked and unmarked individuals is appropriate. The resulting age-1 abundance estimates from the VGAMs were similar to those generated by the conventional Huggins models and only differed substantially in 2 of the years (2010 and 2011) with the greatest number of sampling occasions (Fig. 3). The 4 years for which VGAMs did not converge tended to have fewer sampling occasions and lower recruitment estimates when using the Huggins models.

4. DISCUSSION

4.1. Overview

This study provides the first 10+ year population assessment of Atlantic sturgeon recruitment in the South Atlantic DPS and updates abundance estimates for the Altamaha River last obtained from 2004 to 2007 (Schueller & Peterson 2010).

4.2. Model comparison

The 2 types of models used in this study resulted in comparable abundance estimates across most years; however, the methods differed in the interpretability of covariate effects. The more traditional Huggins closed capture models provided estimates of recruitment for every year of data (in contrast to the yearly VGAMs which did not always converge) but gave little information related to the interpretation of variables affecting the model parameters, p_c and p_r. Although these models do indicate the common inclusion of a time-varying effect, the specific covariates to which 'time' refers are never actually defined. Studies which have used age as an individual covariate to estimate the model parameters have made progress in the way of model interpretation (Bahr & Peterson

2016); however, age is an inconvenient variable to verify for sturgeon and other similarly threatened species for which otolith extraction is not feasible.

In contrast to the Huggins models, the VGAM package allowed for the inclusion of multiple continuous variables for estimating p_c and p_r, and subsequently allowed for more meaningful biological interpretation of measurable covariates, as opposed to the vague covariate of 'time.' Most notably, in this study, occasion-specific sampling effort was featured in the top annual model for multiple years and had a positive association with capture probability. This makes sense given that, although the instantaneous capture probability of any given fish is likely similar, increasing sampling effort within a particular sampling occasion increases the potential to encounter a given individual during that sampling occasion and is interpreted by the model as an increase in capture probability. After plotting the annual recruitment estimates along with their associated confidence intervals, we noticed that years with higher sampling effort tended to have smaller confidence intervals compared to years with less sampling effort. This post-hoc observation indicates that, for this system, 150 net hours may be a reasonable target for minimum yearly sampling effort (Figs. 3 & 4). Water temperature (at river bottom), another covariate used to model capture probability, was featured in the top model for one of the sampling years. In that case, increasing temperatures over the summer led to an increase in predicted capture probability. This was somewhat counterintuitive given that the water tem-
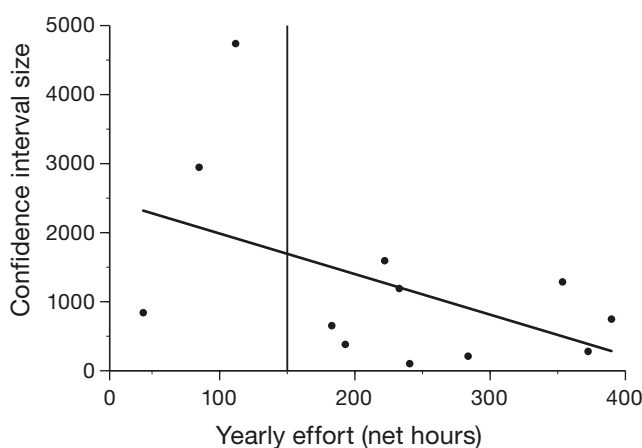

Fig. 4. Size of confidence intervals around yearly estimates of age-1 Atlantic sturgeon abundance in the Altamaha River, GA, USA, 2008–2020. Estimates are based on the top model (Huggins or vector generalized additive model [VGAM]) for each year vs. yearly sampling effort in net hours (Table 3). Solid line represents a linear regression (non-significant); vertical line indicates 150 net hours

peratures reached during the late summer approach the maximum thermal tolerances of Atlantic sturgeon and would be expected to cause decreased activity (Secor & Gunderson 1998, Cech & Doroshov 2004, Niklitschek & Secor 2010). A possible explanation is that the increased water temperatures pushed juvenile sturgeon into thermal refugia in the deeper areas where netting took place. Lastly, the inclusion of FL resulted in a better understanding of how the size of the individual affects its probability of capture — something that was not possible when using age as a covariate, due to the range of sizes within a cohort. In these models, a positive linear relationship was demonstrated between FL and p_c representing the increased gear efficiency when encountering larger age-1 individuals. Given large enough individuals (e.g. adults), this relationship may no longer be linear, but that question was outside the scope of this juvenile-focused study.

