# Calculating adult sex ratios from observed breeding sex ratios for wide-ranging, intermittently breeding species 

J. E. Kahn (D) ${ }^{1, \dagger} \dagger$ J. C. Watterson, ${ }^{2}$ C. H. Hager, ${ }^{3}$ N. Mathies, ${ }^{3}$ and K. J. Hartman ${ }^{4}$<br>${ }^{1}$ National Marine Fisheries Service, Silver Spring, Maryland 20910 USA<br>${ }^{2}$ U.S. Department of the Navy, Naval Facilities Engineering Command, Atlantic, Norfolk, Virginia 23508 USA<br>${ }^{3}$ Chesapeake Scientific, Williamsburg, Virginia 23185 USA<br>${ }^{4}$ Division of Forestry and Natural Resources, West Virginia University, Morgantown, West Virginia 26506 USA

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#### Abstract

A sex ratio is one of the most basic demographic estimates produced because it is easy to collect and provides deeper insight into population dynamics for the species under consideration. For inconsistently or intermittently breeding species, the breeding sex ratio (BSR) and adult sex ratio (ASR), both reported as the proportion of males, can be quite different. The entire adult population of some wide-ranging species may never be present and capable of being sampled in the same time and place. We explore equations to indirectly estimate ASRs and annual abundance estimates from annual surveys of BSRs. We sampled Atlantic sturgeon (Acipenser oxyrinchus oxyrinchus) from 2013 through 2019 and implanted acoustic transmitters during those sampling periods. The BSRs calculated during capture from 2015 through 2019 were $0.65,0.75,0.69,0.75$, and 0.64 each year. Relying on telemetry detections from the lowest potential spawning region, the expected BSRs in the same years were $0.64,0.74,0.67,0.69$, and 0.60 , suggesting telemetry is a reliable and passive way to estimate BSR. The BSRs were used to indirectly estimate ASR to be approximately 0.51 ( $95 \%$ confidence limits of $0.43-0.58$ ). Estimates of annual abundance derived through sex ratios matched previously published mark-recapture estimates of the same breeding population, but provide additional detail on abundances of each sex. For populations where BSR is more accessible, ASR and abundance estimates can be estimated with capture data and acoustic telemetry.


Key words: abundance; adult sex ratio; Atlantic sturgeon; breeding sex ratio; Chesapeake Bay; female; intermittent reproduction; male; telemetry; wide-ranging species; York River.

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$\dagger$ E-mail: Jason.kahn@noaa.gov

## Introduction

A sex ratio is a commonly used demographic metric, typically easy to collect that provides deeper insight into population dynamics for species ranging from human to wildlife. Identifying and understanding the sex ratio of endangered populations may be particularly important because
skewed ratios in very small populations can increase the risk of extirpation (Hays et al. 2010, Morrison et al. 2016). The sex ratio for many species may change through different life stages when sex-specific mortality risks (Hairston et al. 1983, Ramula et al. 2018, Bennett et al. 2019) or differences in longevity between sexes exist (Austad and Fischer 2016, Cheng and Nelson

2018, Daugherty et al. 2019). Therefore, sex ratios at birth may not reflect adult sex ratios (ASRs; Donald 2007), and depending on breeding strategies employed, breeding sex ratios (BSRs; also called operational sex ratios) may be dissimilar from ASRs (Smith et al. 1984, Smith 1985, Collins et al. 2000, Hays et al. 2010, Lasala et al. 2018, Hager et al. 2020). Studying the two simultaneously can help researchers understand the relationship between ASR, BSR, and breeding strategies (Székely et al. 2014).

Estimation of ASR and BSR can vary in complexity depending on the species and/or population being studied. When every adult individual from the population is present in a finite location, identifying ASR and BSR is straightforward (O'Leary and Kynard 1986, Patricio et al. 2017). Alternatively, species may have naturally skewed BSR if males and females have different reproductive intervals (Collins et al. 2000, Hays et al. 2010, Hager et al. 2020) or migratory behaviors (Morrison et al. 2016). For commercially harvested species, sex ratios are often estimated from harvest data (Brown et al. 1995, Wang et al. 2003, Arocha and Bárrios 2009) but these estimates are not necessarily the same as the ASR due to selective capture bias. Bias is even more pronounced for sexually dimorphic species with sex-dependent growth rates or sizes. To keep sex ratios in more understandable terms, Ancona et al. (2017) suggest estimating ASR as the male proportion of the total population,

$$
\begin{equation*}
\mathrm{ASR}=\frac{N_{\mathrm{m}}}{N_{\mathrm{m}}+N_{\mathrm{f}}} \tag{1}
\end{equation*}
$$

where $N_{\mathrm{m}}$ and $N_{\mathrm{f}}$ are the numbers of males and females collected from within the population.

