



Contemporary and historical effective population sizes of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*

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Abstract

Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) is an anadromous fish of considerable conservation concern, following its long history of overfishing and exposure to a variety of other anthropogenic stressors. Though reaching a large size, population abundances (N_c) of Atlantic sturgeon are not easily surveyed using traditional fishery methods because of their relative scarcity and their many age classes, often exhibiting extensive and differential movements that render them not readily amenable to traditional sampling efforts. A metric of their vulnerability to inbreeding and a possible alternative to N_c for abundance monitoring is effective population size (N_e). We surveyed 14 Atlantic sturgeon populations across their range using a suite of DNA microsatellite markers. Contemporary levels of N_e ranged from 1 in the St. Marys River, Florida–Georgia, to 156 in the Hudson River, New York. Historical N_e estimates averaged about 11.5× higher than contemporary estimates, with a high of 927 for the Kennebec River population. Because of a mix of life history characteristics that make traditional N_e estimates based on imperfectly mixed year classes of juveniles questionable, we propose and provide results of a new, more robust and diagnostic approach based on sequential cohorts, termed N_e Max. Although contemporary N_e values obtained were at levels that might be considered troublesome, we suggest that the unique life history factors of this species may render it more resistant than other taxa to inbreeding effects. Because of the many differences among populations in size, age, and sex ratio and in harvest histories, we do not believe that a reliable extrapolation factor between N_e and N_c is yet possible. However, ongoing monitoring of N_e and N_c in populations might be sensitive to population changes and could form the basis of determining a relationship between N_e and N_c .

Keywords Sturgeon · Effective population size · Census size · Anadromous · Polyploidy

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Introduction

Reductions in the populations of the Atlantic sturgeon subspecies (*Acipenser oxyrinchus oxyrinchus*) and its increased danger of extinction resulted in its inclusion in 2012 on the U.S. federal Endangered Species Act list (ESA). Based largely on genetic results, distinct population segments (DPS) of Atlantic sturgeon labeled as New York Bight, Chesapeake Bay, Carolina, and South Atlantic also were adopted and then designated as endangered, whereas the Gulf of Maine DPS was listed as threatened (Federal Register 2012a). The ESA listings follow decades of concern over declining numbers of Atlantic sturgeon. In 1998, a 40-year fishing moratorium was enacted to protect 20 year-classes of females (ASMFC 1998). Prior to the moratorium, the Atlantic States Marine Fisheries Commission (ASMFC) developed a fishery management plan outlining conservation and restoration measures to achieve population levels

that would support harvests at 10% of the historical peak landings (ASMFC 1990). Although the Saint John River and the St. Lawrence River populations in Canada are designated as Threatened (COSEWIC 2011), Atlantic sturgeon is the subject of regulated fisheries in Canada (Dadswell 2006). However, Atlantic sturgeon is not listed under Canada's Species at Risk Act (Hilton et al. 2016).

As for most Atlantic Coast anadromous fish species, Atlantic sturgeon has endured centuries of human-induced population reductions (Limburg and Waldman 2009). An intensive caviar-focused fishery in the Delaware River in the late 1800s produced as much as 2000 metric tons of adult Atlantic sturgeon annually; these harvests ended in the early 1900s (Secor and Waldman 1999), with few adults or juveniles seen in the Delaware until the early twenty-first century (Wirgin et al. 2015b). Other populations were also overfished for caviar or sturgeon meat, with additional reductions stemming from fishery bycatch, poor water quality, blockage of migrations by dams, habitat degradation, chemical pollution and even ship strikes (Smith and Clugston 1997; ASSRT 2007).

Today, there is strong interest in restoring Atlantic sturgeon populations. Historically, Atlantic sturgeon spawned in 38 rivers along the East Coast of North America from the St. Lawrence, Quebec, to the St. Marys River, Florida (ASSRT 2007). A recent assessment (ASMFC 2017) concluded that contemporary spawning is confirmed or highly likely in 19 of these rivers and suspected in 6 additional rivers. Both microsatellite and mitochondrial DNA (mtDNA) studies have indicated that each spawning river of Atlantic sturgeon surveyed to date contains genetically distinguishable populations (e.g., King et al. 2001; Grunwald et al. 2008; Wirgin et al. 2015a, b; Savoy et al. 2017).

Estimation of population census sizes (N_c) is a fundamental aspect of managing extant populations of endangered and threatened species. However, Atlantic sturgeon abundances are difficult to quantify for a number of reasons, many related to complexities of their life history. Young-of-the-year are challenging to survey because they tend to be widely dispersed and not easily caught in sampling gear (Farrae et al. 2009). Unknown proportions of young may leave their natal rivers as early as age-2 to occupy coastal waters for extended durations. Others remain in natal rivers for as many as 8 more years (Caron and Tremblay 1999); however, southern juveniles may remain in natal rivers for fewer years than northern individuals (Schueller and Peterson 2010). While ranging through coastal waters Atlantic sturgeon may seasonally occupy non-natal estuaries, further confounding river-specific population estimates (Waldman et al. 2013; Wirgin et al. 2018).

Census estimates are further complicated by reproductive maturation that is earlier for males than females and that individual adults do not spawn every year. Also, males

may remain in rivers longer and occupy a broader area than females when spawning (Caron et al. 2002). Another complication is that Atlantic sturgeon, in addition to having long-recognized spring spawning runs across the northern and central portions of their range also have more recently defined fall spawning runs in the center (Balazik et al. 2012; Hager et al. 2014; Smith et al. 2015) and southern portions (Ingram and Peterson 2016). Finally, it is hard to obtain sufficiently robust sample sizes for census estimates of a species with relatively few individuals dispersed over wide geographic ranges. Thus, it is likely that any Atlantic sturgeon population is both thinly and widely dispersed at any given time, and sampling any particular life stage at any single location has considerable vagaries as to what proportion of the population it represents, making extrapolation problematic. However, at the pooled-populations level, Kocik et al. (2013) estimated the that mean abundance of Atlantic sturgeon in oceanic waters (excluding any that reside year-round in rivers and estuaries) off the Northeast coast of the U.S. during 2006–2011 was 417,934 individuals, with a 95% confidence interval of 165,381–744,597.

One alternative measure of population size is genetically-based effective population size (N_e). Effective population size is the size of an ideal population experiencing the same rate of random genetic change over time as the actual population under consideration (Wright 1938). N_e is typically much smaller than census population size (N_c) because of the influences of life history and reproductive biology characteristics, such as fluctuating population size, unequal sex ratio, overlapping generations, and variance in reproductive success among individuals (Frankham 1995; Palstra and Ruzzante 2008). N_e , therefore, can be diagnostic of ongoing or impending genetic stress, such as inbreeding, and assessment of such vulnerability is usually why N_e estimates are made. Some conservation geneticists have advocated the 50/500 rule proposed by Franklin (1980) in which animal populations must be above $N_e = 50$ to avoid inbreeding depression in the short-term and above $N_e = 500$ to retain the ability to evolve in perpetuity. Evidence accumulated since 1980 shows that $N_e = 50$ is inadequate for preventing inbreeding depression over five generations in the wild, with $N_e \geq 100$ being required to limit loss in total fitness to $\leq 10\%$ (Frankham et al. 2014). Further, even $N_e = 500$ may be too low for retaining evolutionary potential for fitness in perpetuity, with $N_e \geq 1000$ being a better approximation (Frankham et al. 2014).

However, beyond its importance as an indicator of genetic vulnerability to inbreeding effects, N_e estimates are also a form of population census, albeit indirect and imperfect as a direct measure of census size, and with many caveats in their interpretation, such as the effects of sampling biases and the influences of historical effects of demography and migration on genetic characteristics. For instance, N_e can be

as much as five orders of magnitude lower than census sizes in marine broadcast spawners that have large variances in reproductive success (O’Leary et al. 2013). A recent analysis of the effective number of breeders N_b and the number of spawners (N_a ; developed from mark-recapture studies) in the Atlantic sturgeon population of the Altamaha River, Georgia, however, showed a more even relationship with N_c , with N_b at levels 7–45% lower than N_c (Moyer et al. 2012).

