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Past and Present Processes Influencing Genetic Diversity and Effective Population Size in a Natural Population of Atlantic Sturgeon

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ARTICLE

Past and Present Processes Influencing Genetic Diversity and Effective Population Size in a Natural Population of Atlantic Sturgeon

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Abstract

Threats such as habitat loss, invasive species, and overexploitation cause species extinctions; however, stochastic processes can accelerate extinction rates as census sizes decline. Using molecular and ecological data, we explored the influence of these processes on the demography of a candidate species under the U.S. Endangered Species Act—the Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*. We used molecular microsatellite markers to estimate the effective population size (N_e) and effective number of breeders (N_b) and we used mark–recapture data to estimate the number of spawners (N_a) for Atlantic sturgeon of the Altamaha River, Georgia. We found that estimates of N_b were 7–45% less than the estimated N_a over four consecutive cohorts and that skewed sex ratios could explain the relative decrease of N_b to N_a. Our estimate of contemporary N_e was 125 (95% confidence interval = 75–348) and was at least an order of magnitude less than our estimate of historical N_e. To explain the large discrepancy between these estimates, we tested several alternative evolutionary scenarios that might explain the observed pattern of genetic diversity. Our results indicated that the observed genetic data were indeed best explained (i.e., 0.998 posterior probability of the data given the hypothesis) by overexploitation during the last half of the 20th century.

Population census size (N) is an important parameter in the conservation and management of threatened and endangered species because variability of N determines extinction risk. As N becomes small owing to deterministic events (e.g., natural selection, habitat loss or modification, or overharvest), stochastic factors such as inbreeding and loss of genetic variation (genetic factors), skewed sex ratio or variance in family size (demographic factors), and variation in environmental conditions (environmental factors) can accelerate population decline (Fagan and Holmes 2006). For example, inbreeding and loss of neutral genetic variation associated with a small population size can further reduce the fitness of the population (Reed and Frankham 2003). The rate of these genetic processes, however, is not contingent on N but rather on the effective population size (N_e) of the population. The parameter N_e, which refers to the size of an ideal population experiencing the same rate of random genetic change over time as the real population under consideration (Wright 1938), is typically much smaller than N because of various life history and reproductive biology aspects, such as fluctuating population size, unequal sex ratio, and variance in reproductive

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success (Frankham 1995; Palstra and Ruzzante 2008). Populations, therefore, may become susceptible to stochastic factors at levels where census estimates would provide little indication of a high risk of extinction or extirpation (Turner et al. 2002, 2006).

While N_e is important in evolutionary and conservation biology, it is often difficult to measure in natural populations. Estimates of contemporary N_e (roughly, the N_e that applies to the time period encompassed by the sampling effort) are typically derived from a single sample (Hill 1981) or two samples (Nei and Tajima 1981). The two-sample (temporal) method, which depends on random changes in allele frequency over time, has been widely applied; however, in addition to other simplifying assumptions, the standard temporal method assumes that generations are discrete. This method is thus difficult to apply to iteroparous, age-structured species unless temporal samples are taken several generations apart (Waples and Yokota 2007).

An age-structured population presents a problem for the estimation of N_e because it does not constitute a homogeneous breeding unit; therefore, there will not necessarily be a direct relationship between N_e and temporal allele frequency fluctuations. Instead, variances and covariances in allele frequencies within and among age-classes depend on the age-specific birth and survival rates of each population and will tend to bias estimation of N_e (Waples and Yokota 2007) unless these sampling effects are corrected (Jorde and Ryman 1995). In such situations, demographic information must be accounted for when estimating N_e for observed short-term fluctuations in allele frequency.

Conservation and management of age-structured, iteroparous species thus depend on detailed knowledge of interactions between life history and population dynamics. For example, theoretical findings suggest that species characterized by overlapping generations and multiple mating opportunities are more resistant to the detrimental genetic consequences of years with poor recruitment and low numbers of breeders (Warner and Chesson 1985; Nunney 1993; Ellner and Hairston 1994) and that these characteristics render a population less sensitive to environmental variance (Gaggiotti and Vetter 1999). This resilience, however, may not protect against other random processes or against declines driven by deterministic factors. Therefore, while theoretical connections between N_e and life history, behavioral ecology, and demography are becoming better understood, few empirical studies on long-lived iteroparous species are available to support these findings (however, see Gaggiotti and Vetter 1999).

One such long-lived species is the Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*. During the mid-1800s, this species was very abundant in many of the major river systems along the Atlantic coast of North America (Armstrong and Hightower 2002); however, in less than 10 years after the caviar market was established, annual landings had declined to less than 10% of their former peak (Secor and Waldman 1999). In 1990, after several decades of continued decline, the Atlantic sturgeon fishery was closed; shortly thereafter, this species was petitioned for listing under the U.S. Endangered Species Act (USFWS 1997) and is currently listed as a candidate species (USFWS 2006).

Atlantic sturgeon spend most of their adult life in the marine environment but migrate to freshwater to spawn (in the Altamaha River, which is the focus of our study, the spawning run typically occurs in February–March). The mating system of Atlantic sturgeon is unknown but presumed to be polygamous like that of other sturgeon species (Schueller and Hayes 2010). Available evidence indicates that eggs, which are highly adhesive, are broadcast into flowing water and subsequently settle on bottom substrate, usually on hard surfaces such as cobble (Smith and Clungston 1997). Juvenile Atlantic sturgeon move downstream into brackish waters and eventually become residents in estuarine waters at 2–5 years of age.

As subadults (76–92 cm total length), Atlantic sturgeon typically move to coastal waters (Smith 1985), where they migrate among coastal and estuarine habitats. Despite extensive mixing in coastal waters, Atlantic sturgeon appear to return to their natal river to spawn, as indicated by tagging records (Collins et al. 2000) and relatively low rates of gene flow (King et al. 2001).

Life history characteristics of Atlantic sturgeon show clinal variation, with faster growth and earlier age at maturation in more southerly systems (e.g., Altamaha River) compared with more northerly systems (e.g., Hudson River; Van Den Avyle 1984). The estimated age structure of Atlantic sturgeon in the Altamaha River consists of 19 year-classes (Peterson et al. 2008). Males mature at age 5, whereas females typically mature at 11 years of age (Peterson et al. 2008). Spawning intervals of Atlantic sturgeon range from 1 to 5 years for males (Smith 1985; Collins et al. 2000; Caron et al. 2002) and from 2 to 5 years for females (Van Eenennaam et al. 1996; Stevenson and Secor 2000). Fecundity of Atlantic sturgeon (ranging from 400,000 eggs to 8 million eggs) has been correlated with weight (Van Den Avyle 1984).