In addition to the issue of interpretability, the 2 modeling methods also differed with regard to parameterization. In the Huggins models, each sampling occasion is allowed to have its own capture probability, which in years with large numbers of sampling occasions, creates a cumbersome number of model parameters and potentially results in overfitting when numbers of observed individuals are not large enough (Williams et al. 2002). In contrast, the additive linear nature of the VGAMs meant that time-varying effects were included as single slope parameters, reducing the sample observations needed to acquire a reasonable abundance estimate. As an example, in 2011, when the greatest number of sampling occasions occurred, the unspecified time-varying model contained parameters for each of the 155 sampling occasions. Conversely, the additive model required only 4 parameters to estimate the effects of sampling effort, temperature, and fork length on capture probability. This difference in parameterization also has a large effect on model selection when using AIC_c, since the small sample correction severely penalizes models with much greater numbers of parameters (Burnham & Anderson 2002).

Due to the limitations of the current VGAM package, there were variables of potential biological relevance that could not be investigated. Location of sampling was one such variable which may have affected capture and recapture probabilities. Given the heterogeneous nature of the riverine landscape, sampling at different sites results in varying capture rates. These variations could be due to differences in water depth and velocity, substrate type, forage availability, or any number of other variables that

influence sturgeons' behavior. However, in its current form, the VGAM package is not configured to recognize categorical time-varying covariates, like sample site. Due to the multiple braided channels of the Altamaha River estuary, our sample site locations could not be converted to rkms or other continuous distance units — in single-channel estuaries, this might be a possibility. Another limitation of the software is related to how the package estimates abundance from the capture histories. In 'RMark', the package used for the Huggins models, population abundance can be estimated as group-specific (in our case age-specific) values; even though the model does not count the age-2+ fish as part of the age-1 estimate, it can still use data from those older cohorts to help estimate the time-varying model parameters. In the current version of the VGAM package, no such group-specific abundance estimate exists. This means that only the age-1 captures and recaptures can be used to estimate age-1 abundance, and information about capture probability from older cohorts is lost. In years where the majority of captures are age-2+ sturgeon, this may substantially affect the model parameters and increase the size of confidence intervals around the point estimates. Going forward, the inclusion of a function that allows for group-specific estimates in VGAM would greatly improve the utility of this package for estimating sturgeon recruitment, by allowing more complete use of the available data.

4.3. Atlantic sturgeon recruitment

The Altamaha River is thought to host the largest population of Atlantic sturgeon in the South Atlantic DPS (ASSRT 2007). From 2004 to 2007, annual recruitment in the Altamaha varied from 333 to 1453 individuals (Schueller & Peterson 2010). Our results indicate that from 2008 to 2020, the number of recruits varied from 163 to 4448. Although some years of this study demonstrated much greater recruitment than Schueller & Peterson (2010), there was no overall temporal trend in recruitment within or between the 2 studies — the number of annual recruits did not steadily increase or decrease over time. However, age-1 recruits were observed in every year from 2004 to 2020 in the Altamaha River, indicating that adults were able to successfully spawn each year. Generally, other Atlantic sturgeon populations in the South Atlantic DPS with available recruitment estimates appear to produce far fewer, if any, age-1 fish per year (Farrae et al. 2009, 2016, Fox et al. 2018b). Only the

Savannah River consistently produced age-1 Atlantic sturgeon in every year of sampling: annual recruitment from 2013 to 2017 varied from 528 to 991 age-1 fish (Bahr & Peterson 2016, Cummins 2018).

Although the species has been protected from harvest in Georgia since 1996 (2 yr before the coastwide moratorium; ASSRT 2007), the number of age-1 Atlantic sturgeon produced in the Altamaha River rarely exceeds 3000 yr^{-1}. However, a female Atlantic sturgeon may produce >0.4 million eggs per spawn (Van Eenennaam et al. 1996) — the fact that recruitment is so low in the Altamaha River indicates that there may be a bottleneck at the larval or juvenile stages. Further research is needed to investigate the survival of larval and young-of-year Atlantic sturgeon in this river and to compare these parameters with populations in other rivers. In addition to any existing bottlenecks to population growth, climate change could pose a challenge for Atlantic sturgeon. River systems are experiencing changes in the form of increasingly variable hydrologic regimes and increased water temperatures at times of the year not historically observed (Viger et al. 2011, Sun et al. 2013). Investigating how hydrologic variables, as well as temperature changes, affect all life stages (but especially the early life stages of these fish) will likely shed some light on the mechanisms affecting these population-level trends.