Despite this lack of direct correspondence between N_e and N_c , N_e offers a useful, rigorous, and integrative means with which to compare population-specific information that is at least somewhat reflective of, if not perfectly correlated, with population census sizes. Simulations suggest that contemporary single-sample methods to estimate N_e often can detect population trends as accurately as classical ecological methods (Tallmon et al. 2010). For instance, Portnoy et al. (2009) suggested that for sandbar sharks (*Carcharhinus plumbeus*), the magnitude of N_e appeared to be strongly coupled with, and roughly half the size of N_c . Development of an accepted quantitative relationship between N_e and N_c for Atlantic sturgeon would be valuable for such a species with difficult-to-estimate census sizes.

Several life history characteristics have been demonstrated to potentially impact the ability to accurately estimate N_e in populations of species with overlapping generations (Waples et al. 2014). Two of the most prominent, maximum life expectancy and age at initial maturity (Waples et al. 2013), are problematic to define in Atlantic sturgeon. That is because of the dramatic differences among DPS, and even populations within DPS, for these characteristics. Atlantic sturgeon are potentially very long-lived with a maximum life expectancy of over 60 years (Dadswell 2006) reported for the Saint John River, Canada; however, it is likely that extreme longevity does not apply to most other populations because of the significantly slower growth rates of northern compared to southern populations. Moreover, there are latitudinal differences among populations, and even genders within populations, in age at reproduction. For example, initial spawning ranges between 5 and 32 years (Smith and Clugston 1997), occurring in southern rivers at younger ages than in northern populations. Furthermore, males achieve sexual maturity earlier than females, e.g., in the James River initial spawning occurs at age-10 for males and age-15 for females (Balazik 2012).

To assess reduced genetic variability, to provide a metric of relative population sizes for Atlantic sturgeon, and to explore the relationship between N_e (both historical and contemporary) and N_c , we used a suite of DNA microsatellite markers to estimate N_e and N_b in Atlantic sturgeon populations ranging from Canada to the Georgia–Florida border. Although several alternative methods to estimate N_e are available, we used the linkage-disequilibrium approach, as recommended by Waples and Do (2009). To better

understand the effects of declines of Atlantic sturgeon on their population genetics, we also estimated historical values of N_e for the same populations using a coalescent-based method that incorporates migration between populations. However, because of the many asymmetric aspects of their life histories at the individual, male vs. female, and population levels and because of possible biases inherent in the sampling of Atlantic sturgeon, we also analyzed contemporary N_e on a year-class basis for selected populations for which collections of juveniles were available for multiple years. These annual calculations of N_e based on individual year-classes were then examined in a cumulative fashion over several consecutive years to obtain a more robust assessment of N_e for the entire population, what we termed N_e Max. By then comparing our calculations of historical N_e values with N_e and N_e Max obtained from contemporary samples, our results provide a novel genetic assessment regarding the current status of several populations.

Methods

Atlantic Sturgeon collections

Atlantic sturgeon were collected from across their range from June 1980 to July 2017, for 43 individual collections. In total, 2030 Atlantic sturgeon were analyzed from 14 extant reference spawning populations (Fig. 1). The number of individual collections made within spawning rivers (Table 1) ranged from 1 (Connecticut) to 9 (Hudson). These specimens were either juveniles (defined as ≤ 54 cm TL) or adults (defined as ≥ 127 cm TL), except for those from the St. Lawrence River collected in 1992, which were subadult males of unknown length and 5 two-year old specimens collected from the St. Marys River in 2015. Because of their differential availabilities in individual estuaries, collections are composed of either juveniles or adults, except for the Edisto, James, and Hudson Rivers which contain both life stages. Fin clips were taken from all specimens except for those from the St. Lawrence River in 1992, from which livers were removed and immediately frozen, and from the Kennebec River in 1980, from which DNA was isolated from dried fin spines. Fin clips were stored in 95% ethanol prior to DNA isolations. Except for the Connecticut River, all rivers were sampled over two or more years.

DNA isolations

Fin clips were washed with phosphate-buffered saline and incubated in cetyltrimethyl ammonium bromide (C-Tab) buffer (Saghai-Marroof et al. 1984) and digested at 65 °C with proteinase K (Roche Diagnostics, Indianapolis, IN). Genomic DNA was purified using phenol–chloroform



Fig. 1 Map of rivers in which Atlantic sturgeon collections were made. *DPS* distinct population segment, *MU* management unit

extractions, alcohol precipitations, air drying and resuspension in Tris–EDTA buffer. Concentrations and purities of DNAs were evaluated using a Nanodrop ND-1000 Spectrophotometer (NanoDrop Technologies, Wilmington, DE). DNA concentrations were adjusted to 50 ng/μl for standardization of subsequent analyses.

Microsatellite analysis

Eleven microsatellite loci were scored that were previously shown to be effective in distinguishing spawning populations of Atlantic sturgeon and that behaved in a codominant pattern in pedigree analysis (King et al. 2001; Wirgin et al. 2015a, b). These included LS19, LS39,

LS54, LS68 (May et al. 1997), Aox23, AoxD45 (King et al. 2001), and Aox44, AoxD165, AoxD170, AoxD188, AoxD24 (Henderson-Arzapalo and King 2002). PCR amplifications followed the procedure described in Wirgin et al. (2015a).

Microsatellite genotypes were determined using a Beckman Coulter CEQ8000™ capillary-based DNA sequencer (Beckman Coulter Fullerton, CA). Individual PCR reactions were multi-pooled, diluted up to 1:3 with Sample Loading Solution (Beckman Coulter), 0.5–2.0 μl of reactions were loaded onto 96 well plates along with 0.5 μl of CEQ DNA Size Standard-400 (Beckman Coulter) and 40 μl of Sample Loading Solution (Beckman Coulter), and run with the FRAG 1 program (Beckman Coulter).