The main purpose of this study was to estimate N_e for Atlantic sturgeon from the Altamaha River by using genetic and life history data and, in doing so, to provide empirical evidence for the various processes influencing this value.

METHODS

Field sampling and collection of genetic data.—Fin clips were collected from 194 age-1 (350–500 mm as defined by Schueller and Peterson 2010) Atlantic sturgeon sampled in the tidally influenced portion of the Altamaha River over a 4-year period starting in 2005 (2005: $n = 50$; 2006: $n = 25$; 2007: $n = 23$; 2008: $n = 96$). Sampling sites were randomly distributed within three contiguous 10-km strata comprising the lower 30 km of the Altamaha River estuary. Each stratum was sampled weekly from June to August with monofilament gill nets (Schueller and Peterson 2010). Atlantic sturgeon DNA was extracted from ethanol-preserved fin clips by use of the DNeasy Blood and Tissue Kit (QIAGEN, Valencia, California).

TABLE 1. Summary of molecular microsatellite markers used to examine Atlantic sturgeon effective population size (A = number of alleles; H_o = observed heterozygosity; H_e = expected heterozygosity). Fluorescently labeled forward primers are denoted in parentheses next to each marker. Loci with the same superscript capital letter designate multiplex polymerase chain reactions (see Methods for details).

Marker	Repeat motif	Size range (base pairs)	A	H_e	H_o	Reference
Aox12 (6-FAM)[B]	di (imperfect)	171–202	8	0.8185	0.7889	King et al. 2001
Aox23 (6-FAM)[C]	tri	91–134	10	0.7761	0.7286	King et al. 2001
AoxD44 (PET)[B]	tetra	127–191	7	0.7966	0.7500	Henderson-Arzapalo and King 2002
AoxD165 (VIC)[A]	tetra	187–231	11	0.8763	0.8676	Henderson-Arzapalo and King 2002
AoxD170 (6-FAM)[A]	tetra	132–164	9	0.7123	0.7225	Henderson-Arzapalo and King 2002
AoxD241 (6-FAM)[A]	tetra	182–270	23	0.9214	0.8995	Henderson-Arzapalo and King 2002
LS19 (PET)[C]	tri	133–154	6	0.6182	0.5739	May et al. 1997
LS54 (PET)[C]	tetra	168–188	3	0.1752	0.1709	May et al. 1997
AoxD172 (NED)[B]	tetra	136–212	15	0.8830	0.5372	Henderson-Arzapalo and King 2002
AoxD234 (VIC)[B]	tetra	194–322	25	0.5975	0.3297	Henderson-Arzapalo and King 2002
AoxD242 (NED)[A]	tetra	150–210	17	0.7711	0.7438	Henderson-Arzapalo and King 2002

We used multiplex polymerase chain reaction (PCR) reactions to amplify a suite of 11 microsatellite markers that are known to amplify in Atlantic sturgeon (King et al. 2001; Henderson-Arzapalo and King 2002) and lake sturgeon *A. fulvescens* (May et al. 1997). Multiplex PCR amplifications (Table 1) were performed in 20-μL reactions with the following reaction components: 1 × *Taq* reaction buffer (Applied Biosystems, Foster City, California), 3.75 mM of $MgCl_2$, 0.318 mM of each deoxynucleotide triphosphate, 0.25 μM of each primer, and 0.08 units of *Taq* polymerase (Applied Biosystems). The PCR conditions were an initial denaturation at 94°C (10 min), followed by a touchdown procedure involving 33 cycles and consisting of denaturing (94°C, 30 s), annealing, and extension (74°C, 30 s) cycles, where the initial annealing temperature was initiated at 56°C (30 s) and decreased by 0.2°C per cycle.

Before electrophoresis, 2 μL of a 1:100 dilution of PCR product were mixed with an 8-μL solution containing 97% formamide and 3% GeneScan LIZ 500 size standard (Applied Biosystems). Microsatellite reactions were visualized in an ABI 3130 genetic analyzer (Applied Biosystems) with fluorescently labeled forward primers and were analyzed by means of GeneMapper version 3.7 (Applied Biosystems). The resulting genotypes were assessed for scoring errors attributable to stutter products, large-allele drop-out, or null alleles with MicroChecker version 2.2 (van Oosterhout et al. 2004). Conformance to per-locus Hardy–Weinberg equilibrium, genotypic disequilibrium, and genic differentiation was tested with GENEPOP version 4.0.10 (Raymond and Rousset 1995). All P-values were adjusted for multiple comparisons by means of a sequential Bonferroni method (Rice 1989).

Estimation of the number of spawners and effective number of breeders.—The total number of reproductively capable adult fish (i.e., number of spawners N_a) was estimated for the ith year with mark–recapture data obtained from wild fish during their spawning run for the years 2004–2007 (Peterson et al. 2008; Schueller 2008). Abundance estimates for each year were derived from a Jolly–Seber population model (Schwarz and Arnason 1996). Briefly, the Jolly–Seber model is applicable to an open population in which there is the possibility of death, recruitment, immigration, and permanent emigration (this model appeared to be more appropriate for the Altamaha River population than did closed population models).

The annual effective number of breeders (N_b) was estimated from each annual collection of age-1 individuals (i.e., each cohort) by means of linkage disequilibrium methods (Hill 1981). Burrow's composite measure of linkage disequilibrium (Campton 1987) was estimated for each cohort with the program LDNe (Waples and Do 2008). Allele frequencies close to zero can affect estimates of N_b (Waples 2006); therefore, we excluded alleles with frequencies less than 0.02 for sample sizes less than 95 or alleles with frequencies less than 0.01 for sample sizes greater than 95 (Waples and Do 2010). Confidence intervals (CIs) were calculated via jackknifing disequilibrium values across loci (Waples and Do 2008 2010).

All age-1 fish collected in a given year were assumed to be progeny from the previous year's spawning run. Thus, the N_b estimate for a given sample of age-1 individuals should correspond to the preceding N_a (Waples 2005). For example, age-1 fish collected in 2008 were designated the 2007 cohort (i.e., from the 2007 spawning run) and the subsequent N_b value corresponded to N_{a-2007}.

