

NOTE

Age and Growth of Atlantic Sturgeon in the James River, Virginia, 1997–2011

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Abstract

Historically the Chesapeake Bay supported a large population of Atlantic sturgeon *Acipenser oxyrinchus*, but loss of suitable spawning habitat and overfishing coincided with dramatic in-system declines throughout the 20th century. Atlantic sturgeon harvest moratoriums were implemented in 1974 for Virginia waters and were expanded coastwide in 1998. In 1997, researchers became aware that commercial fishers in the James River, a tributary of the Chesapeake Bay, were catching juvenile and subadult Atlantic sturgeon as bycatch in various fisheries. Genetic studies showed that the Chesapeake Bay population has maintained genetic integrity and qualifies as a distinct population segment. Between 2007 and 2011, almost 150 adults have been caught in the tidal–freshwater portion of the James River during putative spawning runs. Pectoral fin spines from juveniles and subadults collected in the Burwell Bay (rkm 40) and Cobham Bay (rkm 60) areas and mature adult samples from vessel strikes in freshwater around or above rkm 120 were analyzed to create a length-at-age curve for Atlantic sturgeon in the James River. Five models were used to analyze the data, and the double von Bertalanffy ($k_1 = 0.054$, $k_2 = 0.097$, $t_1 = -2.85$, $t_2 = 1.09$, $t_p = 6.03$ years, $L_\infty = 2241$ mm) provided the best fit to the observed data. We estimated an increase in growth coefficient at t_p , which could be an artifact of low sample size or due to ontogenetic changes in habitat use as older fish spend more time in oceanic waters than younger fish. Atlantic sturgeon in the 6–9 year age range are rarely encountered in the James River compared with younger and older age-classes, so a more in-depth analysis of the increased growth coefficient would require ocean sampling.

Prior to extensive commercial harvesting in the late 19th century, many tributaries of the Chesapeake Bay supported abundant stocks of Atlantic sturgeon *Acipenser oxyrinchus*

(Murawski and Pacheco 1977; Smith 1985; ASSRT 2007). After the Virginia fishery collapsed in the early 1900s, Atlantic sturgeon continued to be harvested typically as bycatch until 1974 when the Virginia Marine Resources Commission placed a moratorium on harvest. In 1998, the Atlantic States Marine Fisheries Commission (ASMFC) implemented a moratorium on Atlantic sturgeon harvesting for all U.S. waters (ASMFC 1998). Many researchers considered the Chesapeake Bay population functionally extirpated (Secor 1996; Speir and O’Connell 1996; ASSRT 1998), resulting in it being a candidate for federal protection under the Endangered Species Act (Federal Register Notice RIN 0648-XZ76).

The James River is the southernmost major tributary to the Chesapeake Bay. Historically, the James River supported a large population of Atlantic sturgeon, but loss of spawning habitat and overfishing coincided with dramatic in-system declines throughout the 19th and 20th centuries (Smith 1985; Balazik et al. 2010). Observations in the 1990s of subadults caught by commercial fishers, as well as rare discoveries of dead adult Atlantic sturgeon in the James River (A. Spells, U.S. Fish and Wildlife Service, personal communication), suggested that Atlantic sturgeon inhabited the river. Genetic studies using samples from the James and York rivers showed that the Chesapeake Bay metapopulation has maintained genetic integrity and is distinct from other coastal populations (King et al. 2001). Successful spawning in the James River was verified in 2004 when a 135 mm fork length (FL) young-of-year Atlantic sturgeon was collected at river kilometer (rkm) 110 (Figure 1). It is currently unknown if the James River is the only river in the Chesapeake Bay that sustains Atlantic sturgeon reproduction. However, the James