Table 1 Characterization of Atlantic sturgeon genotyped in this study

| River | N | Length range (cm), mean in parentheses | Collection period | |
|-----------------|----------|--|----------------------------|-------------------------|
| St. Lawrence | 40 | ND | August 1992 | |
| | 50 | 167–197 (177.9) FL | May–June 2015 | |
| Saint John | 66 | 127–244 (170.3) TL | July–August 1992–1993 | |
| | 161 | 162.6–248.9 (199.7) TL | May–August 2014 | |
| Kennebec | 19 | 157–229 (171.0) FL | June–July 1980 | |
| | 43 | 133–197.4 (171.6) TL | June 2010–August 2011 | |
| Connecticut | 47 | 22.5–71.0 (53.7) TL | May–October 2014 | |
| Hudson | 83 | 152.0–244.0 (185.7) TL | June 1990–1994 | |
| | 32 | 155.0–242.0 (192.5) TL | June–July 2006 | |
| | 42 | 172.7–240.7 (190.8) TL | June 2009 | |
| | 50 | 170.2–222.3 (197.7) TL | June 2010 | |
| | 30 | 43.2–54.0 (49.8) TL | March–April 2011 | |
| | 35 | 40.4–52.8 (46.2) TL | March–April 2013 | |
| | 46 | 27.6–50.0 (43.9) TL | April–May 2014 | |
| | 53 | 163.2–249.0 (192.4) TL | June 2015 | |
| | 32 | 37.8–50.0 (46.8) TL | March–April 2016 | |
| | 56 | 164.0–228.0 (197.3) TL | June 2017 | |
| | Delaware | 59 | 22.0–36.7 (30.4) TL | September–November 2009 |
| | | 49 | 23.5–36.3 (28.9) TL | September–November 2011 |
| | James | 58 | 26.0–49.5 (45.7) TL | Unknown |
| 58 | | 122.0–211.0 (161.1) FL | July–September 2014 | |
| Albemarle | 41 | 28.6–48.5 (38.8) TL | May–September 1998 | |
| | 31 | 27.0–49.9 (40.3) TL | December 2006–January 2011 | |
| | 16 | 31.5–49.4 (43.0) TL | January 2013–March 2014 | |
| Edisto-Combahee | 40 | 115.7–233.7 (156.2) TL | March–November 1998 | |
| Edisto | 53 | 27.7–50.0 (39.9) TL | April–October 1996 | |
| | 52 | 32.6–48.5 (42.4) TL | May–September 2005 | |
| Savannah | 50 | 31.6–44.7 (39.1) TL | May–June 2013 | |
| | 50 | 27.4–47.9 (37.0) TL | May 2014 | |
| | 61 | 27.6–45.3 (41.9) TL | May–July 2017 | |
| Ogeechee | 26 | 19.9–52.0 (28.6) TL | June 2007–August 2009 | |
| | 45 | 22.7–31.0 (26.0) TL | July–August 2014 | |
| | 67 | 16.6–44.2 (33.2) TL | May–July 2015 | |
| | 47 | 21.0–52.0 (33.5) TL | May–July 2016 | |
| | 15 | 40.1–50.1 (45.8) TL | June–July 2017 | |
| Altamaha | 49 | 31.9–40.4 (37.9) TL | June–July 2005 | |
| | 40 | 32.7–48.1 (38.6) TL | July–August 2011 | |
| | 55 | 28.1–48.7 (37.2) TL | May–June 2014 | |
| | 64 | 27.5–41.7 (38.3) TL | May–July 2016 | |
| | 37 | 35.0–53.0 (45.6) TL | April–June 2017 | |
| Satilla | 41 | 22.8–42.8 (38.2) TL | June–July 2015 | |
| | 27 | 22.9–52.4 (44.0) TL | June–July 2016 | |
| St. Mary's | 9 | 29.3–40.5 (36.0) TL | May–June 2014 | |
| | 5 | 56.5–75.4 (66.2) TL | May 2015 | |
| Total | 2030 | | | |

FL fork length, *TL* total length

Microsatellite data analysis

Microsatellite data were initially examined using Micro-Checker (Van Oosterhout et al. 2004) for the presence of null alleles, scoring errors, and large allele drop-out. Exact tests in GENEPOP (version 4.2) (Raymond and Rousset 1995; Rousset 2007) were used to test the genotypes at each locus and in each collection for their conformity to Hardy Weinberg equilibrium (HWE). Linkage disequilibrium (LD) was tested for all pairs of loci in each population using contingency tables in GENEPOP. All tests of HWE and LD used default Markov chain parameters in GENEPOP. Significance levels for HWE and LD tests were adjusted using sequential Bonferroni correction (Rice 1989). Microsatellite allelic diversity at all loci and in all collections was quantified in GenAEx (Peakall and Smouse 2006, 2012), FSTAT version 2.9.3 (Goudet 2001), and HP Rare 1.0 (Kalinowski 2005); measures presented (Supplementary Table 1) include mean number of alleles, effective number of alleles, allelic richness, expected heterozygosity, and observed heterozygosity.

Contemporary effective population size and effective number of breeders in their parental generation were estimated for population-specific cohorts of juveniles and adults using the bias-corrected version of the linkage disequilibrium (LDN_e) methods of Waples and Do (2008) implemented in NeEstimator v2 (Do et al. 2014). The LDN_e method has been shown empirically to outperform other approaches in accurately estimating N_e (Gilbert and Whitlock 2015; Wang et al. 2016). Low frequency alleles were screened out with a P crit. of 0.02 (Waples and Do 2008). For each population except that in the Connecticut River, two or more years of collections were pooled to calculate estimates of N_e .

Calculation of N_e max

Because only juvenile specimens were available from rivers in the South Atlantic DPS (except the Edisto River), we were interested in empirically determining how many years of juvenile cohort collections were needed to accurately portray their effective population sizes. This would guide future work with newly discovered Atlantic sturgeon populations from which only juvenile collections were available and other species in which only cohorts of young life-stages are available for analysis. We first identified those populations where tissue samples had been previously collected from juveniles in each of at least 3 years (usually consecutive). These populations included the Altamaha (5 years, $n = 37\text{--}64/\text{year}$, mean = 49), Savannah (3 years, $n = 50\text{--}61/\text{year}$, mean = 54), Ogeechee (4 years; $n = 15\text{--}67/\text{year}$, mean = 44) and Hudson (4 years; $n = 30\text{--}46/\text{year}$, mean 36). After estimating the annual N_b for the initial cohort on each river system, we sequentially combined individual

cohorts and then recalculated their N_e . We then constructed a simple plot of cumulative N_e , for each year, by combining the samples in each successive year. The resulting plots were then used to identify the N_e Max for each population based on the equation of the parabolic function depicted in each of the plots.

Estimating historical N_e and gene flow

To compare current N_e estimates with long-term (historical) N_e , we used a Bayesian framework implemented in the program MIGRATE-n version 3.6.11 (Beerli and Felsenstein 2001; Beerli 2006). MIGRATE-n uses coalescent modeling to jointly estimate long-term effective population size ($\theta = 4Ne\mu$) and gene flow ($M = m/\mu$) over approximately $4Ne$ generations. For these analyses, we used 13 populations, excluding the Connecticut as this population is believed to have been founded in modern times. All samples and loci were included in the analysis, which used a Bayesian analysis strategy (details below) and a microsatellite (Brownian motion) model of evolution. First, we compared three migration models in MIGRATE-N using the strategy outlined in Beerli and Palczewski (2010): (1) full migration model (migration estimated for all possible binary combinations among 13 populations); (2) DPS model (migration estimated between populations within each DPS) (between populations within each DPS; populations grouped into the 5 DPS and the 2 individual populations in Canada); (3) stepping-stone migration (migration between adjacent populations).

In all models, asymmetric and bidirectional migration was allowed. We determined the best-fitting migration model via log marginal likelihood using Bezier scores from MIGRATE-N runs with four heated chains in a Bayesian framework (Beerli and Palczewski 2010). Two shorter initial MIGRATE runs were performed to determine whether parameter space was being captured by the MCMC (four runs sampling 100,000 generations). We then performed a final run including three replicate chains of 10,000,000 steps (burn-in of 1,000,000 steps) for 50,000 recorded steps. A static heating scheme was implemented with the following four chain temperatures: 1.00, 1.50, 3.00, 1×10^7 . We used uniform prior distributions (min, max, delta): $\Theta = (0.001, 100, 10)$; and $M (0, 1000, 10)$. We calculated the effective number of migrants (N_m) as $(\Theta \times M/4)$ where M is the mutation-scaled immigration rate (Beerli and Palczewski 2010). To convert θ to N_e estimates, we used a mutation rate (μ) of 4.15×10^{-4} (CI 1.45×10^{-3} to 4.15×10^{-4}) mutations per locus per generation based on a recent genealogy-based study of microsatellite mutation rate in Atlantic sturgeon (Panagiotopoulou et al. 2017). We incorporated uncertainty in these estimates by creating a script in R (version 3.5.1) (R Core Team 2018) that performed bootstrap resampling 100,000 times from the published 95% confidence intervals

of μ given above and the 95% highest posterior density (HPD) intervals of Θ produced by Migrate-n for each population.

Results

Contemporary and historical N_e estimates

Estimates of contemporary N_e ranged from a low of 1 for the St. Marys population to a high of 156 for the Hudson River population (Table 2). Three of the five DPS had only a single population represented within it: the N_e for the Kennebec River population (the only one from the Gulf of Maine DPS) was 67; the N_e for the James River (the only one from the Chesapeake DPS) was 32; and the N_e for Albemarle Sound (lone representative of the Carolina DPS) was 19. The mean N_e for the Connecticut, Hudson, and Delaware Rivers of the New York Bight DPS was 66; the mean N_e for the Edisto, Savannah, Ogeechee, Altamaha, Satilla, and St. Marys Rivers of the Southeast DPS was 63. Furthermore, the mean N_e for the two rivers in Canada, the St. Lawrence and the Saint John, was 67. The mean contemporary N_e for all 14 populations was 58.4.