Comparison of observed and expected effective number of breeders.—Observed N_b values were compared with expected N_b ($N_{b\mathrm{EXP}}$) based on demographic data to assess the influence of the observed unequal sex ratio on N_b/N_a. The expected reduction in N_b caused by an unequal sex ratio was defined as

$$N_{b\mathrm{EXP}} = \frac{4(N_{\mathrm{male}})(N_{\mathrm{female}})}{(N_{\mathrm{male}} + N_{\mathrm{female}})}$$

(Wright 1931), where N_{male} and N_{female} were the number of males and females observed in the spawning run (note that this

TABLE 2. Atlantic sturgeon life table used for simulations and estimation of effective population size. To model the uncertainty in the parameters of survival (S), proportion of breeders (M_j), and iteroparity, we generated 1,000 simulated life history tables, each time drawing parameters from uniform distributions as indicated in brackets. Prior knowledge of each distribution and weight (kg) at each age-class is outlined in the Methods. The birth rate (b_{ij}) for each age j and sex i was estimated by taking the product of weight, M_j, and iteroparity. The overall birth rate for each age was taken as the average b_{ij} for males and females.

		Males				Females			
Age (years)	Age-class	S	Weight (kg)	M_j	Iteroparity	S	Weight (kg)	M_j	Iteroparity
0	1	[0.53–0.80]		0.00		[0.69–1.00]	0.00	0.00	
1	2	[0.53–0.80]		0.00		[0.69–1.00]	0.00	0.00	
2	3	[0.53–0.80]		0.00		[0.69–1.00]	0.00	0.00	
3	4	[0.53–0.80]		0.00		[0.69–1.00]	0.00	0.00	
4	5	[0.53–0.80]		0.00		[0.69–1.00]	0.00	0.00	
5	6	[0.53–0.80]	20.75	[0.0055–0.0088]	[0.20–1.00]	[0.69–1.00]	0.00	0.00	
6	7	[0.53–0.80]	22.98	[0.024–0.036]	[0.20–1.00]	[0.69–1.00]	0.00	0.00	
7	8	[0.53–0.80]	25.20	[0.085–0.128]	[0.20–1.00]	[0.69–1.00]	0.00	0.00	
8	9	[0.53–0.80]	27.43	[0.200–0.306]	[0.20–1.00]	[0.69–1.00]	0.00	0.00	
9	10	[0.53–0.80]	29.65	1.00	[0.20–1.00]	[0.69–1.00]	0.00	0.00	
10	11	[0.53–0.80]	31.88	1.00	[0.20–1.00]	[0.69–1.00]	0.00	0.00	
11	12	[0.53–0.80]	34.10	1.00	[0.20–1.00]	[0.69–1.00]	47.51	[0.18–0.27]	[0.20–0.50]
12	13	[0.53–0.80]	36.33	1.00	[0.20–1.00]	[0.69–1.00]	50.47	[0.44–0.66]	[0.20–0.50]
13	14	[0.53–0.80]	38.55	1.00	[0.20–1.00]	[0.69–1.00]	53.44	1.00	[0.20–0.50]
14	15	[0.53–0.80]	40.78	1.00	[0.20–1.00]	[0.69–1.00]	56.40	1.00	[0.20–0.50]
15	16	[0.53–0.80]	43.00	1.00	[0.20–1.00]	[0.69–1.00]	59.37	1.00	[0.20–0.50]
16	17	[0.53–0.80]	45.23	1.00	[0.20–1.00]	[0.69–1.00]	62.34	1.00	[0.20–0.50]
17	18	[0.53–0.80]	47.45	1.00	[0.20–1.00]	[0.69–1.00]	65.30	1.00	[0.20–0.50]
18	19	[0.53–0.80]	48.45	1.00	[0.20–1.00]	[0.69–1.00]	65.30	1.00	[0.20–0.50]
19	20	[0.53–0.80]	49.45	1.00	[0.20–1.00]	[0.69–1.00]	65.30	1.00	[0.20–0.50]

equation only applies to a given annual cohort or to a population characterized by discrete generations and assumes that the reproductive variance is zero). Sex was determined by laparoscopy for 105 individuals comprising the 2006 and 2007 spawning runs (Schueller 2008).

Estimation of life table parameters.—To estimate N_e, we needed to correct N_b for sampling effects of overlapping generations. This required the construction of a life table with elements consisting of survival (l_{ij}) and birth (b_{ij}) rates for each sex i at age j (Table 2). The maximum age of Atlantic sturgeon documented in the Altamaha River population over the past decade has been 17 years (Peterson et al. 2008; Schueller 2008). Catch-curve analysis by Schueller (2008) also predicted a maximum age of 19 years (i.e., maximum predicted age averaged over 4 years of catch data), which was younger than ages documented for more northerly populations (Dovel and Berggren 1983). An age-structured population model was created and combined with age frequency data in the Altamaha River spawning run (from Schueller 2008) to estimate sex-specific survival and maturity schedules. Age frequencies from 2004 to 2007 were combined into a single age frequency distribution. Ages ranged from 5 to 17 years, with age-9 Atlantic sturgeon having the greatest frequency of capture. The proportion of males at a given age was estimated from a subsample of individuals sexed via laparoscopic techniques (105 of 281 individuals; Schueller 2008). The youngest female observed by Schueller (2008) was 11 years old, and we assumed that individuals younger than age 11 were all males. The proportion of males at a given age was multiplied by the frequency of each age-class to estimate the frequency of males in each age-class (f_{mi}). The frequency of females at a given age (f_{fi}) equaled the frequency of each age-class minus the estimated number of males. The age-structured model started with a number of age-5 males and females and projected the number that would survive through future age-classes. We assumed that males began to mature at age 5 and were fully mature by age 9, and we assumed that females began to mature at age 11 and were fully mature by age 13. Our age-structured model accounted for the various life history strategies that could be taken by an individual of either sex. We assumed that if an individual became mature at a given age, it would spawn. However, once mature, an individual might not spawn in successive years. The number of newly mature individuals of sex i at age j (NM_{ij}) was calculated as

$$\mathrm{NM}_{ij} = I_{ij-1} \cdot S_i \cdot P_{ij},$$

where I_{ij-1} is the number of immature individuals of sex i at age $j - 1$, S_i is the annual sex-specific survival rate, and P_{ij} is

the probability of an individual of sex i becoming mature if it survived to age j. The number of immature individuals of sex i at age j was

$$I_{ij} = I_{ij-1} \cdot S_i \cdot (1 - P_{ij}).$$

Mature spawners of sex i at age j (MS_{ij}) were a combination of newly mature individuals, mature individuals that spawned the previous year, and mature individuals that did not spawn the previous year:

$$MS_{ij} = NM_{ij} + MS_{ij-1} \cdot S_i \cdot PS_i + MNS_{ij-1} \cdot S_i \cdot PS_i,$$

where PS_i is the proportion of previously mature individuals that returned in a given year, and MNS_{ij} is the number of mature individuals of sex i at age j that did not spawn ($MNS_{ij} = MS_{ij-1} \cdot S_i \cdot [1 - PS_i] + MNS_{ij-1} \cdot S_i \cdot [1 - PS_i]$). The expected MS_{ij} values were summed over all ages to obtain the proportion of age-classes in the spawning run for both males and females (PM_{ij}) such that PM_{ij} equaled $MS_{ij}/\sum MS_{ij}$. The values of MS_{ij} were multiplied by the estimated total number of each sex in the age frequency distribution to yield an expected number of males and females at age in the spawning run. Parameters P_{ij} (ages 5–8 for males; ages 11–12 for females) and S_i (male and female annual survival) were estimated by maximizing the log likelihood of the model

$$\log_e L = \Sigma[\log_e(PM_{ij}) \cdot O_{ij}],$$

where $\log_e L$ is the model log likelihood value and O_{ij} is the estimated frequency of each sex at age (f_{mi} and f_{fi}). The overall proportion at age that were mature for each sex (M_{ij}) was estimated as $M_{ij} = (MS_{ij} + MNS_{ij})/(I_{ij} + MS_{ij} + MNS_{ij})$.