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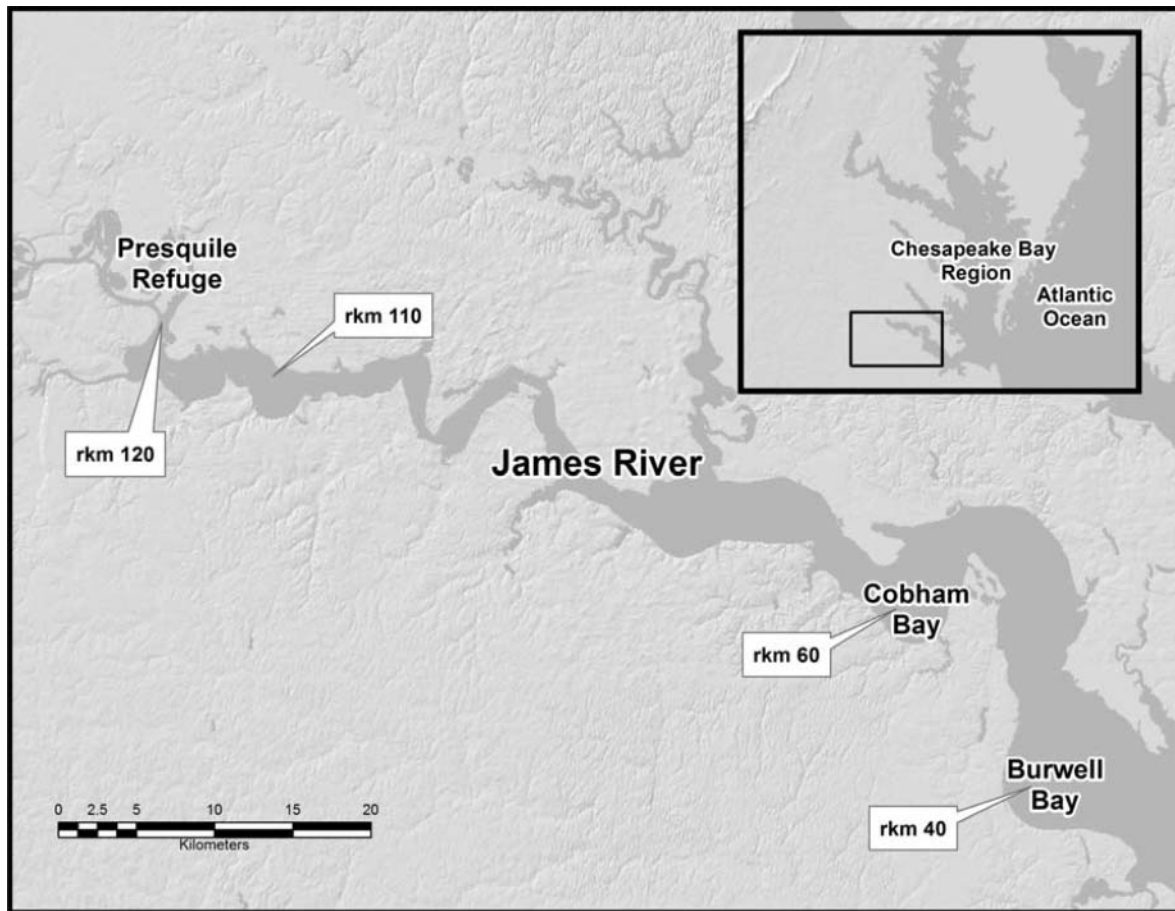


FIGURE 1. Map showing locations of James River Atlantic sturgeon sampling areas. The Burwell Bay (rkm 40) and Cobham Bay (rkm 60) areas are where the 202 juvenile and subadult Atlantic sturgeon were collected between 1997 and 2006. All samples from sexually mature fish ($n = 30$) were vessel strike mortalities collected at or above Presquile National Wildlife Refuge (rkm 120) in August and September of 2006 through 2011 during putative spawning runs. The rkm 110 location signifies where the 135 mm young-of-the-year Atlantic sturgeon was caught in 2004, which verified spawning in the James River.

River is the only river in the Chesapeake Bay watershed where present-day adult Atlantic sturgeon have been collected in freshwater reaches.

