MANAGEMENT BRIEF

Age and Growth of Atlantic Sturgeon from the Saint John River, New Brunswick, Canada

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Abstract

As a long-lived and late-maturing species, Atlantic Sturgeon *Acipenser oxyrinchus* are susceptible to overharvest, which makes knowledge concerning their age and growth essential to sustainable management. The Saint John River, New Brunswick, and the St. Lawrence River, Quebec, support the two remaining commercial fisheries for Atlantic Sturgeon in North America; however, the relationship between age and growth has not previously been modeled for the Saint John River population. Ages of Saint John River Atlantic Sturgeon were estimated by using pectoral fin spine sections collected from 262 individuals of known TL. Most (87%) of the pectoral spine sections were aged by two readers to evaluate possible reader bias. An age–bias plot and coefficient of variation (CV) indicated relatively low between-reader precision (CV = 5.6%) compared with that reported in other studies. Von Bertalanffy growth model (VBGM) parameters were estimated for males ($n = 67$), females ($n = 85$), and the combined sexes. Unsexed juveniles and subadults smaller than 150 cm TL ($n = 110$) were used for the lower part of each curve. The growth models indicated that (1) males reached maximum length sooner than females and (2) females continued to grow more as adults to greater lengths (males: Brody growth coefficient $K = 0.06$, asymptotic length $L_\infty = 230$ cm TL; females: $K = 0.04$, $L_\infty = 264$ cm TL). As predicted, the VBGM parameters estimated for combined sexes of the Saint John River stock ($K = 0.05$, $L_\infty = 254$ cm) were intermediate to those of Atlantic Sturgeon from the Hudson and St. Lawrence rivers, in agreement with a previously observed latitudinal trend in growth.

Atlantic Sturgeon *Acipenser oxyrinchus* historically supported commercial fisheries along the East Coast of North America (Smith 1985). Due to overexploitation and habitat degradation, Atlantic Sturgeon populations have declined from historical levels (Dadswell 2006). The Committee on the Status of Endangered Wildlife in Canada designated Atlantic Sturgeon as threatened (COSEWIC 2011), but the species is not yet listed for protection under Canada's Species at Risk Act. In the United States, four distinct population segments are listed as endangered under the Endangered Species Act, and one distinct population segment is listed as threatened (NMFS 2012). The Saint John River, New Brunswick, and the St. Lawrence River, Quebec, currently support the two remaining commercial fisheries for Atlantic Sturgeon along the coast of North America. Knowledge of the age and growth characteristics of a stock is essential to sustainable management; however, the age–length relationship for the Saint John River Atlantic Sturgeon

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population has not previously been determined. Therefore, the purpose of the present study was to derive a model for the age–length relationship of this population.

Atlantic Sturgeon are highly migratory, anadromous fish (Scott and Scott 1988). After hatching, Saint John River juveniles tend to spend the first several years of life in their natal estuary; upon reaching approximately 70 cm TL, they leave the natal estuary for more-marine habitat. Adult Atlantic Sturgeon (~150 cm TL) return to the Saint John River in late May prior to spawning (DFO 2009). A commercial fishery for meat and caviar is active during this time and harvests approximately 350 adult Atlantic Sturgeon annually, while approximately 50 individuals are taken by recreational fishers (~400 in total). The fishery is closed during June to protect the adults when they begin spawning, which may last until early August. During the summer months, juveniles, subadults, and nonspawning adults from the Saint John River population are present in Minas Basin within the Inner Bay of Fundy (Wirgin et al. 2012). These individuals, along with Atlantic Sturgeon from the Kennebec River, Maine, and Hudson River, New York, aggregate in Minas Basin to feed on abundant benthic invertebrates (McLean et al. 2013). Atlantic Sturgeon in Minas Basin are frequently caught as bycatch by intertidal brush-weir and otter-trawl fisheries (Beardsall et al. 2013). This situation provides multiple geographic locations in which to study different age-cohorts of the Saint John River population.