On the basis of S_i and assuming that S_i was constant from the onset of reproductive maturity until death, we calculated l_{ij} separately for each sex i such that, $l_{ij} = {S_i}^j$ (note that in order to correct N_b for sampling effects of overlapping generations, we were only interested in individuals that contributed to the offspring pool—that is, the adult age-classes; therefore, we needed to account for mortality only across reproductive age-classes; Nunney 1991; Jorde and Ryman 1995). We used average body weight as an indicator of relative gamete contribution and multiplied M_{ij} (as estimated above) and spawning interval (see below) by the mean weight of the fish of that particular age and sex. The resulting product was used as an estimate of b_{ij} for each sex i. We then averaged l_j (i.e., $\bar{l}_j = [l_{mj} + l_{fj}]/2$) and b_j (i.e., $\bar{b}_j = [b_{mj} + b_{fj}]/2$) for all subsequent life table analyses (where the subscripts m and f denote male and female, respectively). The relative reproductive success (p_j) for each age-class was estimated as the product of $\bar{l}_j$ and $\bar{b}_j$. Values of $\bar{b}_j$ were adjusted to result in a constant population size (i.e., $\Sigma \bar{l}_j \bar{b}_j = 1$).

Estimation of contemporary effective population size.—An estimate of N_e was calculated with the equation

$$N_e = \frac{C}{2G\left(\bar{F}\right)}$$

(Jorde and Ryman 1995), where C is a correction factor for overlapping generations (Jorde and Ryman 1995), $\bar{F}$ is the average change in allele frequencies for each consecutive cohort comparison, and G is the generation length and is defined as the mean age of parents (i.e., $\sum p_j \cdot x$ years). The estimation of C followed that of Jorde and Ryman (1995) using the equation

$$C = \frac{f_{1,1}(t) + f_{1,1}(t+1) - 2f_{1,2}(t+t)}{f_{1,1}(t+1) - f_{1,1}(t)},$$

where the f_{ij} values, which are based solely on the demographic parameters l_{ij} and p_{ij} (estimated as above), are variables that trace the process of genetic drift in a population of the present age structure (Jorde and Ryman 1995). The f_{ij} values were all set to zero at some arbitrary initial time ($t = 0$), and their subsequent values were estimated through iterating equations (10) to (13) of Jorde and Ryman (1995) as implemented in the program FactorC (furnished upon request by P. Jorde, University of Oslo, Norway). The estimation of F for each consecutive cohort comparison was calculated with TempFs (Jorde and Ryman 2007) The CI for $\bar{F}$ was calculated by first estimating the SE associated with each consecutive cohort estimate of F; from these SE values, the variance of each estimate was calculated, variances were summed, and an overall SE was recalculated (Sokal and Rohlf 1995).

The accuracy of C, G, and subsequently our estimate of N_e relied on several life history parameters: specifically, survival (S_i), the proportion of male and female mature breeders (M_{ij}), and the spawning interval (i.e., iteroparity rate). To address the uncertainty of our life history parameters and their effects on our estimate of N_e, we treated each demographic parameter at each age-class as a random variable drawn from specific uniform distributions (Table 2). The distribution of each parameter was based on $\pm 20\%$ of the point estimate for each parameter as estimated above except the iteroparity rate. The upper and lower bounds of the uniform distribution for the iteroparity rate were taken from the literature (i.e., 1–5 years for males; 2–5 years for females). We then simulated 1,000 life tables, each time drawing parameter values from each specified uniform distribution given for each age-class (Table 2). New values for C and G were determined and C/G was calculated for each simulated life table (by using FactorC), thus creating a normal distribution of C/G from which an average C/G and 95% confidence values were obtained. Confidence limits (CLs) for C/G were used in conjunction with the CI for $\bar{F}$ in the estimation of N_e uncertainty.

We also explored the effect of demography on N_e by rerunning simulations with an iteroparity rate for females of either 10% or 100% and equalizing the age at maturity for males and

TABLE 3. Prior uniform distributions, posterior probabilities, and summary statistics of coalescent models used to compare competing evolutionary scenarios for Atlantic sturgeon. Each scenario (A–D) consisted of three parameters: contemporary effective population size (N_{ec}), time (in generations G), and ancestral effective population size (N_{ea}). Each parameter was sampled from a uniform distribution with lower and upper bounds indicated in brackets (refer to Methods for details). Also reported are the posterior probability for each evolutionary scenario and the summary statistics (H_e = average expected heterozygosity; M-index = mean ratio of the number of alleles over the range of allele sizes) used to assess the goodness of fit between each model parameter–posterior combination and the observed data set. Test quantities (x), which corresponded to the summary statistics, were interpreted as the probability ($x_{\text{simulated}} < x_{\text{observed}}$); therefore, values greater than 0.95 and less than 0.05 were considered significant.

	Scenario			
Parameter	A	B	C	D
N_{ec}	[75–349]	[75–349]	[75–349]	[75–349]
G	[4–12]	[4–12]	[357–1,071]	[357–1,071]
N_{ea}	[75–349]	[1,100–16,500]	[75–349]	[1,100–16,500]
H_e	1.00	0.25	1.00	0.99
M-index	0.04	0.08	0.01	0.17
Posterior probability	0.0000	0.9998	0.000	0.0002

females by allowing females to spawn at age 5. In doing so, we were able to and assess the influence of a biased sex ratio on N_e for this long-lived iteroparous species.