The long-term migration model that was best supported in Migrate-n was the stepping stone model, with a model likelihood > 84.9%, with the second-ranked model being the

DPS model. Mean estimates of historical N_e ranged from a low of 468 for the St Marys River population to a high of 927 for the Kennebec River population (the Connecticut River was excluded as it is believed to be recently recolonized) (Table 2). Estimates of historical N_e were higher than contemporary N_e for all populations. The percentage of contemporary to historical N_e estimates ranged from less than 1% for the St. Mary’s population to 21.5% for the Altamaha population (Table 2). The mean percentage of contemporary to historical N_e across all populations was 9.2% (with Connecticut River population excluded).

Plots of cumulative N_e from juveniles for each of the four populations yielded N_e Max values near or higher than traditional N_e estimates, varying from a low of 32.2 for the Ogeechee River (vs. 26) to 116.3 for the Savannah River (vs. 123) to 145.9 for the Altamaha River (vs. 149), with a large difference for the Hudson (294.6 vs. 156) (Fig. 2). In all of the southern populations, N_e Max was obtained at 3–4 years of collections, while in the Hudson, N_e Max was still increasing after the 4th consecutive collection.

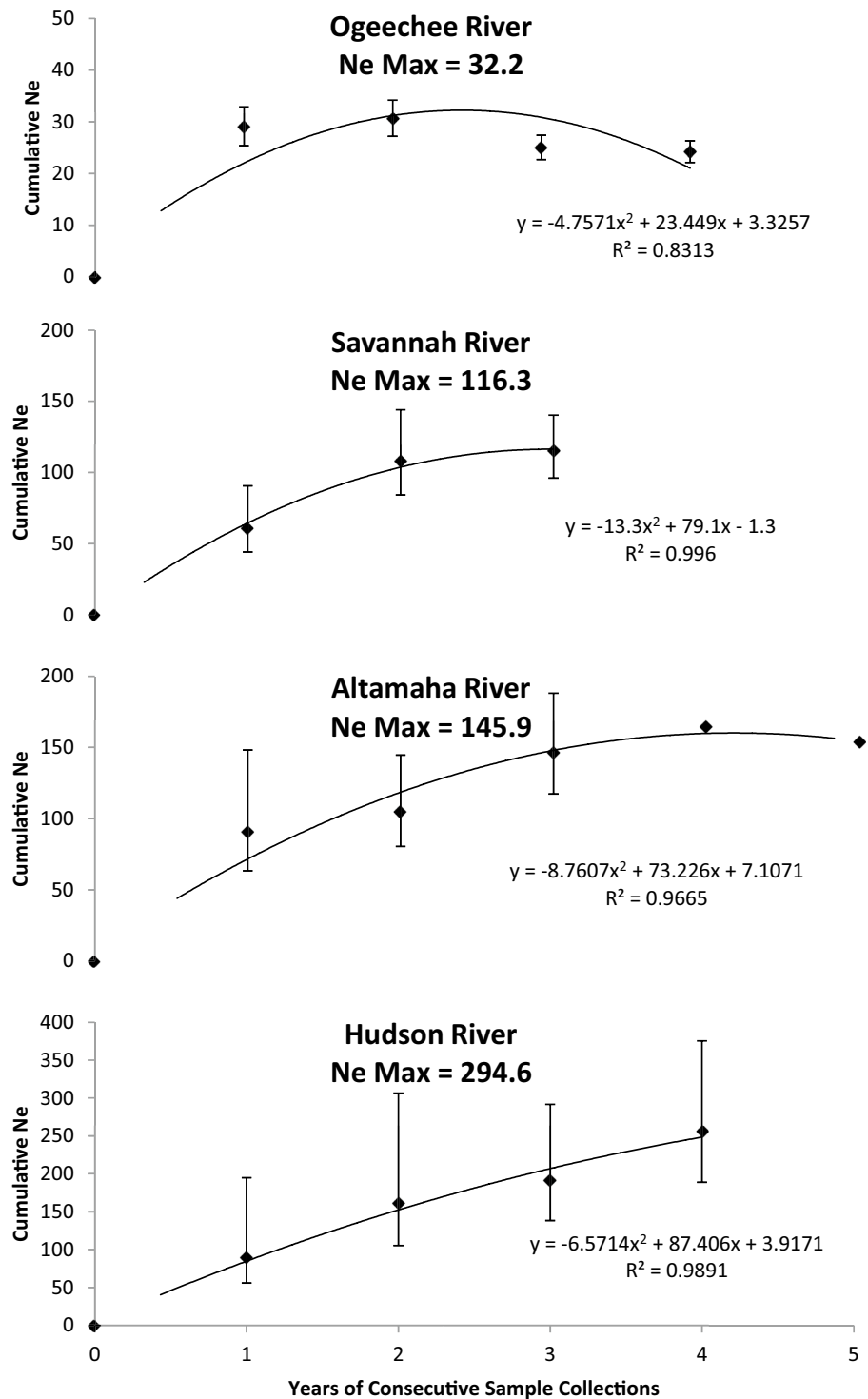
Estimates of the long-term effective number of migrants per generation (4Nem) varied across population pairs, but were generally high, with the exception of low historic gene flow between the St. Lawrence and the Saint John and from the Ogeechee to the Altamaha (Table 3). The highest values were from Hudson to the Kennebec (61.7) and the Savannah to the Ogeechee (60.7).

Table 2 Estimated contemporary and historical N_e for Atlantic sturgeon populations by river

| River | DPS | Sample size | Estimated contemporary N_e | Estimated contemporary N_e 95% CI | Estimated historical N_e | Estimated historical N_e 95% CI | % Contemporary N_e of historical N_e |
|--------------|-----|-------------|------------------------------|-------------------------------------|----------------------------|-----------------------------------|--|
| St. Lawrence | CMU | 90 | 35 | 27.9–43.8 | 630 | 55–732 | 5.5% |
| Saint John | CMU | 227 | 88 | 75.5–104.2 | 539 | 49–716 | 16.3% |
| Kennebec | GOM | 62 | 67 | 52.0–89.1 | 927 | 104–970 | 7.2% |
| Connecticut | NYB | 47 | 2 | 2.0–2.7 | ND | ND | ND |
| Hudson | NYB | 459 | 156 | 138.3–176.1 | 723 | 62–818 | 21.5% |
| Delaware | NYB | 108 | 40 | 34.7–46.2 | 509 | 47–665 | 7.8% |
| James | CB | 116 | 32 | 28.8–35.5 | 708 | 60–801 | 4.5% |
| Albemarle | CAR | 88 | 19 | 16.5–20.6 | 546 | 51–716 | 3.4% |
| Edisto | SA | 145 | 60 | 51.9–69.0 | 635 | 54–767 | 9.4% |
| Savannah | SA | 161 | 123 | 103.1–149.4 | 655 | 59–784 | 18.7% |
| Ogeechee | SA | 200 | 26 | 23.9–28.2 | 792 | 67–868 | 3.2% |
| Altamaha | SA | 245 | 149 | 128.7–174.3 | 764 | 62–834 | 19.4% |
| Satilla | SA | 68 | 21 | 18.7–23.2 | 852 | 90–919 | 2.4% |
| St. Marys | SA | 14 | 1 | 1.3–2.0 | 468 | 45–682 | <1.0% |

Connecticut River excluded from historical analysis because of recency of establishment of current population. DPS designations are CMU (Canadian Management Unit), GOM (Gulf of Maine), NYB (New York Bight), CB (Chesapeake Bay), CAR (Carolina), SA (South Atlantic). ND (No data)