In its 2009 assessment of the Atlantic Sturgeon fishery, the Department of Fisheries and Oceans Canada (DFO 2009) stated that the current harvest quota and size limit for the Saint John River stock would be sustainable for the next 5 years. The DFO (2009) assessment also stated that the lack of an age and growth model was a "source of uncertainty" in the understanding of the Saint John River population. Fish age, length, and rate of growth are among the most essential data for proper management of a fishery (Ricker 1975). Lack of accurate age information can have serious consequences for fisheries management because it can contribute to overexploitation of a species (Lin Lai and Gunderson 1987; Bradford 1991; Yule et al. 2008; Doonan et al. 2013). An accurate growth model for a population can be used to derive the age composition for a sample of fish. Age composition is central to the assessment of recruitment, relative abundance of age-groups, total mortality from a catch curve (Van Den Avyle 1993), and size-selective mortality (Ricker 1975). Managers can also use an accurate growth model to track the abundance of year-classes through time, allowing them to assess the effects of management actions (Devries and Frie 1996) like those recently enacted for Atlantic Sturgeon populations in the USA.

The relationship between age and growth, along with other characteristics, is variable among Atlantic Sturgeon populations (Smith 1985; Stevenson and Secor 1999). Change in length over time has been modeled by using the von Bertalanffy (1938) growth model (VBGM) for populations of the St. Lawrence River (Magnin 1964); the Hudson River (Stevenson and Secor 1999); and the James River, Virginia (Balazik et al. 2012). A review by Smith (1985) provided VBGM parameter estimates for populations of the Kennebec River; Winyah Bay, South Carolina; and Suwanee River, Florida. Stevenson and Secor (1999) provided a summary of the VBGM parameters that had been estimated for each population at that time, showing a range of values; those authors observed that maximum size tended to increase with latitude.

To determine the age–length relationship and VBGM parameters of the Atlantic Sturgeon stock from the Saint John River, we used pectoral fin spine samples collected from juveniles and adults sampled in the Saint John River and from subadults that were sampled in Minas Basin and that were identified by genetic analysis as belonging to the Saint John River stock. We predicted that the VBGM parameters of the Saint John River stock would fall between those previously reported for the St. Lawrence River and Hudson River stocks. Agreement in age estimates between readers was analyzed to evaluate precision of the aging method.

METHODS

Study sites.— The Saint John River, which empties into the Bay of Fundy at Saint John, New Brunswick, is approximately 673 km long and has a drainage that encompasses parts of Maine, Quebec, and New Brunswick. The estuary of the Saint John River stretches 120 km from the tide head at Fredericton downstream to Reversing Falls at Saint John (Metcalfe et al. 1976). Atlantic Sturgeon inhabit the estuary inland to Mactaquac Dam, which is located upstream from Fredericton.

Minas Basin, part of the Inner Bay of Fundy, is located approximately 125 km from the Saint John River. The basin is a mega-tidal (range = 13–16 m), summer-warm (18–22°C), estuarine environment characterized by extensive tidal flats (one-third of the basin's area at low tide) and inflow from several rivers (salinities between 25‰ and 29‰; Bousfield and Leim 1959). Atlantic Sturgeon are found throughout Minas Basin between May and October.

Collection and preparation of samples.— Pectoral fin spine samples were taken from three separate collections: (1) juveniles ($n = 82$) captured in the Saint John River during 1973–1980; (2) subadults ($n = 28$) caught in Minas Basin during 2007–2008; and (3) adults ($n = 152$) harvested as part of the commercial fishery in the Saint John River during 2010–2012. Atlantic Sturgeon were classified as juveniles if they were less than 70 cm TL (the smallest size of confirmed Saint John River Atlantic Sturgeon captured in Minas Basin). Juveniles were caught in 2.5–3.8-cm stretch-mesh gill nets as part of a study on Shortnose Sturgeon *Acipenser brevirostrum* (Dadswell 1979). Subadults (70–150 cm TL) from Minas Basin were caught as bycatch in intertidal brush-weir and otter-trawl fisheries. Sturgeon mortality rates are low for both capture methods (Beardsall et al. 2013). Individuals caught in Minas Basin were identified as originating from the Saint John River