For most species, estimating ASR or BSR can be complicated by a variety of challenges. Many migratory fish, reptiles, birds, and mammals temporally occupy non-reproductive habitats where many distinct populations of the same species overlap (Hays et al. 2010, Wheeler et al. 2016, Covino et al. 2017, Quillfeldt et al. 2017, Freshwater et al. 2019, Turbek et al. 2019, Ponti et al. 2020). Sexually monomorphic species may require invasive sampling to estimate ASR (Ancona et al. 2017). Sexual dimorphism may create bias in capture or detection probability (Smith et al. 1984, Smith 1985, Wang et al. 2003, Donald 2007, Arocha and Bárrios 2009,

Rodrigues and Coelho 2016, Ancona et al. 2017). Bias can be addressed with increased sampling (Rodrigues and Coelho 2016) or accounting for unequal capture or detection probability (Ancona et al. 2017). A number of species may have individuals that skip breeding events or never aggregate to allow for ASR to be estimated.

For this study, we sampled the endangered Atlantic sturgeon, Acipenser oxyrinchus oxyrinchus, a highly migratory, iteroparous, anadromous fish that exhibits intermittent breeding (NMFS 2012). Historically, this species likely spawned in 35 river systems from Hamilton Inlet, Canada, to St. Johns River, Florida, but now may be limited to approximately 22 (NMFS 2007, ASMFC 2017, Kahn et al. 2019). Atlantic sturgeon have several distinct life stages, consisting of river resident juveniles, migratory subadults, and adults (Bain 1997). Determining the sex ratio of river resident juveniles, despite a closed population, is not possible because gonadal differentiation does not occur until ages 1-5 (Van Eenennaam and Doroshov 1998). Once juveniles move offshore and become migratory sub-adults, they are no longer available as a population to sample in the same time and place. Adults eventually return to their natal streams to make spawning runs, typically with males maturing at younger ages and maturity being related to size rather than age (Scott and Crossman 1973, Smith 1985, Caron et al. 2002, Dadswell et al. 2017).

Annually, reproductive aggregations of Atlantic sturgeon can be sampled to estimate BSR following the equation above, but because some adults skip spawning events, all adult individuals from a single population are never present in the same place at the same time to sample. In the population of Atlantic sturgeon presented here, males return approximately once every 1.13 yr and females once every 2.19 yr (Hager et al. 2020). Estimates of the BSR of Atlantic sturgeon in the Edisto River, South Carolina, and Hudson River, New York, suggest 0.75-0.80 may be typical (Collins et al. 2000, Kahnle et al. 2007). Here, we present annual BSR considering different capture probabilities, which we then use to estimate spawning abundance of each sex and ultimately indirectly estimate ASR of the entire population.

## Methods

As an endangered species, all research on Atlantic sturgeon followed federal and state permit requirements as well as standard research protocols (Kahn and Mohead 2010).

## Telemetry implantation and tracking

A select group of adult sturgeon received internal VEMCO V16P-4H, V16P-6x, or V16-6x telemetry transmitters with 6 - to $10-\mathrm{yr}$ batteries. The surgical implantation process is described in Hager et al. (2020). The deployed transmitters were programmed to transmit a 69 kilohertz ( kHz ) signal every 70-150 s. Once lost and failed transmitters, identified by recapturing individuals, were removed from the analysis, we tracked 31 male and 39 female adults.