Fig. 2 Cumulative effective population sizes (N_e) of Atlantic sturgeon in the Ogeechee, Savannah, Altamaha, and Hudson rivers. Juvenile cohorts sampled from each river include Hudson (2013, 2014, 2015, 2016), Savannah (2013, 2014, 2017), Ogeechee (2014, 2015, 2016, 2017), and Altamaha (2005, 2011, 2014, 2015, 2016). Maximum N_e was calculated using the equation of the line depicting cumulative N_e



Discussion

Implications for conservation genetics

As N_e decreases, genetic drift erodes genetic variation, elevates the probability of fixation of deleterious alleles, and reduces the effectiveness of selection, all of which reduce

overall population fitness and limit adaptive responses. These genetic changes can directly or indirectly drive a threatened population closer to extirpation through interactions with population dynamics that create an extinction vortex (Hare et al. 2011). Estimated contemporary N_e values for individual Atlantic sturgeon populations examined in this study fell both within and below the suggested safety

Table 3 Historical migration estimates of Atlantic sturgeon between geographically adjacent spawning populations (Connecticut River is excluded)

| To | From | Effective migrants per generation | Upper 95% CI | Lower 95% CI |
|--------------|--------------|-----------------------------------|--------------|--------------|
| St. Lawrence | Saint John | 1.1 | 1.8 | 0.0 |
| Saint John | St. Lawrence | 2.6 | 3.5 | 1.6 |
| Kennebec | Saint John | 50.5 | 53.5 | 41.5 |
| Saint John | Kennebec | 34.0 | 39.6 | 29.3 |
| Hudson | Kennebec | 52.4 | 55.7 | 48.6 |
| Kennebec | Hudson | 61.7 | 66.0 | 57.7 |
| Delaware | Hudson | 38.9 | 40.0 | 37.0 |
| Hudson | Delaware | 51.8 | 59.2 | 48.2 |
| James | Delaware | 26.6 | 31.5 | 22.0 |
| Delaware | James | 16.2 | 17.2 | 15.2 |
| Albemarle | James | 11.0 | 11.4 | 5.8 |
| James | Albemarle | 29.0 | 42.3 | 28.1 |
| Edisto | Albemarle | 38.3 | 39.5 | 37.0 |
| Albemarle | Edisto | 18.6 | 21.6 | 15.3 |
| Savannah | Edisto | 48.3 | 49.5 | 47.0 |
| Edisto | Savannah | 45.6 | 47.3 | 42.3 |
| Ogeechee | Savannah | 60.7 | 62.8 | 59.9 |
| Savannah | Ogeechee | 52.4 | 53.4 | 51.3 |
| Altamaha | Ogeechee | 2.3 | 3.7 | 0.8 |
| Ogeechee | Altamaha | 23.9 | 24.2 | 16.3 |
| Satilla | Altamaha | 42.5 | 54.5 | 40.8 |
| Altamaha | Satilla | 53.6 | 55.4 | 50.1 |
| St. Marys | Satilla | 15.7 | 17.3 | 14.6 |
| Satilla | St. Marys | 45.3 | 49.0 | 43.3 |

Units are effective number of migrants per generation

zone of 50–500 (Frankham et al. 2014). Even N_e values for populations within this range, nonetheless, were on its lower end, with the highest estimate at 156 for the Hudson River population. N_e values also were somewhat higher at both ends of the distribution of the Atlantic sturgeon, i.e., Canada and the South Atlantic DPS. In fact, the highest regional mean N_e value, for the South Atlantic DPS (63), was about double that of the lowest, the single-river Chesapeake Bay DPS (32).

Following the criteria of Frankham et al. (2014), our results suggest that the 8 of 14 Atlantic sturgeon populations with N_e estimates of 50 or less are in danger of inbreeding and genetic drift. However, concern for these should be tempered by the varied history and status of these populations. For example, the extremely low N_e for the Connecticut River population appears to be the result of a recent recolonization by a small number of founders and, as such, would be expected to have a low N_e (Savoy et al. 2017). In contrast, the James River population, with a N_e of 32, now shows evidence of ongoing recruitment failure, perhaps due to predation from blue catfish *Ictalurus furcatus*, thermal pollution at major nursery areas, or power plant impingement (Pipkin 2017).

Contemporary effective population size versus population status and trends

Differences among populations in our contemporary N_e estimates were largely in keeping with surveys and anecdotal observations of population status. The St. Lawrence River population, at $N_e = 35$, has supported commercial fishing for Atlantic sturgeon for centuries. Since 2000, size regulations and an annual quota of 60 metric tons of subadults only have resulted in a stable population roughly estimated by Dadswell (2006) as 500+ spawning adults.

The other Canadian river included in our study, the Saint John ($N_e = 88$), has also supported a long-term commercial fishery, but with limited participation in recent years and an annual quota imposed since 2009 of 350 individuals or 125 females, whichever comes first. Dadswell (2006) estimated that approximately 200 to 300 adults were captured each year in the fishery (though it is possible that other populations may have contributed very low numbers of individuals) (e.g., 3% of adults; Savoy et al. 2017). Recent analysis of contemporary and historical fishery data by Dadswell et al. (2017) estimated the virgin population in 1880, prior to prosecution of commercial fisheries at 14,200–23,700

individuals. Bradford et al. (2016), using mark-recapture techniques concluded the Saint John River population currently includes 1000 to 3050 spawners, whereas Dadswell et al. (2017) estimated the mean annual population abundance between 2011 and 2016 as 18,000–20,800 adults. Our estimate of $N_e = 88.4$ for the Saint John River population is lower than that of Bradford et al. (2016) who reported an average N_e of 110 using the linkage disequilibrium method as we did, but with an expanded set of microsatellite loci that were analyzed in 232 adult specimens collected over multiple years. They combined their $N_e = 110$ with their empirically determined N_c values of 3050 adults in 2009 and 950 in 2012 to obtain N_e/N_c ratios of 0.04 and 0.12, respectively, for the Saint John population.

Atlantic sturgeon were historically abundant in the Kennebec River and its tributaries, including the Androscoggin and Sheepscot rivers. Sporadic captures since the 1990s suggest a spawning population persists in the watershed (ASSRT 2007), which was validated by the fisheries-independent collection of 32 adults in June of 2010 and 2011 and August of 2011 from the Kennebec River and 8 adults in June 2011 from the Androscoggin. Spawning was confirmed in the Kennebec by the collection in July 2011 of two 15-cm young-of-the-year. Our N_e estimate for the Kennebec population ($N_e = 67$) was near the middle of the overall range found for the 14 populations.

The second lowest value obtained, for the Connecticut River ($N_e = 2$), reflects what appears to be a recent recolonization but presently low abundance (Savoy et al. 2017). Atlantic sturgeon were speared in the river in Massachusetts in the 1700s (Judd 1905) and a limited commercial fishery for adults centered at Cromwell, CT, was reported (Galligan 1960), but access to waters beyond northern Connecticut was cut off by construction of the Enfield Dam in 1827. Substantial numbers of subadult Atlantic sturgeon were surveyed in the lower Connecticut River from 1988 to 2014 (Savoy et al. 2017); however, genetic analysis indicated they were primarily of Hudson River origin (Waldman et al. 2013). There were other occasional catches and sightings in the river but no evidence of reproduction reported by ASSRT (2007) and its authors believed them to be extirpated. However, recent net surveys and genetic analysis indicate that the Connecticut River was recolonized via spawning in 2013 by individuals chiefly from the Chesapeake Bay and the South Atlantic DPS (Savoy et al. 2017). It remains to be determined if successful reproduction occurred in subsequent years.