stock based on mitochondrial and microsatellite DNA analyses in comparison with previously determined reference stock profiles (Wirgin et al. 2012). Sex was determined for all adult Atlantic Sturgeon (>150 cm TL) caught in the Saint John River (males: $n = 67$; females: $n = 85$); sex was not determined for individuals smaller than 150 cm TL.

Atlantic Sturgeon were measured for TL, FL, or both. Growth was analyzed using TL because the minimum size limit for the Saint John River commercial fishery is expressed in TL (120 cm TL; DFO 2009). Total length was measured for most (76%) of the Atlantic Sturgeon in this study. For individuals that were only measured for FL, a linear regression was used to estimate TL (TL = $1.09 \times$ FL + 4.03); this linear regression equation was determined using the FLs and TLs of 286 Atlantic Sturgeon from the Saint John River commercial fishery. Fork length appeared to be a reliable predictor of TL, as indicated by an R^2 of 0.99.

Pectoral fin spines were collected from live juvenile and dead adult Atlantic Sturgeon in the Saint John River, while individuals from Minas Basin had their fin spines removed and were released alive. Removal of pectoral fin spines has been shown to have no deleterious effects on live Atlantic Sturgeon (Collins and Smith 1996). Pectoral fin spines were dried and then sectioned using either a low-speed Isomet saw (all adults) or a jeweler's saw (most of the juveniles and subadults). Section width varied between collections, requiring different types of lighting when observed under a microscope. Sections from juveniles and subadults were between 0.4 and 1.0 mm thick, whereas sections from adults were 5.0 mm thick. For readings under the microscope, thicker sections required reflected light, whereas thinner sections required transmitted light.

Age determination and analysis.— Age was determined for all Atlantic Sturgeon based on counts of annuli on cross sections of fin spines. When samples were viewed using transmitted light, annuli were defined as the translucent bands that marked periods of slow growth (winters), in accordance with published work (Currier 1951; Stevenson and Secor 1999). When samples were viewed with reflected light, opaque bands were considered to be the annuli. Final age was chosen, and between-reader agreement was evaluated by using two readers to estimate age for most (87%) of the pectoral spine samples (reader 1 [N.D.S.]: 1 year of experience; reader 2 [M.J.D.]: >30 years of experience). Spines were read blind without knowledge of fish length, date of capture, or other information. After an initial reading, the two readers met to decide on final age assignments for samples on which they disagreed. Reader agreement was evaluated using an age–bias plot, percent agreement, and the coefficient of variation (CV),

$$\mathrm{CV}_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j},$$

where CV_j is the estimate of precision for the jth fish, R is the number of times each fish was aged, X_{ij} is the ith age assigned for the jth fish, and X_j is the average age assignment for the jth fish. The CV_j values for all fish in the sample were averaged to create an overall mean CV (Chang 1982; Campana 2001). The resulting CV was compared to CVs from other aging studies using sturgeon fin spines. The CV was calculated using R Studio version 0.98.490 (R Development Core Team 2013). A lower CV indicates less disagreement between readers and less bias (Campana 2001).