The implanted transmitters were passively tracked within the freshwater and saline reaches of the York River system, a tributary to the Chesapeake Bay in the eastern United States, yearround from 2014 through 2019 (Fig. 1). Passive Vemco VR2W-69 kHz receiver stations within the York River system helped identify the individual transmitters present at the spawning grounds. Because of the narrow width (most locations $<25 \mathrm{~m}$ ) of the Pamunkey River, a tributary to the York River used preferentially by Atlantic sturgeon for spawning, the receivers acted as gates where every fish that passed a receiver would be within a detectable range, verified through range studies presented by Hager (2016). Atlantic sturgeon were determined to be on a spawning run if they moved at least 20 km upriver of the saltwater interface (Van


Fig. 1. Sampling location and acoustic telemetry receiver placement within the York River system, Virginia, USA.

Eenennaam et al. 1996, Kynard and Horgan 2002) and spent at least 17 consecutive days in freshwater based on ad hoc observations (Hager et al. 2020).

## Capture and breeding sex ratio estimation

Atlantic sturgeon were sampled from the spawning grounds (Pamunkey River kilometer, Prkm, 74, York River system kilometer, Yrkm 129; Fig. 1) of the Pamunkey River during the spawning season (August-October) from 2013 through 2019. The saltwater interface moves depending on river flow and tides, but the freshwater line is generally between Prkm 29 and 34. Sampling was conducted with custom-made gill nets that extended from bank to bank ( $\sim 91 \mathrm{~m}$ long) and surface to bottom ( $>7 \mathrm{~m}$ ). Nylon gill nets had twine ranging from 0.9 to 1.2 mm and ranged from 23 to 41 cm stretched mesh to ensure a wide range of adult sizes were sampled. Three nets of varied mesh sizes were set in sequence in a $0.35-\mathrm{km}$ section of river, such that the largest mesh was set downstream and smallest mesh in the middle. Individuals were sexed during surgical procedures or by expressing gametes via application of pressure to the ventral surface moving from the anterior to posterior ends, ending at the vent.

We calculated observed BSR (OBSR) from the spawning grounds each year following Ancona et al. (2017):

$$
\begin{equation*}
\mathrm{OBSR}_{i}=\frac{N_{\mathrm{bm}_{i}}}{N_{\mathrm{bm}_{i}}+N_{\mathrm{bf}_{i}}}, \tag{2}
\end{equation*}
$$

where $N_{\mathrm{bm}}$ and $N_{\mathrm{bf}}$ are numbers of breeding males and breeding females captured on the spawning grounds while $i$ refers to the year of sampling. If capture probability is the same for each sex, then the OBSR is reflective of the true BSR. However, for many species, including Atlantic sturgeon, capture probability between size-differentiated sexes is not constant. To account for this, we can incorporate the capture probability of each sex into Eq. 2 to produce an estimate of BSR , which is more accurate than our estimate of OBSR.

The values for capture probability by sex were calculated using the proportion of fish captured of a known abundance, in this case, acoustic telemetry transmitters that returned to the river each year:

$$
\begin{equation*}
p_{x i}=\frac{\mathrm{TC}_{x i}}{\mathrm{TR}_{x i}} \tag{3}
\end{equation*}
$$

where $p$ is the capture probability of, $x$, the sex being considered each year of sampling, $i$. The variable TR is a count of transmitters returning to spawning grounds, and TC is a count of the number of transmitters captured during sampling. Transmitters were implanted into the adult Atlantic sturgeon over the course of each spawning season. Only males were telemetered in 2013, so the first year both sexes received transmitters was 2014 and the first year transmitters in both males and females returned to spawning grounds was 2015.
We considered BSR estimates using annually calculated capture probabilities for each sex ( $p_{x i}$; Eq. 3) and also mean capture probability for each sex ( $\bar{p}_{x} ;$ Eq. 4). The equation for $\bar{p}_{x}$ is

$$
\begin{equation*}
\bar{p}_{x}=\frac{\sum_{i=1}^{a} \frac{\mathrm{TC}_{x i}}{\mathrm{TR}_{x i}}}{a} \tag{4}
\end{equation*}
$$

where most variables are defined in Eq. 3 and the value, $a$, refers to the number of years with at least 10 transmitters available for capture. The $\bar{p}_{x}$ estimate limited the stochastic interannual variability observed for $p_{x i}$ that arose from few transmitters being available for capture on the spawning grounds some years. When we introduce capture probability ( $p_{x i}$ or $\bar{p}_{x}$ ) in Eq. 2, we produce abundance estimates of males and females in the spawning population following the canonical abundance estimator:

$$
\begin{equation*}
N=\frac{N}{p} \tag{5}
\end{equation*}
$$

where $N$ is an estimate of abundance, $N$ is the total number of sturgeon captured on a particular spawning run, and $p$ is the capture probability. We used the abundance estimates produced in Kahn et al. (2019) to validate the use of $p_{x i}$ or $\bar{p}_{x}$, which showed $\bar{p}_{x}$ produced the most consistently reliable abundance estimates, which in turn produce more reliable BSR calculations (Ancona et al. 2017):

$$
\begin{equation*}
\mathrm{BSR}_{i}=\frac{\frac{N_{\mathrm{bm}_{i}}}{\bar{p}_{\mathrm{m}}}}{\left(\frac{N_{\mathrm{bm}_{i}}}{\bar{p}_{\mathrm{m}}}+\frac{N_{\mathrm{bf}_{i}}}{\bar{p}_{\mathrm{f}}}\right)} \tag{6}
\end{equation*}
$$

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Here, $N_{\mathrm{bm}}$ and $N_{\mathrm{bf}}$ are still counts of breeding males and breeding females captured and the addition of $\bar{p}_{\mathrm{m}}$ and $\bar{p}_{\mathrm{f}}$ for each year, $i$, estimates the abundance of males or females.

The $95 \%$ confidence limits (CL) of the capture probabilities were calculated by using a standard estimate of variance:

$$
\begin{equation*}
s^{2}=\frac{\sum_{i=1}^{a}\left(p_{x i}-\bar{p}_{x}\right)^{2}}{a-1} \tag{7}
\end{equation*}
$$

where each variable has been defined in the previous four equations. The $95 \%$ CLs were then estimated from a $t$ table using the standard deviation (SD):

$$
\begin{equation*}
95 \% \mathrm{CL}=\mathrm{SD} \times t_{(0.975, a-1)} \tag{8}
\end{equation*}
$$

## Calculation of adult sex ratio

For migratory species that reproduce intermittently, resulting in a situation where all adults are never in the same place at the same time, a calculation must be made to correlate the BSR to the ASR. Here, we rely on telemetry observations with assumptions to calculate the proportion of males and females that reproduce each year. The assumptions were that (1) transmitters are in natal individuals and at sufficient numbers to be representative of the population; (2) those individuals are behaving normally; and (3) all transmitters are detected. The individuals telemetered were verified genetically to be from the York River population, appear to be behaving normally, and all were detected based on the fact that if a transmitter was detected once, it was detected over 1000 times. The ratio of transmitters implanted was skewed because we did not know the sex ratio in the population and females return less frequently so more were needed to achieve at least 10 telemetered females spawning each year.

The relationship between BSR and ASR is described in Hays et al. (2010), who note a skewed ASR for male loggerhead sea turtles of approximately 0.3 , but a BSR of roughly 0.5 , because the male sea turtle reproductive interval is approximately 2.6 times as frequent as females. We employ a similar equation here. The calculation of BSR in a given year is shown in Eq. 6 and the average of each year's BSR, $\overline{\mathrm{BSR}}$, is produced following the methodology from Eq. 4.

An estimate of the expected BSR (EBSR) can be produced by assessing transmitter returns during a given year using the equation:

$$
\begin{equation*}
\operatorname{EBSR}_{i}=\frac{\frac{\mathrm{TR}_{\mathrm{m} i}}{\mathrm{TAL}_{\mathrm{m} i}}}{\left(\frac{\mathrm{TR}_{\mathrm{m} i}}{\mathrm{TAL}_{\mathrm{m} i}}+\frac{\mathrm{TR}_{f i}}{\mathrm{TAL}_{f i}}\right)}, \tag{9}
\end{equation*}
$$

where TR is the number of transmitters returning and TAL is the number of transmitters at large for each sex, during each year, $i$. Transmitters at large were inferred from the final detection recorded for each transmitter, such that a detection of a transmitter implanted in August of 2014 and last detected in October of 2019 was known to be at large during 2016 even if there were no detections of that transmitter during that spawning season. Expected BSRs were calculated based on transmitters returning to a lower station (Prkm 49; approximately 20 km above the saltwater interface), a middle station (Prkm 74), and upper station (Prkm 89). As in Eq. 4, the average EBSR, $\overline{\text { EBSR }}$, can be calculated.

