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ARTICLE

Age and Growth of Atlantic Sturgeon in the New York Bight

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Abstract

Accurate estimates of age and growth of fishes are important in the management and conservation of species and for the development of modeling approaches. Assessments of endangered or rare species typically are limited by poor or inadequate data owing to low abundance, unrepresentative sampling, and/or restrictions on sampling. Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*, which occurs along the east coast of North America, has five distinct population segments (DPSs) listed under the U.S. Endangered Species Act. The New York Bight (NYB) DPS is listed as endangered and represents the largest DPS in the United States. Coastal trawl surveys from 2005 to 2012 were used to evaluate the current age structure of the NYB DPS. A total of 21 year-classes (mean age = 8.89 years, $n = 742$ fish) were observed. Age data for the NYB DPS were combined with other available age estimates from multiple research laboratories and sources ($n = 2,774$) in the Hudson River and Delaware River as well from the coastal regions of New York, New Jersey, and Delaware from 1975 to 2012. Collectively, the combined data set captured much of the age range of the species, minimizing age biases and resulting in improved von Bertalanffy parameter estimates ($L_{\infty} = 278.87$, $K = 0.057$, $t_0 = -1.27$) with high overall model fit ($r^2 = 0.87$). We assessed the effects of individual data sets through a series of leave-one-out bootstrap routines that evaluated the influence of each data set on growth parameter estimates. The parameter estimates of the von Bertalanffy growth function were influenced by sampling location and/or researcher effects. Despite these differences, the combined data set approach used here represents the most comprehensive study on the age-and-growth relationship of Atlantic Sturgeon and provides parameter estimates for the development of population dynamics models and valuable information for future management.

Sufficient understanding of age and growth patterns in fishes is important for species management and conservation (Pardo et al. 2013). In addition to providing information regarding life history, unbiased estimates of growth parameters are essential for age-structured stock assessments (Johnson et al. 2005; Pardo et al. 2013). While length-at-age data for common species is readily available, age samples from endangered species can be difficult to obtain due to low abundance and restrictions on lethal sampling (Goldman 2005; Smart et al. 2013). Although it is possible to model growth curves under data-poor situations (Smart et al. 2013), the results may produce inaccurate or imprecise parameter estimates (Kritzer et al. 2001; Thorson and Simpfendorfer 2009). Often, accurate assessments of age and growth are further complicated by biases due to gear selectivity or inadequate sampling of the complete age range of the species, particularly the youngest and oldest individuals.

Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* is an anadromous species that inhabits the east coast of North America from Canada to Florida (Smith and Clugston 1997). Recently, five distinct population segments were provided federal protection under the U.S. Endangered Species Act (USOFR 2012). At the present time, the largest U.S. population of Atlantic Sturgeon occurs in the Hudson River (Kahnle et al. 2007), which combined with the Delaware Bay stock, comprises the entire New York Bight (NYB) distinct population segment (DPS). The coastal extent of the NYB ranges from Montauk Point, New York, to Cape May, New Jersey, and was the center of a historically important commercial fishery that re-emerged in the 1980s, presumably due to proximity to the Hudson River and Delaware Bay populations (Smith and Clugston 1997; Kahnle et al. 2007). Despite small coast-wide population sizes, aggregations of both adult (mature) and subadult (immature fish that have emigrated

out of natal rivers) Atlantic Sturgeon occur in areas restricted to the mouths of the Hudson and Delaware rivers during spring and fall migrations (Dunton et al. 2010, 2015; Erickson et al. 2011). These coastal aggregations comprise a genetically mixed stock that is primarily composed of fish originating from the NYB DPS, but with other DPS units detected in smaller numbers (Waldman et al. 1996; Dunton et al. 2012; O'Leary et al. 2014). The aggregations contain a high abundance of subadult Atlantic Sturgeon compared with other locations along the coast (Dunton et al. 2010, 2015).

Age structure and growth rates are often biased in Atlantic Sturgeon because of its complex migratory life history. Young juveniles remain resident in natal rivers for 1–6 years before beginning an extended marine migratory stage that includes seasonal formation of mixed-stock aggregations at the mouths of rivers and, ultimately, spawning migrations to natal rivers (Dovel and Berggren 1983; Van Eenennaam and Doroshov 1998). Age-dependent differences in habitat use and mixing of stocks makes it difficult to obtain representative age samples for all life history stages and stocks. Previous work on pre-migrant juveniles and adults has largely focused on natal rivers, with limited at-sea sampling, that has left gaps in life history stages (Dovel and Berggren 1983; Lazzari et al. 1986; Van Eenennaam et al. 1996; Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000) such as marine subadults (Dunton et al. 2010). For example, studies aging Atlantic Sturgeon from marine habitats have been limited to commercial fisheries prior to the 1998 fishing moratorium and predominately sampled older individuals (Van Eenennaam et al. 1996; Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000; Johnson et al. 2005). As a consequence, marine migratory subadults have been frequently excluded in age and growth

TABLE 1. Summary of von Bertalanffy growth curve parameters estimated from previous studies (modified from Stevenson and Secor 2000) in chronological order of publication date. Sample sizes from Smith (1985) represent age-classes and VBGF was calculated using mean size at age. The FL data from Smith (1985), Van Eenennaam and Doroshov (1998), Johnson et al. (2005), and Balazik et al. (2012) were converted to TL using the regression equation: $TL = 1.10FL + 5.02$ (see Figure A.1 in the Appendix for FL to TL conversion). This study also included additional data not shown here.