Hypothesis testing of alternative evolutionary scenarios.—We were interested in testing whether the observed genetic variation present in Altamaha River Atlantic sturgeon could be attributed to overharvest during the late 1800s; therefore, we tested four alternative evolutionary scenarios that might explain the observed genetic variation. The four competing hypotheses (scenarios A–D) evaluated whether the observed genetic data could be attributed to (1) overharvest if the contemporary N_e (as estimated above) remained constant prior to overharvest (scenario A); (2) overharvest given observed estimates of contemporary N_e and ancestral N_e (N_{ea}; estimated from historic abundance estimates, see below; scenario B); (3) historic events, such as Pleistocene glaciations, if the contemporary N_e remained constant over the course of 100–500 generations (scenario C); and (4) more historic events given observed estimates of contemporary N_e and N_{ea} (scenario D). Each scenario therefore consisted of varying three parameters: N_e, N_{ea}, and time (in generations G). An approximate Bayesian computation (ABC) approach (Beaumont et al. 2002) as implemented in the program DIY ABC version 1.0.1.34beta (Cornuet et al. 2008) was employed to model each evolutionary scenario given a uniform distribution of values for each parameter (discussed below) and summary statistics based on the observed microsatellite data. Summary statistics included average number of alleles, expected heterozygosity, allele size variance across loci, and the M-index (mean ratio of the number of alleles over the range of allele sizes; Garza and Williamson 2001). The ABC method entailed generating simulated data sets (based on the 2007 cohort data set because it had the largest sample size), selecting simulated data sets closest to the observed data set, and estimating posterior distributions of parameters through a local linear regression procedure (Beaumont et al. 2002; Cornuet et al. 2008). In doing so, this approach provided a way to quantitatively compare alternative evolutionary scenarios.

The ABC approach relied on prior knowledge of parameters N_e, N_{ea}, and G. The parameter N_e was modeled as having a uniform distribution bounded by the lower and upper CLs for this estimate (as described above; Table 3). The parameter G took on two differing values depending on the evolutionary scenario. The collapse of the fishery took place approximately 137 years ago (1870–2007; Secor 2002), which translated to a G-value of approximately 8 generations (i.e., 137 ÷ 14-year generation time as estimated from our life history table simulations). This value of G was used to model scenarios A and B (Table 3). For scenarios C and D, we chose a G-value of 714 years, which was representative of the end of the most recent glacial event approximately 10,000 years ago (10,000 ÷ 14-year generation time). The Georgia fishery before 1870 comprised approximately 11,000 spawning adults (Secor 2002), suggesting that N_{ea} was between 10% and 50% (1,100–5,500) of this value (Nunney and Elam 1994; Palstra and Ruzzante 2008). This was probably an underestimate of the actual N_{ea} because our estimate was based on spawning adults and not the entire population; therefore, our upper bound for this parameter was based on the assumption that the census size may have been three times larger (i.e., $N_{ea} = 33{,}000 \times 0.5 = 16{,}500$) than the historical spawning abundance estimate. We modeled N_e and G for each scenario as having a uniform distribution bounded by the 95% CI for N_e and $\pm 50\%$ of our point estimate for G (Table 3). For N_{ea}, a uniform distribution was also assumed but bounded by 1,100 and 16,500 (Table 3).

We simulated 1,000,000 data sets per scenario (via DIY ABC) to produce reference data sets by using uniform priors for each parameter (Table 3). Prior information regarding the mutation rate and model for microsatellites was used to supply the default values in DIY ABC. The posterior distribution of each scenario was estimated with local linear regression on logit-transformed data for the 10,000 simulated data sets closest to the observed data set (Cornuet et al. 2008). The exact posterior probability of each scenario was reliant on the model that generated the posterior probability distribution; therefore, poor model

TABLE 4. Per-cohort estimation of temporal changes in allele frequencies (F), the effective number of breeders (N_b), spawning run abundance (N_a), and N_b/N_a ratio for Atlantic sturgeon (n = sample size; 95% confidence intervals [CIs] are shown in parentheses). Note that a negative value of N_b was reported for the 2005 cohort, indicating that the genetic result can be explained entirely by sampling error without invoking any genetic drift. Therefore, the lower bound of N_b was used for the 2005 N_b/N_a estimate (including the 95% CI).

Cohort	n	F	N_b	N_a	N_b/N_a
2004	50		73	89	0.82
			(40–207)	(76–102)	(0.39–2.72)
2005	25	0.008	−70.8	213	0.64
		(−0.011 to 0.027)	(138–∞)	(169–258)	(0.53–∞)
2006	23	0.017	77	139	0.55
		(−0.009 to 0.044)	(31–∞)	(118–160)	(0.19–∞)
2007	96	0.009	86	92	0.93
		(−0.007 to 0.025)	(43–300)	(82–101)	(0.43–3.65)

fit could lead to inaccurate estimation of the model's posterior distribution and subsequent model choice (Cornuet et al. 2010). As recommended by Cornuet et al. (2010), we employed the model-checking function of DIY ABC to assess the goodness of fit between each model parameter–posterior combination and the observed data set by using different summary statistics for parameter estimation and model discrimination. The parameter estimation summary statistics used were average number of alleles and allele size variance, while the model discrimination summary statistics were average expected heterozygosity and the M-index. Finally, we evaluated the level of confidence in the choice of the best supported scenario by estimating type I and II errors. We simulated 450 data sets by using the scenario with the highest posterior probability to estimate parameters to which all other scenarios were compared. We then counted (1) the proportion of times that the scenario with the highest posterior probability did not generate the highest posterior probability among the three competing scenarios when it was the true scenario (type I error) or (2) the proportion of times that the scenario had the highest posterior probability when it was not the true scenario (type II error, estimated from test data sets simulated under the other competing scenarios).

RESULTS

Field Sampling and Collection of Genetic Data

Overall, 194 age-1 Atlantic sturgeon were analyzed by using 11 microsatellite markers. All but two loci conformed to per-locus Hardy–Weinberg equilibrium (all $P > 0.06$ for each cohort). Microsatellite markers *AoxD172* and *D234* had a general excess of homozygotes for most allele size-classes (present in all cohorts), which suggests the potential existence of null alleles. These two loci were removed from all subsequent analyses. Gametic disequilibrium tests between all pairs of loci showed no significant disequilibrium after sequential Bonferroni adjustment (all $P > 0.01$ per cohort; $n = 36$ comparisons for an adjusted α of 0.001). Genic differentiation tests indicated that sampled cohorts were not significant after sequential Bonferroni adjustment (all $P > 0.03$; $n = 9$ comparisons for an adjusted α of 0.005).