The number of males to each female for the entire population is a ratio of mean calculated BSR, derived from OBSR and corrected with capture probabilities, $p$, to the mean expected BSR, $\overline{\text { EBSR. When we apply this ratio to Eq. 1, which }}$ calculates ASR for a population, we produce the following equation:

$$
\begin{equation*}
\mathrm{ASR}=\frac{\frac{\overline{\overline{\mathrm{BSR}}}}{\overline{\mathrm{EBSR}}}}{\left(\frac{\overline{\mathrm{BSR}}}{\overline{\mathrm{EBSR}}+1)}\right.} \tag{10}
\end{equation*}
$$

This equation produces an estimate of ASR for populations even when all members of the population are never present in the same place at the same time.

## Results

From 2014 through 2019, a minimum of 44 and maximum of 86 unique Atlantic sturgeon were captured each year (Table 1). Observed BSRs were corrected for differences in capture probability between sexes. At least 10 telemetered males returned every year during the 5 yr from 2015 through 2019 and in 2018 and 2019 at least 10 telemetered female sturgeon returned (Table 2). Male capture probability in those years was $0.38,0.50,0.45,0.29$, and 0.35 for a mean

Table 1. Annual record of numbers of males and females captured, resulting abundances of each sex when capture probability (Eq. 4) is considered, breeding sex ratio (Eq. 6), spawning run abundance calculated in this study, and validated by published estimates in Kahn et al. (2019).

| Year | Males | Male abundance | Females | Female abundance | BSR | $N / p$ | $95 \%$ CL | Jackknife $\dagger$ | $95 \% \mathrm{CL} \dagger$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 2014 | 46 | 117 | 11 | 41 | 0.74 | 158 | $127-189$ | 152 | $115-215$ |
| 2015 | 49 | 125 | 18 | 68 | 0.65 | 192 | $154-230$ | 182 | $145-243$ |
| 2016 | 44 | 112 | 10 | 38 | 0.75 | 149 | $120-179$ | 219 | $166-298$ |
| 2017 | 59 | 150 | 18 | 68 | 0.69 | 218 | $175-260$ | 215 | $167-292$ |
| 2018 | 36 | 92 | 8 | 30 | 0.75 | 122 | $98-145$ | 154 | $112-222$ |
| 2019 | 60 | 153 | 23 | 86 | 0.64 | 239 | $192-286$ | 330 | $257-434$ |

Note: Abbreviations are BSR, breeding sex ratio; $N$, number captured; $p$, capture probability; CL, confidence limits.
$\dagger$ From Kahn et al. (2019), presenting the optimal model suggested for estimating abundance and including the 2019 spawning abundance.

Table 2. Identification of male (a) and female (b) transmitter returns (TR) at Pamunkey rkm 49, 74, and 89 and transmitters at large (TAL) during that spawning season, used to produce rates of return for each sex at each location.

| Year | TR Prkm 49 | TR Prkm 74 | TR Prkm 89 | TAL | Rate Prkm 49 | Rate Prkm 74 | Rate Prkm 89 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| (a) Male |  |  |  |  |  |  |  |
| 2014 | 8 | 8 | 6 | 9 | 0.89 | 0.89 | 0.67 |
| 2015 | 22 | 22 | 15 | 25 | 0.88 | 0.88 | 0.60 |
| 2016 | 19 | 19 | 18 | 23 | 0.83 | 0.83 | 0.78 |
| 2017 | 20 | 20 | 15 | 26 | 0.77 | 0.77 | 0.58 |
| 2018 | 21 | 21 | 20 | 25 | 0.84 | 0.84 | 0.80 |
| 2019 | 20 | 20 | 18 | 26 | 0.77 | 0.77 | 0.69 |
| (b) Female |  |  |  |  |  |  |  |
| 2014 | 0 | 0 | 0 | 0 | NA | NA | NA |
| 2015 | 2 | 2 | 1 | 4 | 0.50 | 0.50 | 0.25 |
| 2016 | 2 | 2 | 1 | 7 | 0.29 | 0.29 | 0.14 |
| 2017 | 3 | 3 | 0 | 8 | 0.38 | 0.38 | 0.00 |
| 2018 | 10 | 10 | 8 | 26 | 0.39 | 0.39 | 0.31 |
| 2019 | 16 | 12 | 5 | 29 | 0.55 | 0.41 | 0.17 |

Note: NA is not applicable.
male capture probability of 0.39 ( $95 \% \mathrm{CL}$, $0.56-0.23$ ). Female capture probability in 2018 and 2019 was 0.20 and 0.33 for a mean capture probability of 0.27 ( $95 \%$ CL, $0.45-0.08$ ).