5. CONCLUSIONS

With the implementation of any new methodology, the practical question of its usefulness over the existing methods should be investigated. In our study, the VGAM modeling package had some advantages over the conventional Huggins models, although it possesses multiple limitations in its current form. If an abundance estimate is the only desired result, as in many monitoring programs, Huggins models would likely be sufficient. However, these models have limited interpretability of model parameters. The further development of VGAM to overcome its current limitations may offer the best of both: a rigorous mathematical model capable of providing accurate estimates that also allows for meaningful interpretation of its parameters.

Across both modeling frameworks, the results of this study indicate that the Altamaha River Atlantic sturgeon population continues to demonstrate consistent recruitment of age-1 fish each year. Long-term sets of recruitment data provide managers with insights into the effectiveness of management

practices and allow managers to examine population trends over time. In the Altamaha River, 17 yr of continuous monitoring of Atlantic sturgeon recruitment (2004−2007: Schueller & Peterson 2010; 2008−2020: this study) indicate that there is no consistent trend (upward or downward) in recruitment. An understanding of past recruitment can also help with the development of realistic goals related to species recovery and can aid in assessing the effects of natural disasters or anthropogenic activities. Given that populations range-wide have not seen significant increases since the 1998 moratorium, the conservation status of Atlantic sturgeon is not expected to change in the near future (ASMFC 2019). However, continuous monitoring programs — like our work in the Altamaha River — will allow managers to access up-to-date data and make more informed decisions as they develop future management and recovery plans.

LITERATURE CITED

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second International Symposium on Information Theory. Akademai Kiado, Budapest, p 267−281

ASMFC (Atlantic States Marine Fisheries Commission) (1998) Amendment 1 to the interstate fishery management plan for Atlantic sturgeon. ASMFC, Fishery Management Report No. 31. http://www.asmfc.org/uploads/file/sturgeonAmendment1.pdf

ASMFC (Atlantic States Marine Fisheries Commission) (2016) 2016 review of the Atlantic States Marine Fisheries Commission fishery management plan for Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) for fishing year 2013 and 2014. Prepared by the Atlantic Sturgeon Plan Review Team. http://www.asmfc.org/uploads/file/56ba055fSturgeonFMPReview2016.pdf

ASMFC (Atlantic States Marine Fisheries Commission) (2017) 2017 Atlantic sturgeon benchmark stock assessment and peer review report. Prepared by the Atlantic Sturgeon Stock Assessment Subcommittee and Technical Committee. http://www.asmfc.org/uploads/file//59f8d5ebAtlSturgeonBenchmarkStockAssmt_PeerReviewReport_2017.pdf

ASMFC (Atlantic States Marine Fisheries Commission) (2019) Review of the Interstate Fishery Management Plan for Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) 2017 fishing year. Prepared by the Atlantic Sturgeon Plan Review Team. http://www.asmfc.org/uploads/file/63ed2b462017AtlanticSturgeonFMP_review.pdf

ASSRT (Atlantic Sturgeon Status Review Team) (2007) Status review of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*). Report to National Marine Fisheries Service, Northeast Regional Office. https://repository.library.noaa.gov/view/noaa/16197

Bahr DL, Peterson DL (2016) Recruitment of juvenile Atlantic sturgeon in the Savannah River, Georgia. Trans Am Fish Soc 145:1171−1178

Bain MB (1997) Atlantic and shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environ Biol Fishes 48:347−358

Booth GD, Niccolucci MJ, Schuster EG (1994) Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. US Dept of Agriculture, Forest Service, Ogden, UT

Burnham KP, Anderson DR (2002) Model selection and inference: an information theoretic approach. Springer, New York, NY

Cech JJ Jr, Doroshov SI (2004) Environmental requirements, preferences, and tolerance limits of North American sturgeons. In: LeBreton, GTO, Beamish FWH, McKinley SR (eds) Sturgeons and paddlefish of North America. Kluwer Academic Publishers, Alphen aan den Rijn, p 73−86