Some life history characteristics of the Chesapeake Bay Atlantic sturgeon population, including age at maturity and spawning frequency, may be inferred from latitudinally adjacent populations (Smith 1985). Direct determinations of age structure and growth rates are critical for effective restoration and management of vulnerable populations (Campana 2001). Pectoral fin spines are the preferred method for age determination in sturgeon (Brennan and Calliet 1989), and numerous age and growth studies have been conducted on Atlantic sturgeon (Magnin 1964; Squiers et al. 1979; Smith et al. 1982; Dovel and Berggren 1983; Van Eenennaam et al. 1996; Stevenson and Secor 1999) but none for the Chesapeake Bay population. The use of pectoral fin spines to estimate age has been validated for Atlantic sturgeon up to 4+ years of age (Stevenson and Secor 1999) and for lake sturgeon *A. fulvescens* (Rossiter et al. 1995). Even though this technique has been validated for other relatively young sturgeon, age underestimation of older samples is com-

mon and must be taken into consideration (Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003; Hurley 2004; Whiteman et al. 2004). The primary objective of this study was to use pectoral fin spines to create an empirical length-at-age model for Atlantic sturgeon currently inhabiting the James River.

METHODS

Study location.—Juvenile and subadult Atlantic sturgeon samples were collected by anchored gillnet from the Burwell Bay (rkm 40) and Cobham Bay (rkm 60) areas in 1997–1998 and 2006–2007. Samples from sexually mature fish were collected in freshwater around or above rkm 120 (Presquile National Wildlife Refuge) during putative spawning runs (Figure 1) between 2006 and 2011.

Sample collection.—A total of 202 juvenile and subadult (307–1,127 mm FL) Atlantic sturgeon were sampled. The 1997–1998 juvenile and subadult samples ($n = 28$) were collected during the October and November months via a

reward program targeting sturgeon. The remaining juvenile and subadult samples ($n = 174$) were collected in 2006–2007 by commercial fishers conducting a Fishery Resource Grant targeting Atlantic sturgeon. The Fishery Resource Grant provided samples from February through May and used mesh sizes between 10 cm and 35 cm. The wide range of net sizes was used to ensure that a wide range of Atlantic sturgeon size-classes was sampled. Atlantic sturgeon thought to be mature were collected during the Fishery Resource Grant but were not used for the study because of the collection area's close proximity to the ocean. Small, approximately 1–2 cm long, spine samples were removed from juveniles within 1 cm of the articulation (Brennan and Calliet 1989; Van Eenennaam et al. 1996; Stevenson and Secor 1999; Sulak and Randall 2002) using bolt cutters or a hacksaw. No negative effects from spine section removal have been documented (Collins and Smith 1996). All adult samples ($n = 30$, 1,355–2,483 mm FL) were mortalities from vessel strikes found in August and September from 2006 through 2011 and were the only samples for which sex was determined in this study. Maturity and sex was determined visually by inspecting gonads (Mohler 2004). Most adult collections were males ($n = 22$) with only one confirmed female. All male gonads were at stage 4 (large lobular white testis), the one female was a postspawn female that had released eggs within 2 weeks (J. Mohler, U.S. Fish and Wildlife Service, personal communication) of collection. Sex and gonad stage of the remaining freshwater collections ($n = 7$) could not be determined due to decomposition but are thought to be mature due to length (1,355–2,483 mm FL). Atlantic sturgeon are obligate anadromous, highly migratory, and demonstrate site fidelity (Bain 1997; King et al. 2001). The growth rate of Atlantic sturgeon varies clinally with southern groups growing and maturing faster than northern groups (Smith 1985; Balazik et al. 2010). Collections of adult Atlantic sturgeon in freshwater reaches during putative spawning runs are important because the adults were likely spawned in the James River and not from other populations.