The Hudson River population showed the highest contemporary N_e , at 156. Stock composition analysis of Atlantic sturgeon in the New York Bight in 1993 and 1994 (Waldman et al. 1996), off the Delaware coast during the early spring migratory run (Wirgin et al. 2015a), and of coastal bycatch from the Gulf of Maine to North Carolina obtained

in NOAA's Observer program (Wirgin et al. 2015b) indicated that the Hudson River population was the overwhelming contributor (97.2%, 44% and 46%, respectively), suggesting a relatively robust abundance for that population. However, Kahnle et al. (2007) believed there was substantial overfishing before and during the burgeoning caviar fishery in the 1990s which contributed for a low mean annual spawning stock size between 1986 and 1995 of 863 (596 males and 267 females). Tighter harvest regulations in New York followed by the species-wide closure in 1998 may have stemmed further population decline as indicated by increasing numbers of juveniles collected in recent fishery independent surveys (ASMFC 2017).

Hatchery augmentation is another theoretical contributor to low N_e . The only population among those we sampled that had been stocked was the Hudson River, which received 4929 young-of-the-year in 1994 (Waldman and Wirgin 1998). Sampling in the Hudson River from 1995 to 1997 showed that those hatchery-produced individuals comprised 35–53% of the total juvenile catch (Peterson et al. 2000). Despite this, the Hudson population provided the highest contemporary N_e estimate.

The Delaware River may have hosted the largest Atlantic sturgeon population on the Atlantic Coast before it was overfished in the late 1800's (Secor and Waldman 1999). Following this decline, there was uncertainty as to whether a relict Delaware population persisted, due to the almost complete absence of adult or juvenile specimens over many decades of sampling in the river. Genetic analysis of subadults collected between 1991 and 2004 suggested the presence of a relict stock (Wirgin et al. 2007) and successful reproduction there was confirmed beginning in 2009 (and continuing in 2011 and 2014) with the collection of modest numbers of pre-migratory juveniles at, or near, the presumed nursery grounds. A subsequent mark-recapture estimate of age-0 and age-1 juveniles made in 2014 (Hale et al. 2016) indicated a population size of 3656 (95% CI 1935–33041). The moderate N_e estimated for the current Delaware population, 40, may reflect a balance between the pervasive genetic signal from an extremely large historical abundance and a contemporary relict population that experienced a severe bottleneck.

Our N_e estimate of 32 for Atlantic sturgeon from the James River is in the lower range among the populations we examined. However, until recently there was uncertainty as to whether its population remained extant. Grogan and Boreman (1998) used a time series of incidental capture records during annual trawl surveys in the James conducted between 1964 and 1994 to yield probability estimates that the species was extirpated of 0.856 and 0.995%. Nonetheless, a subsequent reward program for commercial fishers demonstrated population persistence, with genetic analysis indicating the presence of a relict stock (Wirgin et al. 2007), and young sturgeon captured in the James in 1996 and 1997 showed

that reproduction was occurring there. Additionally, between 2007 and 2011, Balazik et al. (2012) captured nearly 150 spawning adults in the tidal-freshwater portion of the James River during spawning runs. Balazik and Musick (2015) estimated a N_c for spawning males in the James of 3399 (± 575). Recently, however, the stock appears to be declining (Blankenship 2016).

Albemarle Sound and the Roanoke River have long supported a small commercial fishery for Atlantic sturgeon. Its N_e estimate of 19 is consistent with a relatively small census size. Observations of young individuals indicate that spawning still occurs there, but catch records suggest declining recruitment after year 2000 (ASSRT 2007). In 2010, N-mixture and distance models with data acquired from side-scan sonar surveys were used to quantify abundance of sturgeon in 5 rivers in North Carolina and South Carolina. These results were then used to estimate abundances of sturgeon > 1 m TL in the Carolina DPS as 2031 using a count model and 1912 via a distance model (Flowers and Hightower 2015).

The Edisto River appears to support a relatively robust Atlantic sturgeon population, reflected in its N_e estimate of 60 and also that surveys reveal both young and mature individuals (ASSRT 2007). However, the Edisto enters the ACE Basin, which also includes the Ashepoo and Combahee Rivers, and it may be that individuals captured in the Edisto are part of a single population that spawns in 2 or all 3 of the ACE Basin rivers (Grunwald et al. 2008). In fact, comparisons of mtDNA haplotype and microsatellite allelic frequencies in adults from the Edisto and Combahee did not show significant genetic differentiation between these populations (Grunwald et al. 2008; Wirgin unpublished data).

The Savannah River supports a reproducing Atlantic sturgeon population, with a relatively high N_e value of 123. Mark-recapture analysis by Bahr and Peterson (2016) indicated age-1 cohort sizes of between 528 and 597 individuals from 2013 to 2015. The authors concluded that the Savannah population of Atlantic sturgeon is the second largest within the South Atlantic DPS, a relative estimate that is consistent with our derived N_e value.

We found a relatively low N_e of 26 for the Ogeechee River population. Its only recent census estimate was 450 (CI 203–1125) juveniles (defined as age-1 and age-2 combined) in 2007 (Farrar et al. 2009). The N_e estimate is consistent with the characterization of this population by ASSRT (2007) as having abundant juveniles only rarely, with high interannual variability.

In contrast, Atlantic sturgeon is abundant in the Altamaha River, reflected in its N_e estimate of 149, the second highest for all populations characterized. During the summers of 2004–2007, Schueller and Peterson (2010) performed mark-recapture of age-1 juveniles in the Altamaha and derived annual abundance estimates that ranged from 1072

to 2033 individuals. The authors reported that age-1 and age-2 individuals comprised greater than 87% of the total juvenile population in each year of their study.

A low N_e value of 21 was obtained for the Satilla River population. Only 4 spawning adults and young-of-the-year, all used for genetic analysis (Ong et al. 1996), were collected from this river between 1995 and publication of ASSRT (2007). However, 61 ages-0 to -1 juveniles were collected in the Satilla in summer of 2010. Fritts et al. (2016) speculated that these juvenile specimens were the offspring of a small contingent of “cryptic” subadults that remained in coastal waters since enactment of the 1998 harvest moratorium and only re-entered the Satilla to initially spawn in 2009.

ASSRT (2007) stated that the lack of Atlantic sturgeon captures in either scientific sampling or as bycatch in other fisheries in the St. Mary’s River indicates that the river neither supports a spawning subpopulation nor serves as a nursery ground for Atlantic sturgeon, though no directed sampling surveys had been conducted in years immediately prior. However, genetic samples were collected from 9 pre-migratory juveniles in 2014 (mean TL = 36.0 cm) and tissues were taken in 2015 from 5 pre-migratory juveniles spawned in 2014 (mean TL = 66.2 cm). Collection of juveniles over 2 years from a single cohort confirmed the presence of contemporary spawning in the St. Marys River (Fox et al. In Press). The St. Mary’s collection yielded a N_e estimate of 1, the lowest for all populations characterized, a value likely reduced by its derivation from only 1 year class.

Contemporary versus historical effective population sizes

There were two main findings in the comparison of the contemporary and historical effective population sizes obtained. First, contemporary values for N_e across all 14 populations (range 1–156; $\bar{x} = 58.5$) were very low by conservation biology criteria, and well below the N_e rule of 500 recommended to retain long-term genetic viability of populations. Even when both the Connecticut and St. Marys populations are excluded the mean N_e is only 68.0. Secondly, historical analysis suggests N_e levels were higher in the past (mean across all populations, excluding Connecticut River = 672.9) or about $11.5 \times$ contemporary estimates (also excluding Connecticut River). Thus, contemporary N_e estimates are on average considerably lower and historical N_e estimates somewhat higher than the N_e rule of 500 recommended for retaining long-term genetic viability of populations.