Estimation of the Number of Spawners and Effective Number of Breeders

The Jolly–Seber open population model estimates of N_a for the 2004, 2005, 2006, and 2007 spawning runs were 89, 213, 139, and 92, respectively (Table 4; Peterson et al. 2008; Schueller 2008). Linkage disequilibrium point estimates of N_b were 73, −70.8, 77, and 86, respectively (Table 4). Note that if N_b is large or the sample size is limited, then by chance the measure of linkage disequilibrium can be smaller than the sample size correction, thus producing a negative estimate of N_b (Waples and Do 2010). However, even though the 2005 point estimate was negative, Waples and Do (2010) suggested that the lower bound of the CI can be used to provide a plausible lower limit for N_b. The lower bound of the CI for the 2005 N_b estimate was 138, and this value was used to calculate a conservative N_b/N_a for the 2005 cohort. Taking the point estimate of N_b per cohort yielded N_b/N_a values of 0.82, 0.64, 0.55, and 0.93 for the 2004–2007 cohorts, respectively (Table 4).

Comparison of Observed and Expected Effective Number of Breeders

The sex ratio during the spawning run (as determined from 16 females and 64 males in 2006 and 22 females and 48 males in 2007) revealed that males, on average, comprised 74% of the catch between 2006 and 2007. The $N_{b\mathrm{EXP}}$ values based solely on demographic data for the 2004–2007 cohorts were 68, 164, 107, and 71, respectively (Table 5). The value of $N_{b\mathrm{EXP}}$ was not significantly greater (i.e., CIs overlapped) than the observed N_b for all cohorts (Table 5), indicating that the observed sex bias could explain the reduction in N_b over N_a.

Estimation of Life History Parameters and Contemporary Effective Population Size

Annual survival rates for adult males and females were estimated to be 0.66 and 0.88, respectively, and were similar to that found by Peterson et al. (2008). The estimated proportions of

TABLE 5. Expected effective number of breeders (N_b) for each cohort of Atlantic sturgeon as estimated from the average number of males and females observed in the 2006 and 2007 spawning runs (95% confidence intervals are shown in parentheses). Estimated proportion of males in the spawning runs was 0.74 (Schueller 2008). The expected numbers of males (N_m) and females (N_f) were determined by multiplying the estimated number of spawners (N_a) by the proportion of males and females observed, respectively, during the spawning runs. Expected N_b ($N_{b\mathrm{EXP}}$) was calculated as $N_{b\mathrm{EXP}} = (4N_mN_f)/(N_f + N_m)$. Observed N_b ($N_{b\mathrm{OBS}}$) values were the point estimates in Table 3. Note that a negative value of N_b was reported for the 2005 cohort (Table 3). Therefore, the lower bound of this value was used for the $N_{b\mathrm{OBS}}$ estimate (including the 95% confidence interval).

Cohort	N_a	N_m	N_f	$N_{b\mathrm{EXP}}$	$N_{b\mathrm{OBS}}$
2004	89 (76–102)	66	23	68 (58–78)	73 (40–207)
2005	213 (169–258)	158	55	164 (130–199)	138 (138–∞)
2006	139 (118–160)	103	36	107 (91–123)	77 (31–∞)
2007	92 (82–101)	68	24	73 (63–78)	86 (43–300)

male mature breeders for ages 5–8 were 0.0069, 0.0305, 0.1069, and 0.2550, respectively. The estimated proportions of female mature breeders for ages 11 and 12 were 0.2227 and 0.5538, respectively. Values of $\bar{l}_j$, $\bar{b}_j$, and average p_j, each estimated from 1,000 simulated life history tables, are reported in Table 6. Estimates of F between consecutive cohorts (and associated 95% CLs) based on the Jorde and Ryman (2007) estimator are shown in Table 4. Averaging over all estimates of F yielded a value of 0.011 for $\bar{F}$ (95% CI $= \pm 0.007$). The parameters C and G averaged over 1,000 life table simulations were 39.05 and 14.18, respectively. The parameter C/G averaged over 1,000 simulations was 2.76 (95% CI $= \pm 0.04$; Figure 1). Our point estimate of N_e was 125, determined by using observed values of C/G and $\bar{F}$. The lower and upper 95% confidence values of C/G when multiplied by the 95% CI values for $\bar{F}$ yielded an estimate of N_e that ranged from 75 to 348.

Rerunning life table simulations with an iteroparity rate of 10% or 100% yielded almost identical estimates of C and G (Table 7). At the 10% iteroparity rate, estimates of C and G were 39.66 and 13.64, respectively; likewise, at the 100% iteroparity rate, C and G were 34.86 and 14.68. Similar estimates (37.21 and 13.74) were also found when the maturity schedule was forced to be identical between males and females. These findings indicated that demographic parameters that induce a sex ratio bias in the spawning run had little effect on our estimate of N_e (Table 7).

Hypothesis Testing of Alternative Evolutionary Scenarios

We were interested in testing whether the observed genetic variation present in Altamaha River Atlantic sturgeon could be attributed to overharvest; therefore, we tested four alternative evolutionary scenarios that might explain the observed genetic variation. Scenario B, the model based on our prior knowledge of the number of elapsed generations and adult census size before the collapse of this fishery, produced a posterior probability

TABLE 6. Average values for life history parameters used to infer the correction factor and generation length for Altamaha River Atlantic sturgeon. Each reported value of survival rate (l_j), birth rate (b_j), and reproductive success (p_j) for each age j was the average value based on 1,000 simulated data sets using the life history parameters outlined in Table 2.

Age (years)	Age-class	l_j	b_j	p_j
0	1	1.000	0.000	0.000
1	2	0.7529	0.000	0.000
2	3	0.5742	0.000	0.000
3	4	0.4456	0.000	0.000
4	5	0.3511	0.000	0.000
5	6	0.2785	0.0065	0.0017
6	7	0.2235	0.0219	0.0046
7	8	0.1813	0.0846	0.0143
8	9	0.1479	0.2088	0.0287
9	10	0.1222	0.9319	0.1038
10	11	0.1009	1.0163	0.0922
11	12	0.0837	1.2861	0.0957
12	13	0.0697	1.6509	0.1013
13	14	0.0586	2.2031	0.1132
14	15	0.0492	2.3471	0.1009
15	16	0.0412	2.462	0.0881
16	17	0.0347	2.2698	0.0789
17	18	0.0289	2.7273	0.0684
18	19	0.0244	2.7682	0.0584
19	20	0.0206	2.8275	0.0497

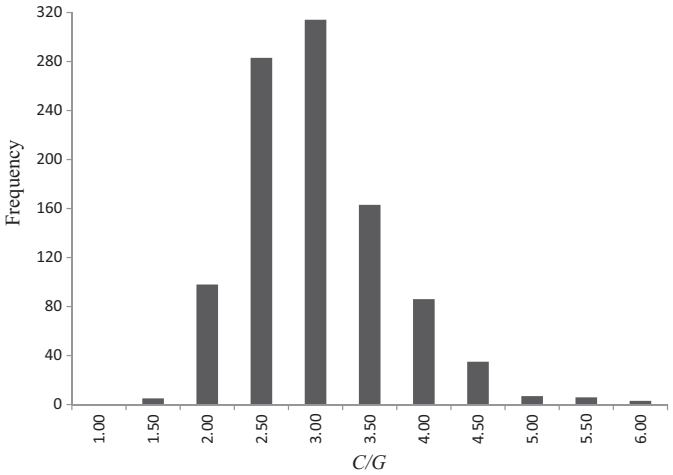

FIGURE 1. Estimated normal probability density function for the parameter C/G (correction factor/generation length) based on 1,000 simulated life history tables for Atlantic sturgeon as reported in Table 2. The mean and median values of this distribution were 2.76 and 2.66, respectively. The 95% confidence interval was ± 0.04 (SE $= \pm 0.6871$).