Sample preparation.—Soft tissue on pectoral spine samples was allowed to decay and spines were scraped clean. Some samples were boiled for approximately 5 s to facilitate the removal of sticky tissue from the surface of the spine. A section (0.4–0.7 mm) from each spine was removed using an isomet saw with a diamond wafering blade (Brennan and Calliet 1989; Van Eenennaam et al. 1996). The section was mounted on a glass slide with thermoplastic resin (Crystalbond) and polished using a METASERV 2000 polish–grinder with 1200-grit lapidary film (Veinott et al. 1999). Fish age was estimated by counting annuli following published criteria (Van Eenennaam et al. 1996; Stevenson and Secor 1999; Veinott et al. 1999): an annulus was determined to be the translucent (hypermineralized) zone between two opaque zones. The translucent zones (inferred annuli) in spine sections were defined and age assignments were estimated.

The spines were read blind (FL and capture date unknown) by an experienced reader (reader 1) using a Nikon Eclipse E200

compound light microscope at $40\times$ magnification (Veinott et al. 1999). A supporting reader (reader 2) read 88% of the spines following parameters used by reader 1 to help support findings. Variables such as secondary rays and double annuli were discussed prior to age estimation (Stevenson and Secor 1999). The coefficient of variation (CV) of age estimation was determined using a paired-sample t -test to evaluate precision between readers, and bias was estimated following Campana et al. (1995).

Growth curve analysis.—Five empirical growth models were fit to the length-at-age data to facilitate model comparison and identify the best description of the data. The use of ordinary least squares to estimate model parameters requires independent observations, normally distributed length observations at each age, and constant variance of lengths across ages (Quinn and Deriso 1999). For Atlantic sturgeon age-classes with more than a few length-at-age observations, histograms of the lengths at age were positively skewed and resembled a lognormal distribution. Examination of the residuals from preliminary model fits showed that the magnitude of the residuals increased with age. The general distributional patterns of the lengths at each age combined with heteroscedasticity suggested that a multiplicative error structure was appropriate for the length-at-age data. (Quinn and Deriso 1999; Zuur et al. 2010).

The von Bertalanffy model is widely used to describe sturgeon age and growth (Morrow et al. 1998; Stevenson and Secor 1999; Sulak and Randall 2002). The traditional von Bertalanffy function (von Bertalanffy 1938), log transformed for multiplicative error, has the following form:

$$\log_e(L_i) = \log_e(L_\infty) + \log_e(1 - e^{-k(t_i - t_0)}) + \varepsilon_i, \quad (1)$$

where L_i is fork length of individual i at age t , L_∞ is the asymptotic length, k is the instantaneous growth coefficient, t_0 is the theoretical age at length zero, and ε_i is the error term. Four additional models, three of which are variations of the von Bertalanffy function, were fitted because of their added flexibility and, in two instances, because they allow growth in proportion to length to change with age. The double von Bertalanffy model (Condrey et al. 1988; Vaughan and Helser 1990; Porch et al. 2002), which allows the rate at which a fish approaches the asymptotic length to change after some pivotal age, t_p , takes the form:

$$\begin{aligned} \log_e(L_i) &= \begin{cases} \log_e(L_\infty) + \log_e(1 - e^{-k_1(t_i - t_1)}) + \varepsilon_i & \text{for } t_i < t_p \\ \log_e(L_\infty) + \log_e(1 - e^{-k_2(t_i - t_2)}) + \varepsilon_i & \text{for } t_i \geq t_p \end{cases} \\ t_p &= (k_2 t_2 - k_1 t_1) / (k_2 - k_1), \end{aligned} \quad (2)$$

where k_1 and k_2 are instantaneous growth coefficients before and after the pivotal age respectively, t_1 and t_2 are age intercepts, and ε_i is the error term. The growth function developed by Porch et al. (2002), which is a generalization of the double von