Length at age was modeled by using the VBGM,

$$L_t = L_\infty [1 - e^{-K(t - t_0)}],$$

where L_t is length at age t, L_∞ is asymptotic length, K is the Brody growth coefficient, and t_0 is the theoretical age at which length equals zero (von Bertalanffy 1938; Ricker 1975). The VBGM parameters were estimated for all aged Atlantic Sturgeon, adult females, and adult males by using the nonlinear least-squares method in the Fisheries Stock Assessment package (FSA) for R (Ogle 2012). Unsexed individuals were used to complete the lower part of the growth curves for both males and females. Sex-specific curves were created to determine (1) whether they provided a better fit to the data than a single combined curve and (2) whether separate curves should be used for management. The fit of each curve was assessed by using the least-squares model of Akaike's information criterion (AIC; Akaike 1973) in the following form (Kimura 2008; Balazik et al. 2012),

$$\mathrm{AIC} = n[1 + \log_e(2\pi \times \mathrm{RSS}/n)] + 2p,$$

where n is the number of individuals in the sample, RSS is the residual sum of squares, and p is the number of parameters for the growth equation ($p = 3$ for the VBGM). The VBGM parameters for combined sexes of Saint John River Atlantic Sturgeon were compared to those estimated for other populations so as to assess their agreement with previously observed latitudinal trends.

RESULTS

Age Determination and Agreement

Total lengths of the 262 Atlantic Sturgeon that were aged ranged from 21.7 to 257.0 cm. Lengths ranged from 21.7 to 149.7 cm TL for unsexed individuals, from 150.0 to 233.7 cm TL for males, and from 173.0 to 257.0 cm TL for females. Age assignments ranged from 1 to 26 years for unsexed individuals, from 18 to 43 years for males, and from 25 to 51 years for females.

For the 228 Atlantic Sturgeon that were aged by both readers, 37% of the pectoral fin spine samples had exact age agreement between readers, 23% had age estimates that differed by
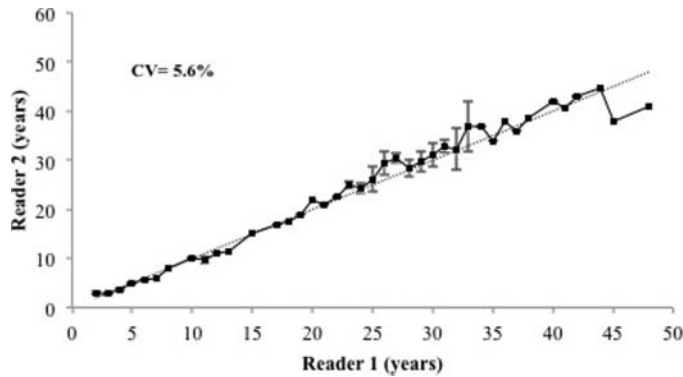
FIGURE 1. Age–bias plot displaying differences in Atlantic Sturgeon age assignments between readers 1 and 2. The dotted line shows what we would expect to see if readers 1 and 2 had assigned identical ages to all fish. The solid line and dots show the average age assigned by reader 2 for each age that was assigned by reader 1. Error bars indicate 95% confidence intervals for age-classes that were represented by five or more individuals.

1 year, 19% had age estimates that differed by 2 years, and 21% had age estimates differing by 3 years or more. The maximum disagreement on age for a sample was 15 years; however, this was attributed to the poor quality of the section. The between-reader CV was 5.6%; according to the age–bias plot, reader 2 tended to assign a higher age than reader 1. The age–bias plot also showed that disagreement between readers increased with fish age (Figure 1).

Von Bertalanffy Growth Models

Of the three growth curves evaluated, the growth curve for males had the best fit, as indicated by the lowest AIC value (Table 1). The curve for females showed the greatest maximum length, while the curve for males had the lowest maximum length, and the combined curve had an intermediate value (Figure 2). Atlantic Sturgeon from the Saint John River exhibited L_∞ and K values that were intermediate to those of Atlantic Sturgeon from the Kennebec and St. Lawrence rivers (Table 2).