The BSR, presented as proportion male in Table 1, ranged from 0.64 in 2019 to 0.75 in 2016 and 2018. When correcting BSR, we produced estimates of male and female abundance on spawning runs in those years, which were validated with estimates from Kahn et al. (2019) in the table. Point estimates of spawning run abundance and 95\% CLs from 2014 through 2019 were produced for each sex participating in those runs (Table 1). Spawning abundance most years typically ranged from 150 to 225 adults.

From 2015 through 2019, 22, 19, 20, 21, and 20 male transmitters, respectively, and 2, 2, 3, 10,
and 16 female transmitters, respectively, returned to spawning habitats in the Pamunkey River. During those years, 25, 23, 26, 25, and 26 male transmitters and $4,7,8,26$, and 29 female transmitters were present in the population (Table 2). The calculated BSR values (Eq. 6) were 0.65, 0.75, $0.69,0.75$, and 0.64 for the same time period (Table 1).

The expected BSR values at Prkm 49, 74, and 89 varied based on the number of telemetered sturgeon that made it to each station (Table 2). Eq. 9 produces expected BSR values at the lowest possible spawning location of $0.64,0.74,0.67$, 0.69 , and 0.58 from 2015 through 2019 (Table 3). These expected BSR values increase moving upriver as males are more often detected at all stations. A comparison of expected to calculated

Table 3. Expected BSR at the lower, middle, and upper Pamunkey River stations between 2015 and 2019.

| Year | Prkm 49 EBSR | Prkm 74 EBSR | Prkm 89 EBSR |
| :---: | :---: | :---: | :---: |
| 2015 | 0.64 | 0.64 | 0.71 |
| 2016 | 0.74 | 0.74 | 0.85 |
| 2017 | 0.67 | 0.67 | 1.00 |
| 2018 | 0.69 | 0.69 | 0.72 |
| 2019 | 0.58 | 0.65 | 0.80 |

BSR values (Fig. 2) shows consistent values at the lower and middle stations, but males are more common in upriver locations. At Prkm 49 and 74, observed BSR values are very similar to expected BSR values. Relying on expected BSR values at lower Pamunkey River stations to ensure detection of all individuals on the spawning run, Eq. 1 produces an overall population ASR of 0.51 with $95 \%$ CLs between 0.43 and 0.59 .

## Discussion

For highly migratory species with intermittent reproduction, resulting in an adult population that is never congregated in the same time and place, estimating the adult sex ratio can be


Fig. 2. Expected BSRs at Prkm 49 (gray triangle), Prkm 74 (gray diamond), and Prkm 89 (gray circle) along with calculated BSR (yellow square) for each year.
locations throughout the spawning reach while males seem to cover nearly the entire area seeking ovulating females. This is important because it suggests male movements can be used to define spawning areas in a particular year, but for calculating the BSR in that year, a station(s) with all adults present is best. The Pamunkey River is narrow and effectively linear, meaning all sturgeon pass the lowest station on their way to further upriver locations where more males are detected. Calculating the BSR in the lowest reach where all individuals meet the pre-determined definition of spawning is most accurate. For other species with large, three-dimensional study areas, it is important to be able to detect all telemetered reproductive individuals to produce the best BSR estimate. The other problem our limited female transmitters from 2015 through 2017 helped identify was that individual variability can have an outsized effect on BSR when few transmitters are present. In 2018 and 2019, when more than 10 telemetered males and females returned to spawn, the BSR estimates in upper and lower stations were more similar to what we observed during capture events (Table 3, Fig. 2).