Bertalanffy model in that it allows the growth rate in proportion to length to decrease gradually with age rather than at some abrupt pivotal point, takes the form:

$$\log_e(L_i) = \log_e(L_\infty) + \log_e(1 - e^{-\beta_1 - k_0(t_i - t_0)}) + \varepsilon_i$$

$$\beta_1 = \frac{k_1}{\lambda}(e^{-\lambda t_i} - e^{-\lambda t_0}), \quad (3)$$

where λ is the damping coefficient that governs how the overall growth coefficient changes with increasing age. The other two growth models considered were the Richards function (Richards 1959),

$$\log_e(L_i) = \log_e(L_\infty) + \left(\frac{1}{\delta}\right) \log_e(1 - \delta e^{-k(t_i - t_0)}) + \varepsilon_i, \quad (4)$$

where δ is a shape parameter, and the sigmoidal Gompertz function (Quinn and Deriso 1999):

$$\log_e(L_i) = \log_e(L_\infty) - \left(\frac{\lambda}{k}\right) e^{-kt_i} + \varepsilon_i. \quad (5)$$

The parameters of all growth models were estimated using nonlinear least squares with the software package R version 2.11.0 (*nls* function; R Core Development Team 2010, Vienna, Austria). Growth models were compared using the Akaike information criterion (AIC; Akaike 1973; Burnham and Anderson 2002), which for growth model m can be written in terms of least squares output as follows (Kimura 2008):

$$AIC_m = n(1 + \log_e(2\pi \cdot RSS_m/n)) + 2p_m, \quad (6)$$

where n is the number of data points, RSS_m is the minimized residual sum of squares for model m , and p_m is the number

of estimated parameters for model m , including the error parameter. The most parsimonious model that best balances the trade-off between fit and number of estimated parameters has the lowest AIC value. Because AIC is on a relative scale, it is often important to calculate AIC differences, which are defined as $\Delta AIC_m = AIC_m - AIC_{\min}$, where AIC_{\min} is the smallest AIC value within the candidate set of models. Generally, ΔAIC_m values between 0 and 2 are indicative of substantial empirical support for the fitted model and values between 4 and 7 are associated with models that have less empirical support (Burnham and Anderson 2002).

RESULTS

Age Estimation

Of the 203 samples read by both readers, 70% ($n = 143$) had exact age agreement, 23% ($n = 46$) differed by 1 year, 6% ($n = 12$) differed by 2 years, and 2% ($n = 2$) differed by 3 years. There was an average between-reader difference of 1.3 years when age estimation was discrepant. The CV was 1.8%, and there was a significant difference ($t = 7.75$, $P < 0.05$) between age determinations by the two readers. The bias plot indicates that reader 1 consistently estimated a higher age (Figure 2). There were three fish estimated to be 10 years old collected above rkm 120 in which gonads were too decomposed for sexual maturity to be determined, the smallest of which was 1,355 mm FL. The youngest confirmed male with stage 4 gonads was 11 years old with a FL of 1,390 mm. The only confirmed female was 21 years old and was 2,005 mm FL.

Growth Curve Statistical Analysis

Numerical convergence was achieved and parameter estimates with accompanying standard errors were calculated for