Study	Sample size	K	L_{∞} (cm TL)	Sex	Study area
Magnin (1964)	582	0.03	315	Combined	St. Lawrence (Canada)
Smith (1985)	7	0.06	236	Combined	Kennebec (Maine)
Smith (1985)	24	0.12	242	Combined	Winyah Bay (South Carolina)
Smith (1985)	17	0.14	184	Combined	Suwannee River (Florida)
Van Eenennaam and Doroshov (1998) ^a	142	0.064	290	Female	Hudson River (New York)
	161	0.11	226	Male	Atlantic Ocean
Stevenson and Secor (2000) ^a	634	0.08	225	Combined	Hudson River (New York)
	225	0.07	251	Female	Atlantic Ocean
	301	0.25	180	Male	
Johnson et al. (2005) ^a	303	0.144	197	Combined	Atlantic Ocean
	86	0.122	224	Female	
	79	0.147	203	Male	
Balazik et al. (2012)	202	0.05–0.097	251	Combined	James River (Virginia)
This study	2,774	0.06	279	Combined	Atlantic Ocean, Hudson River (New York), Delaware River and Bay (Delaware)

^aData from these studies are also included in this study.

studies because of size restrictions on the harvest of Atlantic Sturgeon or because they were not targeted by commercial fisheries.

The von Bertalanffy growth function (VBGF) relates individual length to age using parameters for the x -intercept (t_0), a growth coefficient (K), and the asymptotic maximum length (L_{∞}), with the assumption that the data represent the species' full life cycle. Acipenserid ages have been estimated using otoliths, scutes, opercula, and pectoral-fin spines (Stevenson and Secor 2000), with the latter technique being nonlethal (Collins and Smith 1996). While analysis of pectoral-fin spines is not ideal for all sturgeon species due to biased age estimation that can result in an underestimation of older age-classes (Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003; Hurley et al. 2004), annulus formation has been supported for Atlantic Sturgeon in both juveniles and adults using marginal increment analysis and oxytetracycline marking (Stevenson and Secor 2000). Age and growth of Atlantic Sturgeon has been studied in both research surveys (Dovel and Berggren 1983; Kehler 2007) and commercial fisheries (Johnson et al. 2005) and also by using a combination of fisheries-dependent and independent sampling techniques (Van Eenennaam et al. 1996; Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000; Balazik et al. 2010, 2012). Growth estimates performed on commercial data represent a limited scope of the Atlantic Sturgeon's life stages and likely

introduce bias to parameters (Stevenson and Secor 2000; Johnson et al. 2005; Kahnle et al. 2007). Previous studies based on commercial data have estimated asymptotic maximum lengths (L_{∞}) ranging from 184 to 315 cm TL and growth coefficients (K) from 0.03 to 0.14 among various populations (Table 1).

Combining data from multiple sources in data-poor situations can reduce bias from gear selectivity and increase the robustness of parameter estimates by increasing sample size and including a better representation of the species' life cycle. Focusing on the NYB DPS, the objectives of this study were to (1) evaluate the current age structure of Atlantic Sturgeon through fishery-independent surveys, (2) create an updated estimate of VBGF parameters utilizing previous aging studies combined with new age estimates, and (3) evaluate the impact of each data set on the overall VBGF for the NYB in order to identify potential bias resulting from the combination of disparate data sources.

METHODS

Current collections and age estimation.—Atlantic Sturgeon were sampled during bottom trawl surveys conducted by Stony Brook University (SBU), New York, and by the New Jersey Department of Environmental Protection (NJDEP) from 2005 to 2012; collectively these surveys will be referred to as Dunton (this study) throughout the paper (Figure 1). Detailed