Reduced contemporary N_e values may most readily be explained by more than a century of overfishing across almost all populations as well as other stressors that led to a 40-year moratorium on their harvest and then to listing of Atlantic sturgeon under the ESA. Thus, it is not surprising that contemporary N_e estimates are lower than their

associated historical N_e estimates. These stressors, while impacting all populations, may have been particularly intense on some populations such as that in the Delaware, which went from what was likely the largest to one of the smallest due to rampant historic overharvest and more recently, low dissolved oxygen concentrations in nursery areas (Kahn and Fisher 2012), reduced suitable freshwater spawning and nursery habitats (Moberg and DeLucia 2016) because of dredging, and a relatively large numbers of vessel strikes (Brown and Murphy 2010).

Moyer et al. (2012) obtained a N_e value of 125 for Atlantic sturgeon of the Altamaha River, which is similar to our estimate of 149, the second highest for all populations. However, the historical estimate of N_e by Moyer et al. was an order of magnitude more (1100–5500) than their contemporary N_e estimate, whereas our historical N_e estimate ($N_e = 764$) was only $5.1 \times$ that of our contemporary estimate. Why did Moyer et al. (2012) estimate a higher historical N_e for the Altamaha River population compared with our results? A likely possibility is the mutation rate applied for their historical analyses. We used a recently determined, empirically-derived, species-specific microsatellite mutation rate for Atlantic sturgeon (Panagiotopoulou et al. 2017) based on analysis of mutations between parents and their offspring of Atlantic sturgeon, whereas Moyer et al. (2012) used a rate $4.15 \times$ higher (Jarne and Lagoda 1996), which would help account for their higher historical N_e estimate.

Furthermore, the method employed here to estimate historical N_e (Migrate-n), assumes migration-drift equilibrium; violations of this assumption from processes above can result in underestimated N_e values (Beerli 2009). While Migrate-n and other coalescent methods have been applied to many species with overlapping generations (e.g., Shrimpton and Heath 2003; Hughes et al. 2012; Moore et al. 2013; Bracken et al. 2015), it is important to recognize that the effect of high variance in reproductive success, e.g., of a small number of individuals having many more offspring than others can result in a smaller effective population size (Eldon and Wakeley 2006) and a non-linear relationship between genetic diversity and population size (Wakely and Sargsyan 2009). Additional simulation studies, while outside the scope of the present work, are needed to determine the behavior of coalescent-based methods such as Migrate-n using realistic life history parameters. Moreover, these estimates of historical N_e will be reduced if populations experienced dramatic demographic events such as prolonged bottlenecks, near-extirpations, or extirpation-recolonization events, either due to recent overharvest or earlier climatic events such as glaciations. Geological history indicates that all Atlantic sturgeon populations from the Hudson River northward were derived following deglaciation, i.e., within $\sim 15,000$ years; this hypothesis is corroborated by mtDNA analysis

(Waldman et al. 2002) that shows a pattern of sequential decreases in haplotype diversity in populations from the Hudson to the St. Lawrence.

The low contemporary N_e estimates across populations (and relative to large historical catches in rivers such as the Delaware, obtained from known large populations), may reflect several factors known to reduce N_e . First, the particular life history demographics of Atlantic sturgeon likely serve to reduce N_e far below census sizes, perhaps more so than for most other species. These include uneven sex ratios among breeders, overlapping generations, fluctuating population sizes, variation among individuals in mating success, migration among spawning populations, and several factors which severely limit the number of actual breeders at any given spawning cycle from the overall potential pool. Among these are non-annual spawning of sexes, discrete spring and fall spawning in some rivers in the middle and perhaps southern portion of their range with consequent subdivision of river populations, and the late age of initial spawning, particularly for northern populations.

It has been shown that unequal sex ratios reduce N_e by an average of 36% (Frankham 1995). Sex ratios have not been measured in all populations of Atlantic sturgeon but do exist for a small subset that hosted fisheries. These studies have demonstrated that sex ratios vary considerably among populations with males tending to outnumber females, sometimes by considerable margins. For example, male:female sex ratios ranged from 1.2:1.0 in the Saint John River (Dadswell et al. 2017), 3.0:1.0 in the Edisto and Combahee rivers (Collins et al. 2000), 4.0:1.0 in the Hudson River (Dadswell and Nack 2012), 4.9:1.0 in the St. Lawrence River (Caron et al. 2002), and 60:1 in the James River (Balazik et al. 2012). However, it is possible that these sex ratios are skewed by differential catchability of the sexes based on the gear type employed in these fisheries or research efforts (Hilton et al. 2016). This is particularly true for estimates based on fishery-dependent data as reported for the Saint John, St. Lawrence and Hudson Rivers. Additionally, males may spend more time on the spawning grounds than females, thereby biasing sex ratios (Bain 1997; Whippelhauser et al. 2017).

Given the longevity of Atlantic sturgeon, particularly of northern populations, it is conceivable that individuals spawned across several decades may reproduce in any given year, a factor which lessens estimates of N_e (Felsenstein 1971). Moreover, most N_e estimation methods assume discrete generations and produce a per-generation estimate; however, in species with overlapping generations, it is difficult to define (and challenging to collect) a random sample from an entire generation (Hare et al. 2011). Generally, mixed-age adult samples such as those collected from northern populations in our study (St. Lawrence, Saint John, Kennebec, Hudson, and James Rivers) produce downwardly biased estimates of N_e , which can be attributed to a

two-locus Wahlund effect (mixture LD) caused by combining parents from different cohorts in a single sample (Waples et al. 2014).

Variation in mating success among spawners and subsequent variation in family size is known to greatly decrease N_e , but to our knowledge, there are no empirical studies that have addressed this phenomenon in sturgeon populations. However, it is likely that this occurs, particularly because of the differential age at first spawning for the two sexes. Hauser and Carvalho (2008) believed this to be the most important factor in reducing N_e among marine fishes. With modern bioinformatic approaches to analyze molecular data sets such as ours, estimation of variation in spawning success and family size should now be addressed.

Intermittent spawning is another factor likely decreasing N_e relative to N_c in Atlantic sturgeon populations. This behavior severely reduces the number of mature adults engaging in breeding in any given year. Intermittent spawning likely occurs in all populations, but its frequency varies between genders and among populations. For example, the spawning interval in females was reported at 2–5 years in South Carolina rivers (Smith 1985) and 3–5 years in the Hudson River (Bain 1997). Intervals between spawnings in males is reported to be shorter, occurring at 1–5 years (Smith 1985) or maybe every year in some southern populations (Hilton et al. 2016).

Spawning in both the spring and fall, recently suggested for some populations of Atlantic sturgeon, is another phenomenon that may serve to reduce N_e relative to N_c . Rivers where dual spawning has been reported include the James (Balazik et al. 2012) where significant genetic differentiation at microsatellite loci was reported between two spawning cohorts of adult males collected in the spring and fall (Balazik et al. 2017). We anticipate that the potential dual spawning in this and perhaps other populations serve to reduce their N_e to N_c ratios by limiting the opportunities for mating among complete adult gene pools within the populations. The decreased N_e in these populations should be reflected when calculating N_e from their juvenile aggregations, which will be comprised of offspring from both spawning cycles.

Variable migration rates among some sturgeon populations is another factor that may significantly impact estimates of N_e . Waples and England (2011) showed that pulse migration of genetically divergent individuals can decrease N_e in a local population. Conversely, low rates of migration between populations differentiated by low F_{st} values serve to increase estimates of N_e . Historical rates of migration differ among our 14 populations of Atlantic sturgeon, from very low between the Canadian populations to high in the South Atlantic DPS, and between the Gulf of Maine and NY Bight DPS. Two of the populations with the highest migration rates leading to them lay near the middle of their zoogeographic provinces, the Kennebec in the Acadian, and

the Ogeechee in the Carolinian. We speculate that such sitings may make these rivers a crossroads for migrating sturgeon, some of which may stray reproductively. Similarly, mean F_{st} among populations within the South Atlantic DPS ($F_{st}=0.049$) is lower than among more northern populations, suggesting greater contemporary migration among these rivers. That may be a function of the greater proximity of contemporarily active spawning rivers in the South Atlantic DPS through the intracoastal waterway. Thus, estimates of N_e among southern populations may be deflated by the extensive migration among some populations. While these estimates cannot capture the complex and variable history of source-sink dynamics and pulse migrations in the past, they may provide a useful perspective on relative migration rates across populations.