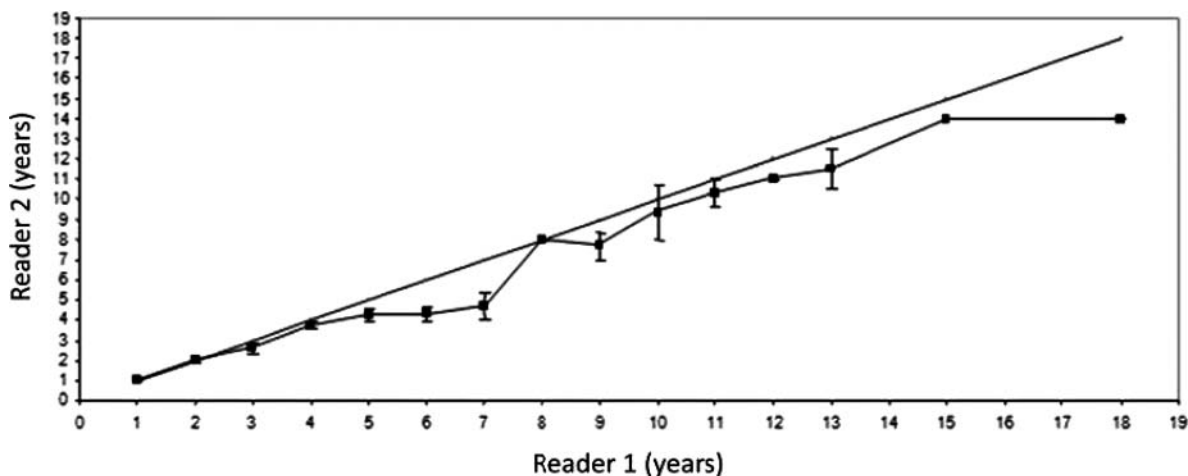


FIGURE 2. Age-bias plot visually displaying bias between reader 1 and supporting reader (reader 2) using James River Atlantic sturgeon pectoral fin spines for age estimation. The straight 1:1 background line indicates what one would expect if both readers had identical age estimates. The bias lines and points are consistently lower than the 1:1 line for older fish indicating that reader 1 consistently gave a higher age estimate than the supporting reader (reader 2). The error bars on the points indicate 95% confidence intervals of the mean age of reader 2 for all samples estimated to be a specific age by reader 1.

TABLE 1. Residual sum of squares (RSS), Akaike information criterion (AIC) and ΔAIC for the five growth models fitted to Atlantic sturgeon length-at-age data from the James River, Virginia. The double von Bertalanffy had the lowest AIC value indicating it is the best fitting model.

Model	RSS _m	Number of parameters	AIC _m	ΔAIC_m
Double von Bertalanffy	1.89	6	-415.9	0.0
Gompertz	1.98	4	-410.1	5.8
Richards	1.98	5	-408.1	7.8
Porch	1.98	6	-406.1	9.7
von Bertalanffy	2.02	4	-405.3	10.6

all models fitted to the James River Atlantic sturgeon length-at-age data. Based on AIC_m and thus ΔAIC_m , the double von Bertalanffy model provided the best fit ($L_\infty = 2,241$ mm, SE = 271.9; $k_1 = 0.054$, SE = 0.009; $k_2 = 0.097$, SE = 0.033; $t_1 = -2.85$, SE = 0.23; $t_2 = 1.09$, SE = 1.36), while the other four remaining models received considerably less empirical support (Table 1). A plot of residuals from the double von Bertalanffy model showed no apparent bias (mean of residuals = 2.9×10^{-3} , constant variance across age-classes), and the parameters were estimated precisely with the exception of t_2 . The estimate of k_2 was larger than the estimate k_1 .

Visual examination of the raw data showed an increasing rate trend in length at age between ages 5 and 10. The fitted double von Bertalanffy model captured this increase and is likely why the double von Bertalanffy model fit the data better than other growth functions considered (Figure 3). The estimated pivotal age, t_p , was 6.03 years, which coincided with the approximate age that Atlantic sturgeon increasingly utilize oceanic habitats.

DISCUSSION

The CV, 1.8%, was low compared with other sturgeon studies: 4.8% for Stevenson and Secor (1999; Atlantic sturgeon) and 7.8% for Rien and Beamesderfer (1994; white sturgeon *A. transmontanus*). When an age discrepancy occurred reader 1 gave a higher age estimate (Figure 2). Even though a bias occurred in age determination, the low CV and average age discrepancy adds confidence to age estimations.

The youngest confirmed sexually mature male was 11 years old and had a FL of 1,390 mm. The youngest freshwater samples were 10 years of age ($n = 3$) and ranged in size from 1,355 to 1,458 mm FL. All three samples were too decomposed for sexual maturity to be determined. However, due to sample location we infer that these fish were likely mature; therefore, James River male Atlantic sturgeon may mature as early as 10 years of age. Atlantic sturgeon maturation varies with age, with age of maturity decreasing with lower latitudes (Smith 1985). Our age of male maturity results are between the estimations of 8 years for South Carolina and 11–20 years for the Hudson River (Dovel 1979; Smith 1985). The only confirmed female