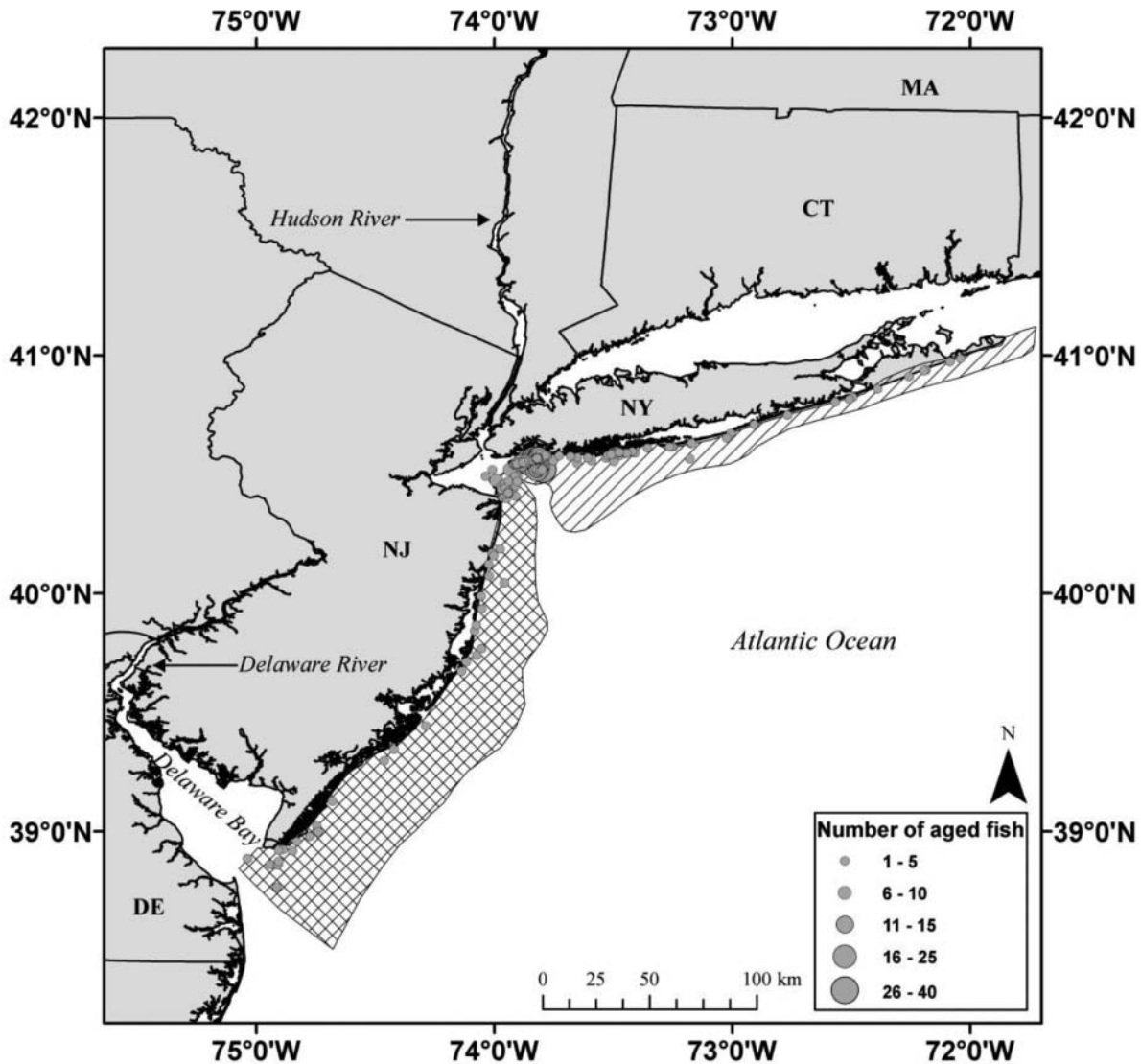


FIGURE 1. Collection locations for pectoral-fin spines used to age Atlantic Sturgeon. Samples were taken during bottom trawl surveys conducted by New Jersey Department of Environmental Protection (cross-hatched area) and Stony Brook University (hatched area) from 2005 to 2012. Other important areas where additional length-at-age data for NYB Atlantic Sturgeon (Table 2) was used are also noted: Hudson River (Dovel and Berggren 1983; Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000; Kehler 2007), Atlantic Ocean (Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000; Johnson et al. 2005), Delaware Bay and Delaware River (M. T. Fisher, unpublished data).

descriptions of the surveys can be found in Dunton et al. (2010, 2015). Trawl surveys utilized a three-to-one, two-seam trawl with a 25-m headrope and either a 30.5-m (NJDEP) or 30.6-m (SBU) footrope. Nets consisted of 12-cm-stretched-mesh forward netting, which tapered down to the rear netting of 8-cm stretched mesh, lined with 6.0-mm mesh. All bottom trawls conducted by SBU after 2009 had the 6.0-mm liner removed. The NJDEP surveys occurred from Delaware Bay, Delaware, to the New York Harbor entrance, while the SBU surveys occurred from the New York Harbor entrance to Montauk Point (Figure 1). Trawls were restricted to depths less than 30 m. Trawl locations in the NJDEP surveys were selected using a random stratified design, while SBU surveys

included both random and targeted efforts for Atlantic Sturgeon. A majority of captures occurred during spring and fall (Dunton et al. 2015).

Atlantic Sturgeon were measured to the nearest centimeter (TL and FL) and weighed (kg). Samples for aging were collected using a nonlethal and nondeleterious technique that consisted of removing a small 1–2-cm section of the primary pectoral-fin spine close to the point of articulation with a pair of cutting pliers or a saw (Collins and Smith 1996; Stevenson and Secor 2000). After April 2012, samples were collected under National Marine Fisheries Endangered Species Permit 16422 issued to SBU. Fin spines were air-dried and soft tissue was allowed to undergo microbial decay (Stevenson and Secor

TABLE 2. Summary information of sampling and biological information of Atlantic Sturgeon studies, by chronological order of publication date, used in this study for parameter estimation of the von Bertalanffy growth function.

Study	Collection method	Sample years	Sample location	Sample size	Size range (cm TL)	Age range (years)
Dovel and Berggren (1983)	Research trawl	1975–1978	Hudson River	124	16–239	0–29
Van Eenennaam and Doroshov (1998)	Commercial fishery	1992–1995	Hudson River and Atlantic Ocean	303	56–277	2–43
Stevenson and Secor (2000)	Commercial fishery	1993–1995	Hudson River and Atlantic Ocean	490	43–277	1–34
Johnson et al. (2005)	Commercial fishery	1992–1994	Atlantic Ocean	303	97–219	5–26
Kehler (2007)	Research gill net	2003–2005	Hudson River	520	36–110	1–8
Hattala (unpublished data)	Hatchery release	1994–2005	Various	238	40–200	2–17
Fisher (unpublished data)	Research gill net; mortalities	2008–2011	Delaware Bay and Delaware River	59	24–255	0–31
Dunton (this study)	Research trawl	2005–2012	Atlantic Ocean	742	54–258	2–35

2000). Any remaining tissue was removed through washings under warm water (Balazik et al. 2012). Spines were sectioned transversely from the proximal end to distal end by cutting directly with a Buhler Isomet low speed saw, equipped with double blades to allow for two simultaneous cuts. Two to four sections, ranging in thickness from 0.4 to 0.6 mm, were taken from each fin spine. Samples too small to be directly sectioned were embedded in epoxy and then sectioned. All sectioned fin spines were briefly sanded and polished using lapping film (3M 266x series; 3 and 30 μm) and/or 1,200 grit sandpaper before being examined with transmitted light under a microscope (Nikon Eclipse 80i) at 10 \times magnification. In addition to reading directly under a microscope, all spines were photographed (Nikon DXM 1200c) and annuli were examined visually and with ImageJ or ImagePro software. A single annulus is defined by one opaque and one translucent zone that could be distinctly and readily identified around the spine (Stevenson and Secor 2000). All age samples were read blindly a minimum of 2–3 times, and precision among readings was estimated by the CV as follows:

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^R \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j} \quad (1)$$

where CV_j is the precision of the age estimate for the j th fish, X_{ij} is the i th age estimate for the j th fish, X_j is the mean estimate of the j th fish, and R is the number of times a fish is aged (Campana 2001). Final age assignment was determined when two or more blind readings agreed. Bias among readers was evaluated using a subset of randomly selected spines that were examined by a second reader and

compared with a 1:1 line. Readers estimated ages without any prior knowledge of biological data, previous age estimates, or collection dates.