DISCUSSION

Aging Accuracy and Bias

It is difficult to accurately and precisely estimate age for long-lived fishes (Campana 2001; Andrews et al. 2005). The difficulty in age estimation for older adult sturgeon

(>30 years) is mainly attributable to the close spacing of annuli near the edge of the pectoral fin spine, which is caused by intermittent spawning and slower growth at older ages (Roussow 1957; Dadswell 1979). Problems with age estimation have been reported by other researchers in studies of Atlantic Sturgeon (Stevenson and Secor 1999), White Sturgeon *Acipenser transmontanus* (Brennan and Cailliet 1989; Rien and Beamesderfer 1994), Shortnose Sturgeon (Dadswell 1979), Lake Sturgeon *Acipenser fulvescens* (Rossiter et al. 1995), and Shovelnose Sturgeon *Scaphirhynchus platorynchus* (Whiteman and Travnichek 2004).

In the present study, agreement in age estimates between readers was lower for older Atlantic Sturgeon (Figure 1). Our CV was higher than those reported in two other aging studies of Atlantic Sturgeon (4.8%: Stevenson and Secor 1999; 1.8%: Balazik et al. 2012). However, the maximum age in our study was greater than that reported in either of those studies. Many researchers suggest that a CV of 5% or less is satisfactory for fish species of moderate longevity and reading complexity (Campana 2001). Our slightly higher CV was likely the result of between-reader variation caused by closely spaced annuli at the outer edge of the pectoral fin spine in older individuals and variation in the assignment of the first one or two annuli. Early annuli were often difficult to see or were absent due to where the pectoral spine was sectioned or due to degeneration of the pectoral spine material; thus, the position of early annuli had to be assumed based on familiarity with sections from younger fish for which these annuli were visible. The annuli representing the first 2 years of growth have a characteristic star-shaped appearance, which makes them easy to recognize when present.

Our age estimation method was partly supported by the inclusion of one female Atlantic Sturgeon that was caught in Minas Basin and sampled for its pectoral fin spine during 2008 and later recaptured and harvested in the Saint John River during 2012 (4 years at large). This individual was 194 cm TL in 2008 and 203 cm TL in 2012. The female's age and length in 2012 were included in the VBGM curve, but both of the pectoral fin spine samples were aged blind. The 2008 sample was aged at 29 years, and the 2012 sample was aged at 32 years. These data provide some evidence of fairly accurate aging, particularly for an older, larger female Atlantic Sturgeon, as the concern over inaccurate aging is greatest with such individuals (Stevenson and Secor 1999).

TABLE 1. Von Bertalanffy growth model values (SE in parentheses) of asymptotic length (L_∞), Brody growth coefficient (K), and theoretical age at zero length (t_0) for Atlantic Sturgeon from the Saint John River, New Brunswick. Sample size (n) and Akaike's information criterion (AIC) are also presented.

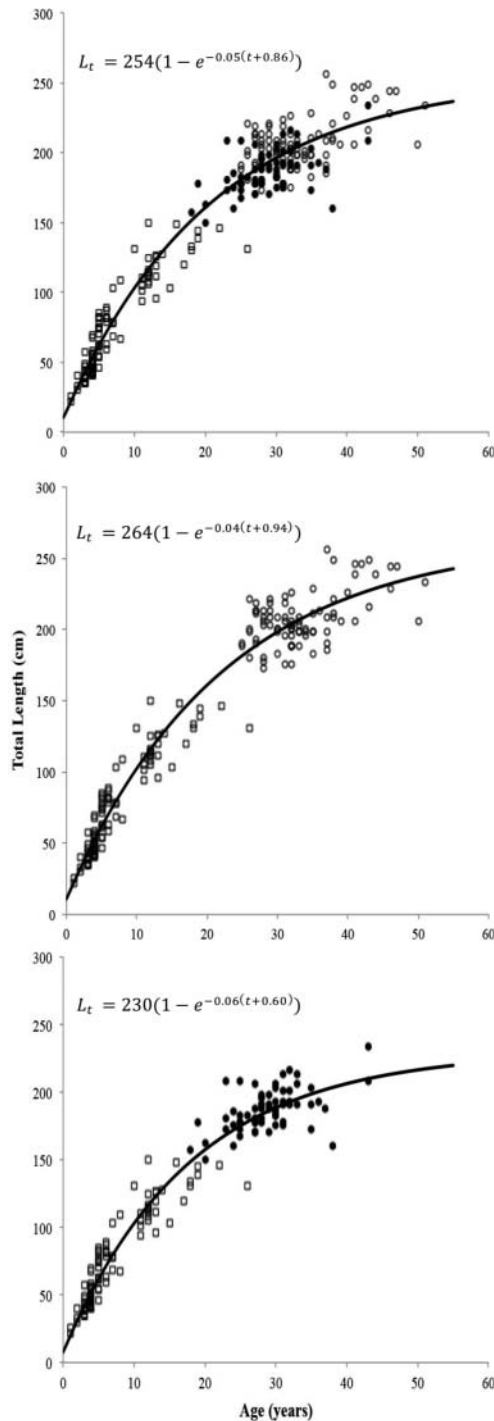| Model	n	L_∞ (cm)	K	t_0	AIC
Males and unsexed individuals	177	230 (7.85)	0.06 (0.005)	−0.60 (0.31)	1,412
Females and unsexed individuals	195	264 (9.51)	0.04 (0.004)	−0.94 (0.35)	1,603
Combined sexes and unsexed individuals	262	254 (7.69)	0.05 (0.004)	−0.86 (0.34)	2,196