TABLE 7. Estimation of the correction factor (C), generation length (G), C/G ($\pm$95 confidence interval [CI]), and effective population size (N_e; 95% CI in parentheses) of Atlantic sturgeon given various demographic parameters (observed = parameter estimates based on the life history parameters in Table 2; 10% or 100% iteroparity = parameter estimates obtained after modifying Table 2 so that the female iteroparity rate was held constant at 10% or 100%, respectively, for all age-classes; ESR = parameter estimates obtained after modifying Table 2 so that males and females exhibited an equal sex ratio, accomplished by equalizing the age at maturity for males and females—i.e., setting female maturity at age 5 instead of age 11).

Parameter	Observed	10% iteroparity	100% iteroparity	ESR
Average C	39.05	41.01	36.69	38.39
Average G	14.12	13.64	14.69	13.75
Average C/G	2.76 $\pm$ 0.04	3.01 $\pm$ 0.04	2.50 $\pm$ 0.04	2.79 $\pm$ 0.04
N_e	125 (75–348)	137 (84–376)	114 (69–312)	127 (78–349)

of 0.9998 (95% CI = 0.9997–1.000; Table 3), which suggests that this scenario explained the observed data significantly better than the competing hypotheses. Scenario B was also the only scenario for which none of the test quantities used to assess model misfit had low tail probability values (Table 3), thus indicating a good fit of the scenario–posterior combination to the pseudo-observed data set. Over the 450 data sets simulated with scenario B, 389 (86.4%) indicated that scenario B had the greatest posterior probability when compared across competing scenarios; thus, our estimate of type I error was 13.6%. The proportion of times that scenario B had the largest posterior probability when data sets were created with scenarios A, C, and D was zero, which indicated that the type II error was infinitesimal.

DISCUSSION

Methodological and Theoretical Bias

Temporal and linkage disequilibrium methods assumed that mutation was unimportant, alleles were selectively neutral, the population under consideration was closed to migration, and samples were random with respect to the population under consideration (Waples 1989). The linkage disequilibrium method also assumed that mating was random (Waples 1989), which if violated, appears to have only minor effects on linkage disequilibrium estimates (Weir and Hill 1980). Except for the assumption of a closed population (see below), these assumptions have been met. Mutations should be insignificant over the time period of this study, and the short-term effects of natural selection are predicted to be negligible (Allendorf and Luikart 2007). Finally, sampling sites were randomly distributed across the Altamaha River estuary, and collections were performed weekly over a 3-month time interval (Schueller and Peterson 2010).

The Jorde and Ryman (1995) method assumed that the population maintains a constant size and age distribution over time and that reproduction and survival of individuals in a given year are independent of whether those individuals reproduced in an earlier year. We evaluated the effect of demographic variability by computing C and G for a reasonable range of life history parameters for the population via sensitivity analyses. Jorde and Ryman (1995) showed that if C/G values were similar over a reasonable range of demographic values, then the estimator should be unbiased. Our simulations indicated that C/G remained stable over a wide range of life history parameters; therefore, we were confident that our estimate of N_e was unbiased. The assumption of independence between reproduction and survival was probably violated to some degree for our data; however, only for instances where most of the mortality is associated with breeding (which is not the case for Atlantic sturgeon) does this violation bias N_e (Jorde and Ryman 1995). Thus, our estimate of N_e for Atlantic sturgeon across four consecutive cohorts appears to be unbiased over a wide range of life history parameters.

The algorithm employed by DIY ABC for coalescent simulations assumed an ideal Wright–Fisher model, which is a discrete-generation model (Hudson 1990). This assumption is clearly violated for Atlantic sturgeon; however, while the average value of C indicated that F between subsequent cohorts was expected to be 39 times greater than that of a discrete-generation case, this large discrepancy was tempered by the fact that the generation time for Atlantic sturgeon was rather long (i.e., approximately 14 years). Thus, the parameter C/G may provide an indication about the extent of bias affecting our ABC results. For an organism with nonoverlapping generations, the value of C/G should be 1 (Jorde and Ryman 1995); therefore, if we did not correct our estimate of N_e for overlapping generations, then we would have underestimated our observed value (i.e., 55 versus 125). This bias, while noticeable, was minimal because C/G, which was close to a value of 1, caused little difference in uncorrected and corrected N_e estimates (i.e., the 95% CIs overlapped: 45–250 versus 75–348, respectively). Thus, the bias caused by assuming discrete generations for coalescent simulations should also be minimal, but until a theory with regard to ABC and overlapping generations is established our results should be treated with caution.

Effective Population Size of Altamaha River Atlantic Sturgeon

Defining minimal viable populations is a difficult challenge faced by conservation biologists. In small populations, random events (e.g., genetic, environmental, and demographic events) can accelerate problems caused by events such as habitat loss or modification and overexploitation (Fagan and Holmes 2006).

Therefore, predicting the fate of small populations requires incorporating both demographic and genetic information into realistic models of extinction (Lande 1988; Reed et al. 1988). Demographic data are often limited; therefore, general conservation goals based on genetic considerations are frequently established at an N_e value of 50 to minimize inbreeding depression and an N_e value of 500 to maintain sufficient evolutionary potential (Franklin 1980; Franklin and Frankham 1998). The empirical estimate of N_e (125; 95% CI = 75–348) for Atlantic sturgeon in the Altamaha River was above critical threshold levels for inbreeding and were similar to other estimates of N_e for populations of conservation concern (Palstra and Ruzzante 2008). These findings suggest that genetic factors do not appear to be of immediate importance to the persistence of Atlantic sturgeon of the Altamaha River; however, our estimate of N_e does not take into account the consequence of gene flow.