Additional age data for NYB Atlantic Sturgeon.—Length-at-age data from Dunton (this study) were combined with data from several published and unpublished studies on Atlantic Sturgeon (Table 2). Collectively the data covered a wide range of size and life stages, more so than any of the data sets contained alone (Figure 2). All ages were estimated using fin spine sections, except those from K. A. Hattala (unpublished data) that had fish of known age and length, as individuals were recaptures of hatchery-released fish (described in Mohler et al. 2012). Ages from M. T. Fisher (unpublished data) were estimated through fin spines collected from directed sampling as well as mortalities within the Delaware River and Delaware Bay systems. Based on the location, timing of sample collections, and genetic evidence, fish used in this analysis largely represented the NYB DPS, suggesting that the influence of genetic effects on growth rates by other DPS units is likely negligible. A genetic study, which was concurrent with fish collections from the New York–New Jersey coastal commercial fishery during the 1990s (Van Eenennaam et al. 1996; Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000; Johnson et al. 2005), showed that $97.2 \pm 6.8\%$ (mean \pm SD) of fish caught within the NYB were of local origin (Waldman et al. 1996). Collections of early juvenile fish that came directly from the Hudson River (Dovel and Berggren 1983; Kehler 2007; Hattala, unpublished data) or Delaware River (Fisher, unpublished data) were assumed to be of NYB origin since they were below the documented age of emigration from natal rivers (Dovel and Berggren 1983).

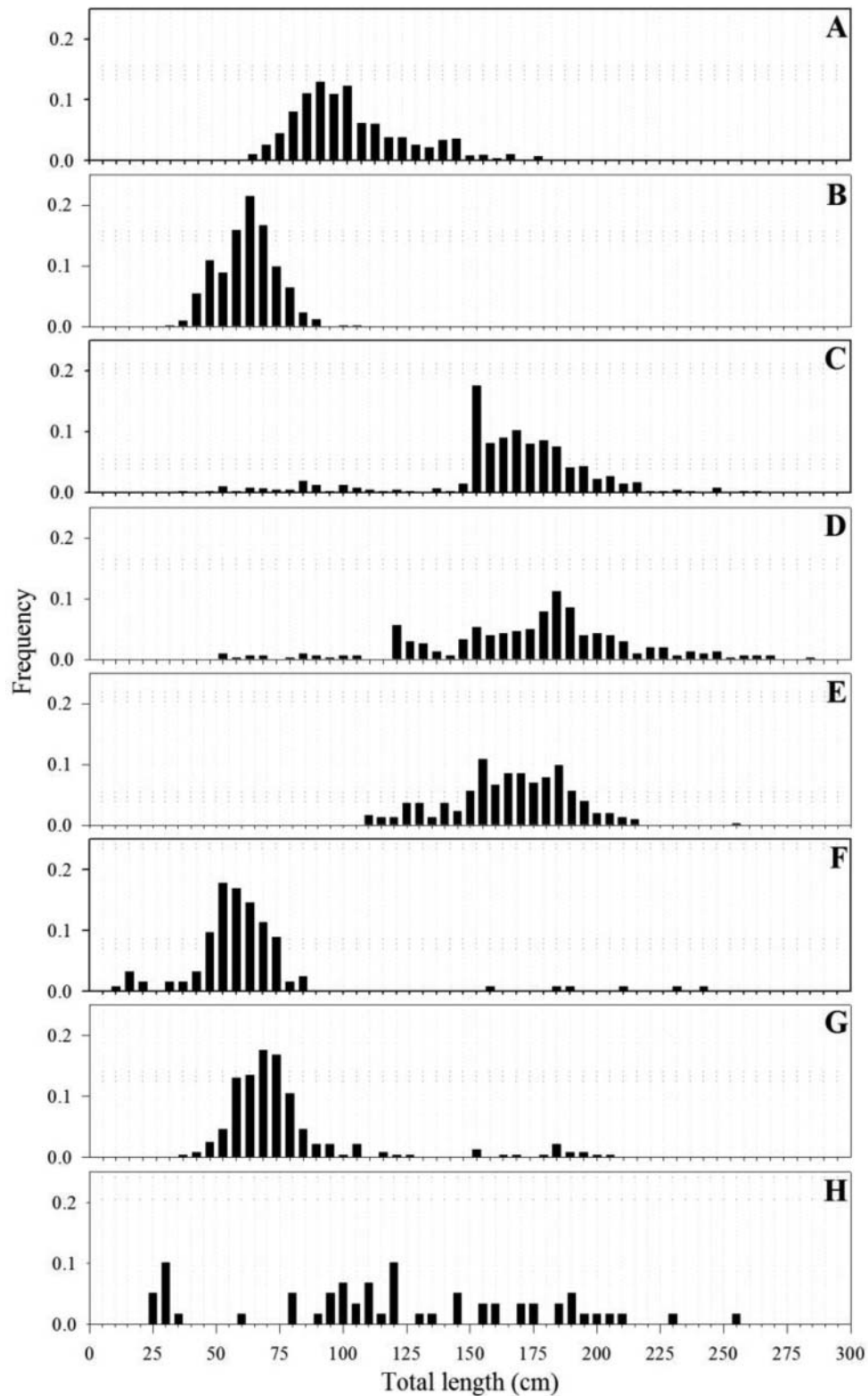


FIGURE 2. Length frequencies of aged Atlantic Sturgeon used in the von Bertalanffy growth function: (A) Dunton (this study), (B) Kehler (2007), (C) Stevenson and Secor (2000), (D) Van Eenennaam and Doroshov (1998), (E) Johnson et al. (2005), (F) Dovel and Berggren (1983), (G) Hattala (unpublished data), and (H) Fisher (unpublished data). See Table 2 for details regarding each specific study's metadata.