FIGURE 2. Von Bertalanffy growth models of Atlantic Sturgeon from the Saint John River for all aged samples (upper panel), females and unsexed individuals (middle panel), and males and unsexed individuals (lower panel; shaded circles = males; open circles = females; open squares = unsexed individuals). Unsexed individuals (<150 cm TL) were used for all three curves.

To assess the validity of age estimation from pectoral fin spines, a complete age validation study should be conducted on Atlantic Sturgeon in the future, similar to studies conducted for White Sturgeon (Paragamian and Beamesderfer 2003),

Lake Sturgeon (Bruch et al. 2009), and Pallid Sturgeon *Scaphirhynchus albus* (Hurley et al. 2004).

Growth

Our use of unsexed juveniles and subadults to construct the lower portion of the growth curves for males and females was based more on availability of data than on the assumption that growth does not become sexually dimorphic until Atlantic Sturgeon reach 150 cm TL. Because age at maturity is variable between and within sexes and stocks and because length is variable within age-classes (Smith 1985; Stevenson and Secor 1999), there is no specific age or length that could be chosen at this time. Van Eenennaam and Doroshov (1998) reported that based on ovarian development of females in the Hudson River, sexual maturity occurs at 150–170 cm TL; the smallest mature male in that study was 150 cm TL. Male Atlantic Sturgeon apparently return to the Saint John River at around 140 cm TL, and females return at approximately 160 cm TL (C. Ceapa, unpublished data). Therefore, although these data support the use of 150 cm TL as an approximate minimum size for maturity, sexually dimorphic growth may occur before this. Ideally, all juveniles and subadults would have been sexed, collected during the same season, and equally distributed across each age-group. However, we believe that the data set analyzed here provides an appropriate and comprehensive look at the majority of the Saint John River Atlantic Sturgeon population.

Our data also provided evidence of sexually dimorphic growth. The lower AIC values for the sex-specific growth models in comparison with the growth model for the combined sexes indicate that sex-specific curves more accurately estimated length at age. The sex-specific VBGM parameters suggested that males reach their maximum length sooner, while females continue to grow to larger sizes as adults. This has been previously observed for Atlantic Sturgeon (Stevenson and Secor 1999). Female Atlantic Sturgeon likely attain larger sizes because fecundity increases with length, which favors large body size (Van Eenennaam and Doroshov 1998). Male Atlantic Sturgeon, similar to males of some other species, likely attain smaller maximum lengths because they reach sexual maturity at an earlier age (Van Eenennaam and Doroshov 1998) and spawn more frequently than females (Smith 1985; Stevenson and Secor 1999; Erickson et al. 2011). The better fit of sex-specific growth curves suggests that separate growth curves should be used for males and females when assessing the age structure of the Saint John River population.