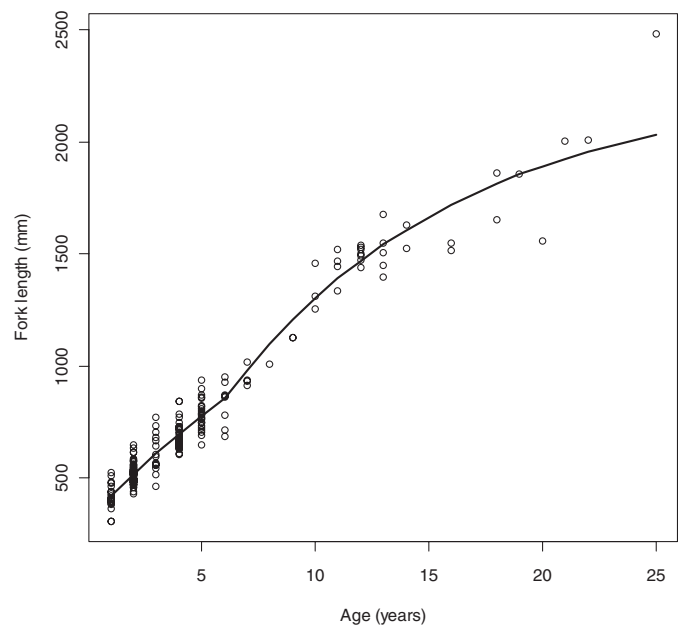


FIGURE 3. Observed length-at-age data and the fitted double von Bertalanffy model for Atlantic sturgeon in the James River. The pivotal age, denoted t_p , was estimated to be 6.03 years. The bias correction factor based on the standard error of the estimate (SEE = 0.093) was incorporated into the back-transformed model prediction (Sprugel 1983).

from this study was 21 years old with a FL of 2,005 mm; however, only one specimen precludes reliable determination of female age at maturity. Female Atlantic sturgeon do grow larger than males (Stevenson and Secor 1999) and the high male to female sex ratio in our samples likely lowered the right portion of the growth curve and the estimated L_∞ . However, the one confirmed female in the study was only 9 cm larger than what the curve predicted.

Surprisingly, the growth function developed by Porch et al. (2002) had the second largest AIC_m value, despite the fact that it allows for the growth rate in proportion to length to vary gradually with age rather than having no variation (as with the standard von Bertalanffy function) or changing abruptly at a pivotal age (as with the double von Bertalanffy model). The higher estimate for k_2 over k_1 is unusual since the rate at which a fish approaches its maximum length generally decreases with age. However, the oldest sturgeon in the present study had an estimated age of 25 years, which is well below the historical estimated maximum age of 60 years (Magnin 1964).

Historical records document Atlantic sturgeon growing up to 4.5 m total length (Scott and Crossman 1973), almost three times greater than any samples in this study. The current James River population structure has changed from the historical population (Balazik et al. 2010). The present data set reflects the typical truncated age structure of a critically depleted population. Since the oldest sample was estimated to be 25 years, large degrees of age estimation error are not likely in this study as compared with sturgeon studies with 40+ to 100+ year old samples (Rien and

Beamesderfer 1994; Stevenson and Secor 1999; Bruch et al. 2009).

Sampling effort for 6–9 year old fish was comparable to that for other age-classes, yet few animals in this age range were collected. Tracking data in the James River indicates that Atlantic sturgeon in the 6–9 years of age size-class are not utilizing the river as much as younger or older size-class fish (Virginia Sturgeon Partnership, unpublished data). The perceived decreased presence of fish in this age–size range may indicate disproportionately higher utilization of oceanic habitats than habitat utilization of other age-classes. An increase in the growth coefficient around 6 years of age could be indicative of faster growth once in the ocean, possibly due to different prey resources. Larger sample sizes in the 6–9 years of age range are necessary to confirm patterns of ontogenetic habitat shifts during the first decade of life.

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