Estimation of VBGF parameters.—Age and length data were used to evaluate growth of Atlantic Sturgeon in the NYB DPS with the VBGF. Model fitting was achieved with nonlinear least-squares regression using the *nls* function in R (R Core Team 2013). The VBGF takes the following form:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \quad (2)$$

where L_t is length at age t , L_∞ is the asymptotic length, t_0 is the theoretical age at zero length (i.e., the x -intercept), and K is the growth coefficient. Sexes were combined in a single growth model because sex determination was not available in all studies. In addition, we performed a series of bootstrap routines to examine the impact of each data set on parameter estimates of the overall growth model. For this, we first ran a 10,000-replicate bootstrap on the full combined data set, selecting values with replacement irrespective of particular data sources. Next we ran a set of leave-one-out bootstraps (also of 10,000 replicates each), where we sequentially removed one of eight component data sets at a time. Each of the routines produced 95% CIs for K , L_∞ , and t_0 .

Normally when implementing a bootstrap analysis, one samples with replacement to create a pseudosample with an equal number of observations as the source data. However, the size of the source data changed in each of the bootstrap operations above, as individual data sources that were removed each had different sample sizes. To ensure that our results were not influenced by differences in sample size during the leave-one-out routines, we also ran all of the analyses above while keeping the sample size of the pseudosamples constant. Because the data collected for this study had the largest number of observations ($n = 742$), its removal in the leave-one-out bootstrap created the smallest sample size for the remaining combined sources ($n = 2,038$). Therefore, we did the leave-one-out bootstrap as outlined above, but kept the size of pseudosamples constant at 2,038. The impact of sample size on the overall interpretation was negligible, so the results are not presented herein.

RESULTS

Current Age Structure within the NYB

A total of 742 ($n_{\text{SBU}} = 657$, $n_{\text{NJDEP}} = 85$) of the captured Atlantic Sturgeon had readable spines suitable for aging (Figure 3). The number of sturgeon captured, and hence available spines for reading, varied each year from 12 to 316. Total length ranged from 54 to 248 cm, and had a mean of 109.30 cm (SD = 22.67) (Figure 2A). The 21 estimated age-classes ranged from 2 to 35 years old with a mean of 8.89 years (SD = 3.027), and 84.7% represented by fish less than 12 years of age (Figure 3). Precision of age estimates by different readers was determined for a subset of 64 spine samples and indicated a CV of 3.78%, and an age-bias plot showed no evidence of bias in the estimation between readers (paired

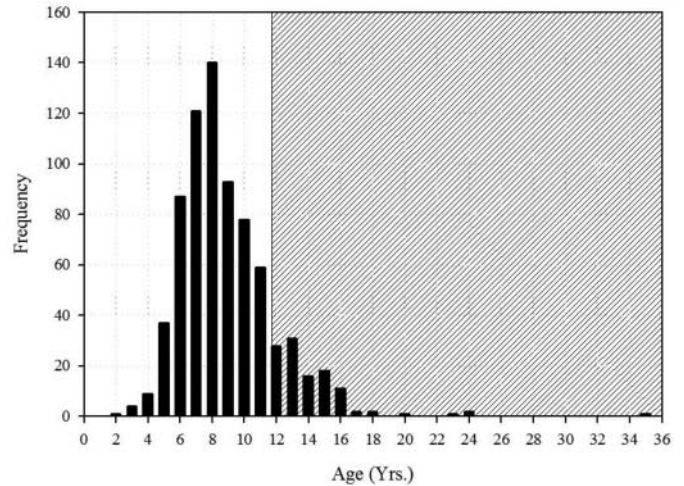


FIGURE 3. Age distribution of Atlantic Sturgeon ($n = 742$) estimated from pectoral-fin spines captured within Dunton (this study). Shaded box represents the estimated minimum age of maturity for the NYB DPS (Van Eenennaam and Doroshov 1998).

t -test: $P = 0.469$) (Figure 4). Age estimates between readers agreed exactly 62.5% of the time, within 1 year 28% of the time and within 2 years 7% of the time, and one fish had a discrepancy of ± 3 years, indicating that no systematic errors were found.

Growth curves.—The quantity and range of estimated age and size data varied among studies and comprised 2,774 samples collected and processed from the Hudson and Delaware rivers and coastal New York, New Jersey, and Delaware from 1975 to 2012 (Table 2; Figure 5). These data were used to estimate VBGF parameters for ages ranging from 0 to 43 years and sizes from 16 to 277 cm TL (mean 114.35 cm, SD = 48.69) (Figure 5). Pooled ages using the VBGF produced

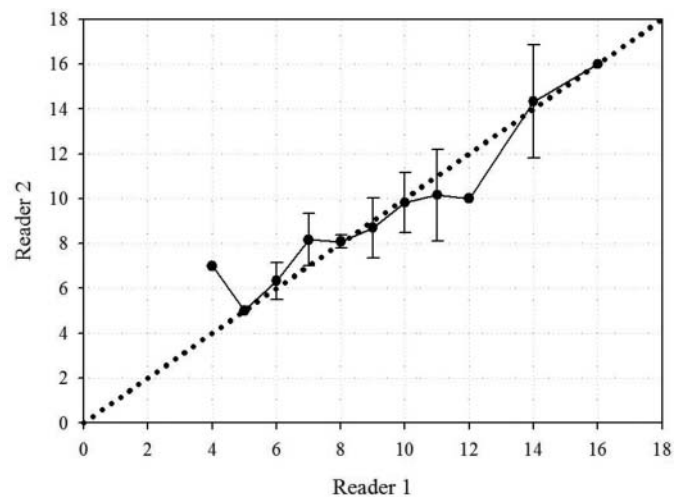


FIGURE 4. Age-bias plot for a randomly selected subset ($n = 64$) of Atlantic Sturgeon age estimates obtain in Dunton (this study). The dotted line represents the 1:1 relationship between readers; CV = 3.78%.