Colligan M, Collins M, Hecht A, Hendrix M and others (1998) Status review of Atlantic sturgeon (*Acipenser oxyrinchus*). Prepared by Atlantic Sturgeon Status Review Team for U.S. Fish and Wildlife Service and National Marine Fisheries Service, Washington, DC

Collins MR, Rogers SG, Smith TIJ (1996) Bycatch of sturgeons along the southern Atlantic coast of the USA. N Am J Fish Manage 16:24−29

Collins MR, Rogers SG, Smith TIJ, Moser ML (2000) Primary factors affecting sturgeon populations in the southeastern United States: fishing mortality and degradation of essential habitats. Bull Mar Sci 66:917−928

Cormack RM (1964) Estimates of survival from sighting of marked animals. Biometrika 51:429−438

Cummins AJ (2018) Recruitment of Atlantic sturgeon and shortnose sturgeon within the Savannah River, Georgia and South Carolina. MS thesis, University of Georgia, Athens, GA

Darroch JN (1958) The multiple-recapture census: I. Estimation of a closed population. Biometrika 45:343−359

Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27−46

Dovel WL, Berggren TJ (1983) Atlantic sturgeon of the Hudson Estuary, New York. NY Fish Game J 30:140−172

Farrae DJ, Schueller PM, Peterson DL (2009) Abundance of juvenile Atlantic sturgeon in the Ogeechee River, Georgia. Proc Annu Conf SE Assoc Fish Wildl Agencies 63:172−176

Federal Register (2012a) Endangered and threatened wildlife and plants; final listing determinations for distinct population segments of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Northeast region. Fed Reg 77: 5880–5912

Federal Register (2012b) Endangered and threatened wildlife and plants; final listing determinations for two distinct population segments of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the Southeast. Fed Reg 77:5914–5982

Fox AG, Peterson DL (2019) Movement and out-migration of juvenile Atlantic sturgeon in Georgia, USA. Trans Am Fish Soc 148:952–962

Fox AG, Stowe ES, Dunton KJ, Peterson DL (2018a) Seasonal occurrence of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the St. Johns River, Florida. Fish Bull 116:219–227

Fox AG, Wirgin II, Peterson DL (2018b) Occurrence of Atlantic sturgeon in the St. Marys River, Georgia. Mar Coast Fish 10:606–618

Fritts MW, Grunwald C, Wirgin I, King TL, Peterson DL (2016) Status and genetic character of Atlantic sturgeon in the Satilla River, Georgia. Trans Am Fish Soc 145:69–82

Grunwald CL, Maceda L, Waldman J, Stabile J, Wirgin I (2008) Conservation of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*: delineation of stock structure and distinct population segments. Conserv Genet 9:1111–1124

Hilton EJ, Kynard B, Balazik MT, Horodysky AZ, Dillman CB (2016) Review of the biology, fisheries, and conservation status of the Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus* Mitchill, 1815). J Appl Ichthyology 32:30–66

Huggins RM (1989) On the analysis of capture experiments. Biometrika 76:133–140

Huggins RM (1991) Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732

Ingram EC, Peterson DL (2016) Annual spawning migrations of adult Atlantic sturgeon in the Altamaha River, Georgia. Mar Coast Fish 8:595–606

Jolly GM (1965) Explicit estimates from capture-recapture data with both dead and immigration-stochastic model. Biometrika 52:225–247

Kahnle AW, Laney RW, Spear BJ (2005) Proceedings of the workshop on status and management of Atlantic sturgeon Raleigh, NC, 3–4 November 2003. Special Report No. 84 of the Atlantic States Marine Fisheries Commission

Kieffer MC, Kynard B (1993) Annual movements of shortnose and Atlantic sturgeons in the Merrimack River, Massachusetts. Trans Am Fish Soc 122:1088–1103

Laake JL (2013) RMark: an R interface for analysis of capture-recapture data with MARK. AFSC processed rep 2013-01. Alaska Fish Sci Cent, NOAA, Natl Mar Fish Serv, Seattle, WA

Lincoln FC (1930) Calculating waterfowl abundance on the basis of banding returns. U.S. Department of Agriculture Circular 118, Washington, DC

Niklitschek EJ, Secor DH (2010) Experimental and field evidence of behavioral habitat selection by juvenile Atlantic *Acipenser oxyrinchus oxyrinchus* and shortnose *Acipenser brevirostrum* sturgeons. J Fish Biol 77: 1293–1308

Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations. Wildl Monogr No. 62. Wiley, Washington, DC

Petersen CGJ (1896) The yearly immigration of young plaice into the Limfjord from the German Sea. Rep Dan Biol Station 6:1–48

Peterson DL, Bednarski MS (2013) Abundance and size structure of shortnose sturgeon in the Altamaha River, Georgia. Trans Am Fish Soc 142:1444–1452

Peterson DL, Bain MB, Haley N (2000) Evidence of declining recruitment of Atlantic sturgeon in the Hudson River. N Am J Fish Manage 20:231–238

Peterson DL, Schueller P, DeVries R, Fleming J, Grunwald C, Wirgin I (2008) Annual run size and genetic characteristics of Atlantic sturgeon in the Altamaha River, Georgia. Trans Am Fish Soc 137:393–401

Pine WE III, Allen MS, Dreitz VJ (2001) Population viability of the Gulf of Mexico sturgeon: inferences from capture-recapture and age-structured models. Trans Am Fish Soc 130:1164–1174

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rogers SG, Weber W (1995) Movements of shortnose sturgeon in the Altamaha River system, Georgia. Georgia Department of Natural Resources, Coastal Resources Division, Brunswick, GA

Schnabel ZE (1938) The estimation of total fish populations of a lake. Am Math Mon 45:348–352

Schueller P, Peterson DL (2010) Abundance and recruitment of juvenile Atlantic sturgeon in the Altamaha River, Georgia. Trans Am Fish Soc 139:1526–1535

Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa

Seber GAF (1965) A note on the multiple-recapture census. Biometrika 52:249–259

Secor DH, Gunderson TE (1998) Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, *Acipenser oxyrinchus.* Fish Bull 96: 603–613

Secor DH, Anders PJ, Van Winkle W, Dixon D (2002) Can we study sturgeons to extinction? What we do and don't know about the conservation of North American sturgeons. In: Van Winkle W, Anders PJ, Secor DH, Dixon DA (eds) Biology, management, and protection of North American sturgeons. American Fisheries Society Symposium 28, Bethesda, MD, p 3–10

Sheldon JE, Alber M (2002) A comparison of residence time calculations using single compartment models of the Altamaha River estuary, Georgia. Estuaries 25: 1304–1317

Sun G, Caldwell PV, McNulty SG, Georgakakos AP and others (2013) Impacts of climate change and variability on water resources in the Southeast USA. In: Ingram KT, Dow K, Carter L, Anderson J (eds) Climate of the southeast United States: variability, change, impacts, and vunerability. NCA Southeast Technical Report Series. Island Press, Washington, DC, p 210–236

Van Eenennaam JP, Doroshov SI, Moberg GP, Watson JG, Moore DS, J Linares (1996) Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries 19:4 769–777

Viger RJ, Hay LE, Markstrom SL, Jones JW, Buell GR (2011) Hydrologic effects of urbanization and climate change on the Flint River Basin, Georgia. Earth Interact 15:1–25

Vladykov VD, Greeley JR (1963) Order Acipenseroidei. In: Olsen YH (ed) Fishes of the western North Atlantic. Sears Foundation for Marine Research, Yale University, New Haven, CT, p 24–60

Waldman JR, King T, Savoy T, Maceda L, Grunwald C, Wirgin I (2013) Stock origins of subadult and adult Atlantic sturgeon *Acipenser oxyrinchus*, in a non-natal estuary, Long Island Sound. Estuaries Coasts 36:257–267

Waldman J, Alter SE, Peterson D, Maceda L, Roy N, Wirgin I (2019) Contemporary and historical effective population sizes of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus.* Conserv Genet 20:167–184

White SL, Kazyak DC, Darden TL, Farrae DJ and others (2021) Establishment of a microsatellite genetic baseline for North American Atlantic sturgeon (*Acipenser o. oxyrinchus*) and range-wide analysis of population genetics. Conserv Genet 22:977–992

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA

Yee TW (2015) Vector generalized linear and additive models: with an implementation in R. Springer, New York, NY

Yee TW, Stoklosa J, Huggins RM (2015) The VGAM package for capture-recapture data using the conditional likelihood. J Stat Softw 65:1-33. www.jstatsoft.org