Year class-specific contemporary N_e analyses

Although derivations of N_e Max may not be necessary or desirable for most other fishes, our calculations suggest that N_e Max may provide a more robust measure of effective size for some Atlantic sturgeon populations than traditional methods of calculating contemporary N_e . For many populations in the Carolina and South Atlantic DPS, only juveniles are available for genetic analysis. Because of its intermittent spawning, collections of single year classes of Atlantic sturgeon juveniles may only harbor a small fraction of the total gene pool in any given population; therefore, N_e Max may provide a more comprehensive view of their actual N_e . In our study, final N_e Max values were not far from the contemporary N_e values calculated across year classes in 3 of 4 populations (Fig. 2). However, in 2 of these (Savannah and Altamaha), a N_e estimate based on a single year class would have yielded substantially lower values (Fig. 2). Moreover, there was a large difference between N_e Max and N_e for the Hudson (294.9 vs. 156), with the cumulative N_e Max still ascending at the fourth consecutive cohort. The number of years required to reach N_e Max, likely reflects the “average” spawning interval for both sexes in each population. Hence, the reason that the Hudson curve is still ascending may be because in northern climates, the spawning interval is longer for both sexes compared to southern populations. This is potentially important because it provides an important indicator of how many years of sampling juveniles is required to reach a good estimate of N_e Max.

The N_e calculation should, intuitively “peak” at N_e Max, at which point juvenile cohorts in the population have been fully represented. The decline in N_e after N_e Max, occurs because additional sample years begin to increase the number of juveniles within the total sample that were produced from repeat spawners. Essentially, these juveniles (from repeat spawners) effectively add partial siblings to the total cumulative juvenile sample population. This addition of

partial siblings causes the resulting N_e estimate to decline after N_e Max. Hence the parabolic function was not only the best fitting function we observed, but it best represents the reproductive cycle of Atlantic sturgeon with respect to how each result cohort is produced and how the genetic diversity of the adult population is propagated throughout that reproductive cycle.

Additionally, the use of river-resident juveniles for calculation of N_e Max allows researchers to include small populations in these comparisons, populations where spawning adults are rare or not easily sampled. Inclusion of small populations in genetic analyses of N_e is especially important within the context of species recovery because N_e is of particular concern for smaller populations. Unfortunately, no standardized sampling approach has yet been established for assessment of N_e among Atlantic sturgeon populations; N_e has been calculated from spawning adults in some rivers while river-resident juveniles or combinations of adults and juveniles have been used in one other, the Hudson River. Given the protracted and variable spawning period that has been well documented for Atlantic sturgeon, the calculation of N_e Max provides a less variable estimate of N_e , one that is standardized among populations and hence, may provide a more accurate comparison of the genetic composition of different populations throughout the range. Future studies are needed to examine the differences in N_e calculated from single and multiple years of adult and river-resident juvenile collections to identify the best sampling method for monitoring N_e as one important measure of species recovery.

Does polyploidy play a protective role in preventing inbreeding effects at low effective population sizes?

A possible, as yet unexplored, but potentially important question for Acipenseriformes, including Atlantic sturgeon, is whether their polyploidy exerts an ameliorating effect on what may appear to be low N_e levels for some populations. Sturgeon species are allopolyploid and their chromosome numbers range from around 120 (tetraploid) in multiple species, including Atlantic sturgeon (Hilton et al. 2016), to 372 (dodecaploid) in shortnose sturgeon (*Acipenser brevirostrum*) (Vasil'ev 2009).

One benefit of allopolyploidy involves the fixing of divergent parental genomes. Whereas heterozygosity and heterosis decay in the progeny of a diploid F_1 hybrid (at each generation half the heterozygous loci become homozygous), the enforced pairing of homologous chromosomes in allopolyploids prevents intergenomic recombination, effectively maintaining the same level of heterozygosity through the generations (Comai 2005). Another advantage of polyploidy is gene redundancy. Gene redundancy can mask recessive alleles by dominant wild-type alleles (Comai 2005). This effect can act at two life stages, one of which is the haploid

stage. Although this form of the organism has reduced complexity, its function requires the activity of many genes. This exposes the egg to the action of lethal and deleterious loss-of-function mutations. In the second, 2N phase, polyploidy can reduce the incidence of homozygous recessives.

Comai (2005) speculated that the protective effect of polyploidy against deleterious recessive mutations might be important when isolated and severely bottlenecked populations are forced to inbreed, at a time when the purging of deleterious alleles is made difficult by the reduced number of breeding individuals. Such a protective response would have value for organisms such as sturgeons, which because of the large sizes of some species, would not likely maintain highly abundant populations, particularly for potentially more food limited landlocked forms and, thus, would be subject to inbreeding risks. Furthermore, Yi and Strelman (2005) concluded that genome size in ray-finned fish is negatively correlated with N_e and that reduced N_e underlies the evolution of larger and more complex genomes. If polyploidy is an ancestral trait in sturgeons, it would be expected to appear in all species, as in fact, it does. Additional research is needed as to whether any dangers from the low N_e seen in Atlantic sturgeon are modulated by their polyploidy.

Is effective population size predictive of census size for Atlantic sturgeon?

Given the challenges of conducting census estimates of Atlantic sturgeon, estimation of N_e may be a way to at least crudely estimate census sizes, but only if there is reasonable confidence in the accuracy of extrapolation factors from N_e to N_c . Theory suggests that N_e/N_c ratios for animals in the wild should be ≥ 0.10 (Hare et al. 2011). In most fish species, N_e is ~ 0.05 – 0.10 the census population size (Hare et al. 2011) but estimated N_e/N_c ratios in marine species are often as low as 10^{-5} (Hauser and Carvalho 2008; Palstra and Ruzzante 2008). A complication is that the relationship between N_e and N_c is not linear but rather, a power function in which the ratio decreases with increasing population size.

Bradford et al. (2016) obtained N_e/N_c ratios of 0.04 and 0.12 for two collection years of spawning adults for the Saint John River Atlantic sturgeon population, values near the 0.5–0.10 proposed by Hare et al. (2011). The Saint John is the only population in which there are whole-population N_c estimates with which to make comparison with contemporary N_e . For the Hudson, our N_e estimate of 156 compares with an estimate of mean annual adult spawners of 863, for a ratio of 0.18. However, we are unable to address the generality of their estimate to other populations. Additional whole-population N_c estimates are needed to attempt to develop an extrapolation factor between N_e and N_c .

It may be that tracking individual populations using N_e would be more reliable than applying an extrapolation factor

between N_e and N_c . However, it would be important to monitor both N_e and N_c for periods long enough to determine how sensitive N_e is to changes in N_c and over what time frame.

Conclusions

Atlantic sturgeon show low contemporary N_e values; these may be of concern given current conservation biology guidelines for vertebrates. However, four factors temper this notion: (1) to date there is no evidence of any genetically-based problems, e.g., alarmingly low estimates of genetic diversity or morphological abnormalities for Atlantic sturgeon populations, (2) historical N_e values, while higher than contemporary values, are also considerably lower than might be expected based on historical catch records, suggesting that the particular life history attributes of the subspecies result in low N_e levels, (3) calculations of N_e Max suggest that some estimates of N_e are likely biased low because of inadequate representation of the population, and (4), although speculative, polyploidy may provide a buffering effect for low N_e in Atlantic sturgeon populations.

Additionally, N_e may be a useful monitoring tool as a surrogate for N_c , but there is not yet enough information to propose a reliable adjustment factor. To achieve that goal, there needs to be more research on N_e , N_e Max, and N_c simultaneously on individual populations across a sufficient number of year classes to achieve a flattening of the curve of N_e Max.

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