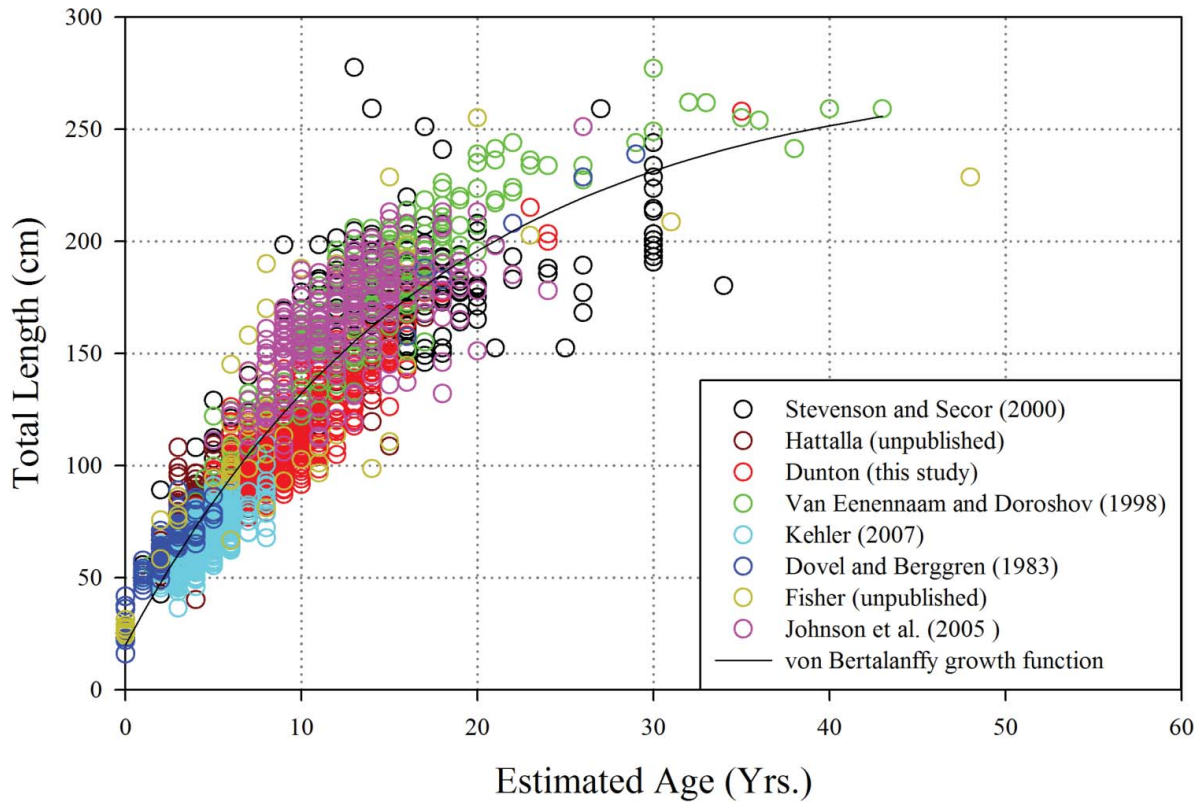


FIGURE 5. Length at age for all samples used to estimate the von Bertalanffy growth function (black line) for Atlantic Sturgeon. Inset indicates which study age estimates are from. See Table 2 for details regarding each specific study's metadata.

estimates of $L_{\infty} = 278.87$, $K = 0.057$ and $t_0 = -1.28$ ($r^2 = 0.87$) (Figure 5). The 95% CIs from bootstrap estimates of the VBGF ranged from 267.42 to 292.60 for L_{∞} , from 0.052 to 0.062 for K , and from -1.45 to -1.11 for t_0 (Figure 6).

With the exception of the Stevenson and Secor (2000) data set and data presented here, removal of individual data sets resulted in 95% CIs for L_{∞} and K that overlapped with CIs from the combined data sets (Figure 6). Relative to the other VBGF parameters, t_0 was most sensitive to the removal of data (Figure 6). With the removal of Dunton's (this study) data, the overall L_{∞} decreased, while K and t_0 increased ($L_{\infty} = 249.51$, 95% CI = 241.42–259.01; $K = 0.077$, 95% CI = 0.0711–0.0823; $t_0 = -0.71$, 95% CI = -0.86 – -0.55 ; Figure 6). In contrast, removal of data from Stevenson and Secor (2000) caused an increase in L_{∞} and decreases in K and t_0 ($L_{\infty} = 382.99$, 95% CI = 350.31–448.19; $K = 0.035$, 95% CI = 0.028–0.039; $t_0 = -1.93$, 95% CI = -2.23 – -1.70 ; Figure 6). The results are not completely unexpected as the age distribution is restricted to older fish in Stevenson and Secor (2000) and juveniles and subadults in Dunton (this study) (Figure 2).

DISCUSSION

Complex long-distance migrations, mixing of stocks, large variation in body size, and changing habitat use with both age

and season make representative sampling of the endangered Atlantic Sturgeon a challenge. Together, the combined data set of contemporary and historical age estimates provided a range of lengths covering much of the life cycle of Atlantic Sturgeon. Growth estimates from combined data sets also provided an improved statistical fit ($r^2 = 0.82$) over previous estimates for the NYB DPS with fairly narrow bootstrap-estimated 95% CIs for all parameters. Despite a broad representation of length groups, the combined VBGF parameter estimates were sensitive to sampling location and/or researcher effect on estimated growth parameters. The sequential removal of data sets with bootstrap methods demonstrated strong study effects on estimated values of K and L_{∞} . This phenomena can be seen with the exclusion of Dunton's (this study) data, consisting of primarily subadults (lower L_{∞} , higher K), and the Stevenson and Secor (2000) study that focused on larger individuals (higher L_{∞} , lower K). In general, previous studies that focused on juvenile stages produced faster growth rates, leading to the overestimation of K . Such studies produce nearly linear growth functions (Balazik et al. 2012). Research that focused on a single life stage or geographical area resulted in a strong influence on estimated growth parameters, which argues for large-scale and coordinated aging studies that represent all life stages and habitats of the species.