Our VBGM parameters for the combined sexes further corroborated the trend of increasing Atlantic Sturgeon maximum length with increasing latitude (Smith 1985; Stevenson and Secor 1999). The DFO (2009) suggested that the growth rate of Atlantic Sturgeon in the Saint John River would fall between those of the Hudson and St. Lawrence rivers but would likely be closer to that in the St. Lawrence River due to

TABLE 2. Von Bertalanffy growth model (VBGM) parameters (defined in Table 1) for several Atlantic Sturgeon stocks (combined sexes) grouped by Stevenson and Secor (1999). Our VBGM parameters and those calculated from Balazik et al. (2012, via M. T. Balazik, Virginia Commonwealth University, personal communication) were added for comparison. Stock locations are listed in descending order based on latitude. Asterisks indicate data from Smith (1985), where n is the number of age-classes; Smith (1985) cited Beamesderfer (1993) for conversion of FLs to TLs (FL = 1.11 × TL), which were presented as mean length by age-class.

Location	Source	n	L_∞ (cm)	K
St. Lawrence River, Quebec	Magnin 1964	582	315	0.03
Saint John River, New Brunswick	Present study	262	254	0.05
Kennebec River, Maine	Smith 1985	7*	236	0.06
Hudson River, New York	Stevenson and Secor 1999	634	225	0.08
James River, Virginia	Balazik, personal communication	203	444	0.025
Winyah Bay, South Carolina	Smith 1985	24*	242	0.12
Suwannee River, Florida	Smith 1985	17*	184	0.14

climate similarity. This prediction proved to be correct based on our values of K, a parameter that describes how quickly individuals reach the theoretical maximum length; however, both K and L_∞ were closer to parameters reported for the Kennebec River population. Increases in maximum length and decreases in growth rate with increasing latitude have been observed in other fish species, such as the American Shad *Alosa sapidissima* and Striped Bass *Morone saxatilis*, and are attributed to water temperature and the length of the growing season (Conover 1990).

Although our estimated maximum TL of female Atlantic Sturgeon from the Saint John River population was 264 cm, in 1924 a female that measured 427 cm in length (converted from feet) was caught in the Saint John River estuary (Vladykov and Greeley 1963). Between 1973 and 1975, five Atlantic Sturgeon larger than 400 cm TL were caught in the Saint John River, but they were too large to remove from the water for accurate measurements (M. J. Dadswell, personal observation). More recently, the largest female caught in the Saint John River since 2010 was 257 cm TL. Other authors have previously observed this disparity between growth models and historical records for other systems (Stevenson and Secor 1999; Balazik et al. 2010). There are several possible explanations for the difference between current estimated maximum size and historical records of Atlantic Sturgeon size in the Saint John River. First, our sample may have lacked the largest Atlantic Sturgeon from this population, thus resulting in a VBGM that underestimated maximum length. Gear used by the fishery may select against any much larger (>400 cm TL) Atlantic Sturgeon in the system, or individuals of these sizes may be extremely rare. Second, historical periods of overfishing, causing the removal of the largest Atlantic Sturgeon from the Saint John River, may have left us with a size-truncated population (Smith 1985). Whether or not these large Atlantic Sturgeon still exist in the Saint John River, they are probably not as common now as in the past, and our growth model likely describes the age–length relationship for the greater majority of the population.

This study provides an example of how historical samples can be used to develop a comprehensive growth curve. The VBGM parameters we estimated for the Saint John River stock can be used to determine the growth of individuals and the age structure of the population and to evaluate and predict the sustainability of harvest limits and quotas. With continued cooperation between researchers and the commercial fishery to examine Atlantic Sturgeon growth, spawning periodicity, and population size, sustainable management of the Saint John River stock can be expected.

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