We had anticipated the ASR would be slightly skewed toward males because males reach sexual maturity at a younger age (Dovel and Berggren 1983, Smith 1985). The sex ratio can become skewed if there are differences in age at maturation, survival between the sexes, selective mixing/migrating, small population sizes, or selective harvest removal (Hays et al. 2010, Coleman et al. 2011, Székely et al. 2014, Morrison et al. 2016, Ancona et al. 2020). Survival in this population, estimated over a $6-\mathrm{yr}$ period, ranges within $95 \%$ confidence limits for males and females from $91.4 \%$ to $99.8 \%$ and $83.4 \%$ to $99.4 \%$ (J. E. Kahn et al., unpublished manuscript). If adults have high annual survivorship until senescence, a 6-yr study design would not have detected whether females live longer than males. However, if females live longer and males mature earlier, that would balance the ASR. We are not aware of studies suggesting female Atlantic sturgeon longevity differs from male, but this may be an interesting topic of future research.

As Székely et al. (2014) note, studying BSR and ASR simultaneously can shed light on breeding strategies employed by species. In the case of Atlantic sturgeon, BSR differs considerably from

ASR due to their breeding strategy. Skewed BSRs are often considered evidence of population stress (Lens et al. 1998, Ingraldi 2005, Steifetten and Dale 2006). However, for a highly fecund species like Atlantic sturgeon (Mitchill et al. 2020), such an approach may be more likely to increase genetic diversity, particularly when eggs are fertilized externally. Female sturgeon release their eggs directly above the benthos and the nearest male has the highest likelihood of successfully fertilizing the most eggs. Therefore, males battle to be in close proximity, either beside or above the female in the act of spawning. This implies a BSR exceeding 0.75 may be sub-optimal as a breeding strategy for the population. When Atlantic sturgeon BSR exceeded 0.75 , as an estimate of 0.8 in the Hudson River (Kahnle et al. 2007), there was a simultaneous recruitment failure (Peterson et al. 2000) and fishery closure (ASMFC 1998). In addition, Atlantic sturgeon females require 2.19 yr between spawning events, while males need only 1.13 yr (Hager et al. 2020), so a population-level balance of a roughly even ASR maintains this BSR (Hays et al. 2010, Székely et al. 2014). Similar BSRs have been estimated for other Atlantic sturgeon spawning populations (Collins et al. 2000) but are notably different from those reported from commercial harvest (Smith et al. 1984, Dadswell et al. 2017).

Incorporating capture probability into the calculation of BSRs also produces an estimate of annual breeding abundance. Kahn et al. (2019) examined 11 different closed population models to estimate annual breeding abundance of this population, confirming the modeling done by Grimm et al. (2014) that the jackknife model $\left(M_{\mathrm{h}}\right)$ produced the most reliable estimates. Table 1 shows the estimate produced using the capture probability derived in this study with the jackknife model used previously (Kahn et al. 2019) and reveals the point estimates and $95 \%$ confidence limits are very similar. Additionally, the estimates relying on capture probability provide estimates of the abundance of each sex of Atlantic sturgeon during a breeding period for the first time since the commercial fishery (Kahnle et al. 2007), which is critical to understanding population dynamics and recovery potential. In addition to being difficult to estimate ASR for adults of a population that is never in the same place at
the same time, it is also difficult to estimate the total adult abundance. Kahnle et al. (2007) demonstrated it is possible to estimate the total adult abundance by calculating the capture probability from the entire population (Kahnle et al. 2007) but it may also be possible to estimate total abundance indirectly using ASR in the same way we were able to estimate ASR indirectly from BSR.

Estimating BSRs each year can be labor-intensive. This study shows expected BSRs (Eq. 9) were nearly identical to BSRs (Eq. 6) each year. As various forms of acoustic and radio telemetry continue to improve animal movement data across diverse taxa (Iverson et al. 1996, Steward 1997, Kjellén et al. 2001, D'Angelo et al. 2005, Schofield et al. 2009, Fossette et al. 2014), a greater insight into the BSRs for various species will emerge. This study provides validation that over time relatively few telemetry transmitters can provide similar sex ratio estimates as higher intensity mark-recapture studies.

## AckNowLeDGMENTS

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15-023, and 16-036 for 2013, 2014, 2015, and 2016 respectively), VDGIF Permit (numbers 047061, 051600, 053337, 055949, 060198, 061577, and 065154 for 2013, 2014, 2015, 2016, 2017, 2018, and 2019 respectively), and NMFS Permit Numbers 16547 and 19642.

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