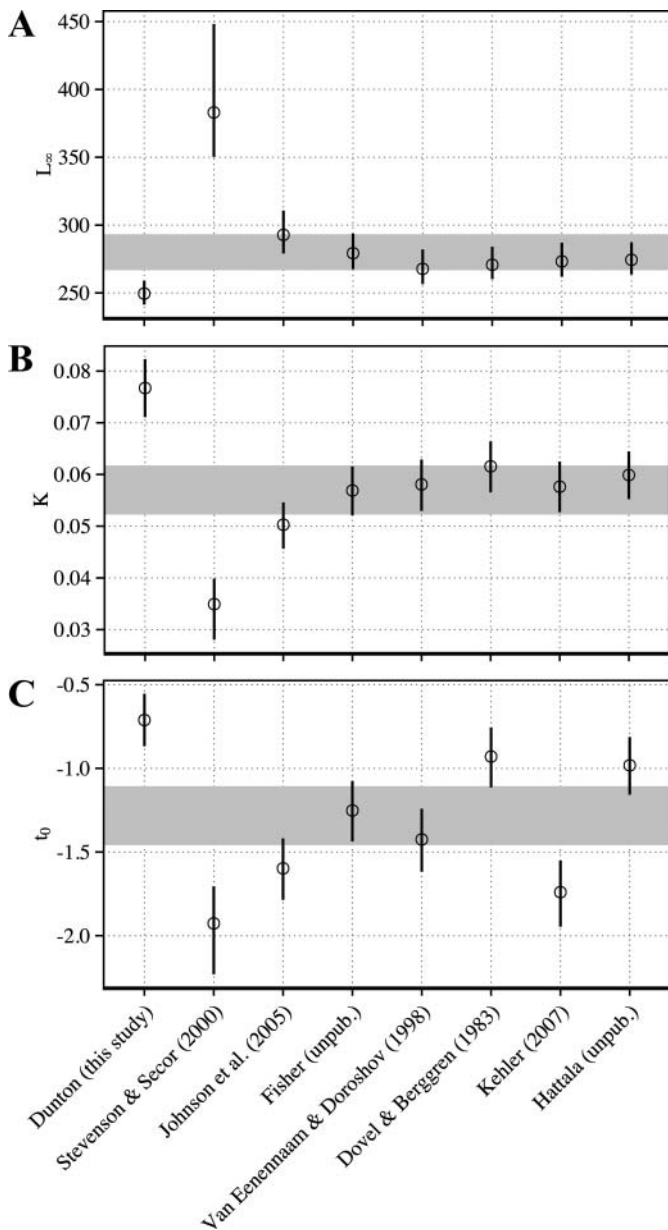


FIGURE 6. The 95% CIs on fitted (A) L_{∞} , (B) K , and (C) t_0 from bootstrap routines on the von Bertalanffy length-at-age model for Atlantic Sturgeon. Vertical lines represent 95% CIs for bootstrap analyses with one data source removed (indicated on x -axis). Original parameter estimates are displayed as open circles. For comparison, the 95% CI for the entire data set is shown as a gray, horizontal bar.

A combined data set approach was used here to overcome nonrepresentative sampling. Similar methods have been shown to improve estimates of VBGF parameters in Bluefin Tuna *Thunnus thynnus* (Restrepo et al. 2010). Omission of specific life stages or lengths has been cited as a primary factor affecting the accuracy of parameter estimates (Smart et al. 2013). The combined growth model filled a previous gap in age data (i.e., marine-captured subadults), covered all size ranges, and increased sample size. Still, the growth model

could be improved further through the addition of data from older fish. Distribution of older fish is important in the VBGF (Kritzer et al. 2001), and while this study includes age estimates of fish up to 43 years old, age estimates from fish greater than 21 years were scarce. In most cases only one estimate per age-class was included, far below the 5–10 samples per age-class recommended to capture natural variation (Sokal and Rohlf 1981; Kritzer et al. 2001).

Age estimates derived from pectoral-fin rays in other sturgeon species underestimated the age of older individuals (Rien and Beamesderfer 1994; Paragamian and Beamesderfer 2003; Hurley et al. 2004; Bruch et al. 2009). It is unclear if this systematic error is prevalent in the aging of Atlantic Sturgeon with fin spines. The use of spines in Atlantic Sturgeon is currently considered the best available method, since otoliths are hard to interpret in older ages (Stevenson and Secor 2000). If the ages of older individuals are in fact underestimated, this would lead to an overestimation of the growth rate.

The observed age distribution in Dunton's (this study) marine surveys was skewed towards subadults (84.7%), resulting from either differential habitat use among life stages, reduced catchability of adults, or low abundance of adult fish. Recent genetic analyses suggest that Atlantic Sturgeon populations have a low effective number of breeders and show evidence of inbreeding (O'Leary et al. 2014). Consequently, low CPUE of adults may reflect a continuing legacy of the fisheries effect on the populations. While the oldest aged Atlantic Sturgeon on record was a 60-year-old, 233-cm individual taken from the St. Lawrence River in Canada, fish of this size and age are uncommon. The rarity of large fish is consistent with the common trend of truncated size–age frequencies resulting from size-selective commercial fishing (Stevenson and Secor 2000; Johnson et al. 2005). Peak fisheries for Atlantic Sturgeon occurred from 1880 to 1890 and focused primarily on large females for caviar. Reports from that period provide a source of comparison for large females captured in the fishery. Ryder (1890) stated that females averaged 244 cm TL and sometimes reached 305 cm, while averages for males ranged from 183 to 213 cm. Additionally, Cobb (1900) reported the weight of females averaged 159 kg and that of males averaged 30 kg and noted that lengths of 305 cm were not uncommon.