Gene flow can bias the estimation of N_e, with the bias being dependent on two factors: the amount of gene flow and the extent of genetic differentiation between the focal and source populations (Wang 2003; Palstra and Ruzzante 2008). An estimate of genetic differentiation (i.e., F_{ST}) between the Savannah River and Altamaha River populations was approximately 0.011 (T. King, U.S. Geological Survey, personal communication), indicating that gene flow is occurring between the Altamaha River and other nearby river systems. Continual gene flow and low genetic differentiation are expected to reduce the genetic drift signal, which could bias our N_e estimate upwards (Palstra and Ruzzante 2008). Therefore, while genetic factors are not of immediate concern, we urge caution in its interpretation because our estimate may be somewhat inflated. Clearly, there is a need to elucidate the influence of gene flow on N_e for Georgia populations of Atlantic sturgeon. In principle, the extent of this bias could be evaluated by including reference samples from the other rivers and the use of assignment testing to remove putative migrants.

Another concern is that the Altamaha River population is regarded as the second most abundant Atlantic sturgeon population, rivaled only by that in the Hudson River (Kahnle et al. 2007). Assuming that the genetic diversity of other populations was influenced by the same historical factors affecting the Altamaha River population (see below), then this could place all but the Altamaha River and Hudson River populations at or below critical threshold values for inbreeding depression. Evaluating whether stochastic genetic factors are indeed impeding recovery of other Atlantic sturgeon populations should therefore be of high priority.

Ratio of the Effective Number of Breeders to Spawner Abundance for Altamaha River Atlantic Sturgeon

In 2007, the Atlantic Sturgeon Status Review Team indicated that accurate estimation of the number of spawners is an essential factor in determining the extinction risk for Atlantic sturgeon (Atlantic Sturgeon Status Review Team 2007). We have shown that the genetic analysis of known-age collections of Atlantic sturgeon can serve as a viable alternative to mark–recapture methods for estimating the number of annual spawners. In fact, genetic estimates may provide for a more accurate understanding of the number of spawners that actually have contributed offspring to the next generation. Our data indicated that the N_b was between 10% and 45% less than N_a. There are several explanations for the observed lower N_b/N_a ratio for Atlantic sturgeon; however, demographic data indicated that a biased sex ratio (approximately 1 female to 3 males) during the spawning run could explain the lowered N_b relative to N_a. Alternatively, variance in reproductive success and immigration of genetically differentiated individuals from other populations could have a similar effect on linkage disequilibrium estimates of N_b (Waples and Do 2010). Regardless, demographic data can explain our results without invoking stochastic environmental factors or deterministic events. Can the same be said for our estimate of N_e?

If we estimate N_e from historical catch data (approximately 11,000 spawning adults; Secor 2002) and apply an N_e/N ratio of 0.10–0.50 (Nunney and Elam 1994; Frankham 1995; Palstra and Ruzzante 2008), we obtain an estimated historical N_e of 1,100–5,500. This estimate is approximately an order of magnitude greater than our contemporary N_e estimate. There are several demographic, life history, and environmental parameters that could explain this discrepancy. As mentioned previously, gene flow could be biasing our results, but the bias is expected to be in an upward direction. Consequently, this parameter can be ruled out as negatively influencing our estimate of N_e. Furthermore, a large generation time suggests that the effect of environmental fluctuations on the level of genetic variability should be small (Gaggiotti and Vetter 1999) unless the environmental variance and or time period considered is large (Engen et al. 2005).

Alternatively, Wright (1938) indicated that when generations are nonoverlapping, any sex ratio bias should act to lower N_e. Therefore, we would expect that the elimination of the proportion of nonbreeders (i.e., 100% incidence of iteroparity) or the observed sex ratio bias (due to survival) would increase our estimate of N_e. Yet, in doing so, we found little difference in C, G, and subsequently N_e. This seems counterintuitive to Wright's (1938) finding; however, the proportion of nonbreeders and sex ratio bias can have relatively little influence on N_e when the generation time is long (Nunney 1991). The effect of generation time is easily observed when one considers the theoretical expectation of N_e under a mating system that involves the random union of gametes and Poisson-distributed female fecundity. In such a situation,

$$N_e = N/\{2 + [(1 - 2\alpha_{\text{male}})/(\alpha_{\text{male}} \times T_{\text{male}}) + (1 - 2\alpha_{\text{female}})/(\alpha_{\text{female}} \times T_{\text{female}})]/2)\}$$

(Nunney 1991, 1993), where N is the census size, α is the proportion of breeders for each sex, and T is the mean generation time for each sex. Thus, as the proportion of breeding males (or

females) increases, the average generation time (if large) acts to buffer against a large departure from the theoretically expected value of $N/2$. These findings hold for a variety of mating systems (Nunney 1993; Nunney and Elam 1994), including a polygamous system, as found in Atlantic sturgeon. Variance in reproductive success (i.e., in excess of Poisson variation) could also act to reduce our estimate of N_e; however, similar to an unequal sex ratio, the decrease in N_e is proportionally lower as the generation time increases (Nunney 1991). In brief, the life history as well as gene flow and potential environmental fluctuations appeared to have little influence on our estimate of contemporary N_e, thus indicating that one or more deterministic factors have played an important role in shaping this estimate.

The reduction in N_e may have been due to severe overexploitation, habitat degradation, or both during the last half of the 20th century (Peterson et al. 2008). However, alternative evolutionary hypotheses do exist. For example, Atlantic sturgeon may be predisposed to have reduced N_e because of their larger and more complex genome size (Yi and Streelman 2005). To eliminate this (modeled as scenario A; Table 3) and competing hypotheses, we tested alternative scenarios that might also explain the observed pattern of genetic diversity in the Altamaha River population of Atlantic sturgeon. Our results indicated that the observed genetic data were indeed best explained by overexploitation during the last half of the 20th century. This scenario was better supported than other competing hypotheses, such as large genome size and past Pleistocene events.

In summary, molecular data in conjunction with demographic data provided for an understanding of past and present processes influencing the genetic diversity of a natural population of Atlantic sturgeon. The life history of Atlantic sturgeon suggests that the genetic consequences of factors acting in a single spawning season do not directly translate to reductions in N_e over the entire generation length. Instead, processes associated with past anthropogenic events have shaped present estimates of N_e. While genetic (e.g., inbreeding or loss of genetic variation), demographic (e.g., biased sex ratio and variance in family size), and environmental factors currently do not appear to pose a critical threat to Atlantic sturgeon inhabiting the Altamaha River, findings should be tempered until the effect of gene flow on N_e is fully understood. In the interim, the population should be monitored for and protected against any depression of the demographic rate, which could cause the population to decline and thereby reinforce interactions with other stochastic factors.

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