The L_{∞} estimates reported here are within the range for Atlantic Sturgeon captured in the late 1880s and early 1900s, suggesting that reported parameters fall within the observed biological range of the species. The maximum size of Atlantic Sturgeon has been proposed to be as large as 540 cm (Bigelow et al. 1953; Smith 1985), and the largest reported specimens in the northern DPS measured 426.72 cm (Vladykov and Greeley 1963). However, the VBGF based on the combined data set failed to estimate L_{∞} values near maximum observed sizes, likely because of a lack of older and larger specimens. The lack of these large fish is likely the direct result of the fishery that existed for Atlantic Sturgeon. The historical fishery (before 1900 to the early 1900s) led to the collapse of the

Atlantic Sturgeon population by targeting the largest individual fish during spawning migrations. The following period (after 1990) was governed by a minimum size limit that targeted the largest juveniles and subadults. Such long-term selection for the largest individuals suggests evolutionary effects of size selection (towards smaller individuals) are possible (*sensu* Conover and Munch 2002). These fishing practices would have selected for precocious maturation and smaller individuals, especially since populations were driven close to extirpation with the long-term and consistent removal of the largest individuals. Similarly, minimum size limits may have led to selection for faster-growing fish, which would be harvested at a younger age as they entered the fishery. Recently, O'Leary et al. (2014) has shown a detectable amount of inbreeding occurring within the Delaware River and Hudson River populations, indicating that genetic effects of overfishing a century ago may still be prevalent in contemporary populations. Evolutionary effects of fishing have the potential to be reversed over time, but it would take several generations to build a broad and more balanced age distribution (Conover et al. 2009).

Sexual dimorphic growth patterns in Atlantic Sturgeon have been suggested as early as 1890–1899 (Ryder 1890; Cobb 1900) and more recently it has been shown that females grow slower but reach a larger maximum size than do males (Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000). The VBGF parameters were initially estimated for each sex, but due to the limited number of age samples and the restriction of those samples to certain size- and age-classes for each sex class, the resulting VBGF estimates (L_{∞} for females = 247.93, L_{∞} for males = 196.66) were much lower than the overall model's estimate. The lack of sex-specific age samples and combining both sexes together is likely to cause L_{∞} to be underestimated for females. Age and gender information of fish greater than 200 cm TL needs to be collected to further delineate this sex-based difference in mature individuals. Due to data limitations, we were unable to build on previous research documenting the influence of sex and latitude on growth parameters, and additional research is needed to better understand growth in the species (Ryder 1890; Cobb 1900; Van Eenennaam and Doroshov 1998; Stevenson and Secor 2000). Given the potential effects of sex, region, and genetics on VBGF parameters, current estimates for Atlantic Sturgeon should be used with caution until research can address the full demographic complexity of the species.

Many years have passed since enactment of the 1998 fishing moratorium on Atlantic Sturgeon and signs of population recovery should be observable in rivers as the first round of protected year-classes begin to spawn. Population monitoring (Sweka et al. 2007) and indices of early juvenile abundance are crucial for the detection of strong year-classes and can serve as early detection of population recovery and the success of protective measures (Woodland and Secor 2007). Since both annual spawning and recruitment success is highly

variable, and may even be nonexistent during unfavorable conditions (Bemis and Kynard 1997), several strong year-classes will be needed for rapid population growth and recovery (Woodland and Secor 2007). Although the link from early juvenile to subadult survival is unknown, continued sampling of the marine environment is needed to estimate how many individuals are recruiting from one life stage to the next. The next 20 years will present an opportunity to detect signs of population recovery and understand demographic shifts that may become apparent. If no improvement occurs in juvenile or adult abundances, then attention will have to shift to a broader range of impacts. Managers will need to identify sources of mortality through population modeling approaches using length-at-age and other population parameter estimates. This information can then be used to develop rebuilding plans and identify potential threats to the Atlantic Sturgeon's recovery.

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Appendix: Additional Information on the Calculation of the von Bertalanffy Growth Function for Atlantic Sturgeon.

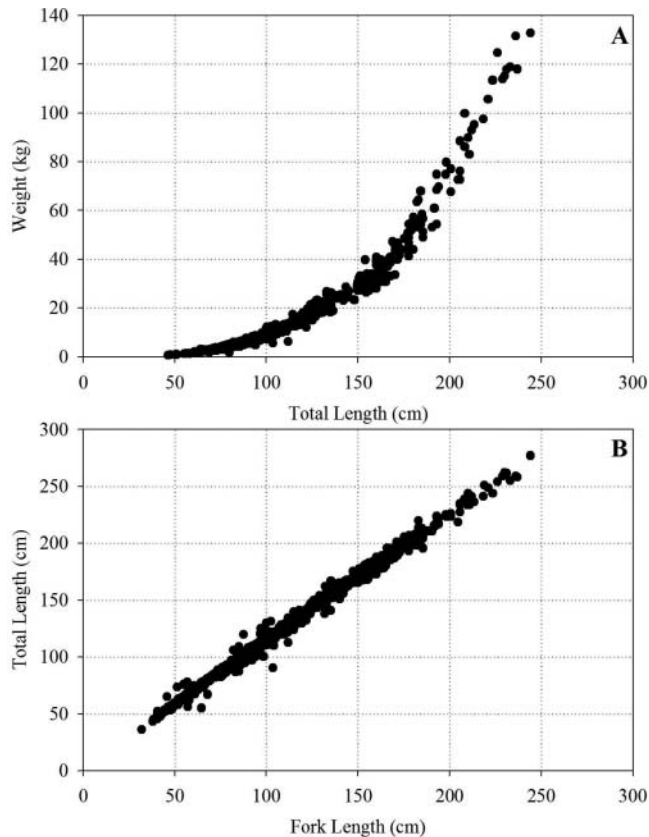


FIGURE A.1. (A) Total length versus weight ($n = 1,364$) and (B) fork length versus total length ($n = 1,829$) relationships for all available Atlantic Sturgeon used to estimate the von Bertalanffy growth function. The linear relationship of FL to TL was determined as $TL = 1.10FL + 5.02$ ($r^2 = 0.993$).