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# Population and sex-specific survival estimates for Atlantic sturgeon: addressing detection probability and tag loss

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ABSTRACT: Survival estimates of animal populations provide managers with critical information on productivity, population stability, and demography. Telemetry-based survival estimates can be obtained remotely. The Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* is a wide-ranging species whose populations overlap along the East Coast of North America, complicating survival estimation. The objective of this study was to estimate apparent annual survival of the York River population using a Cormack-Jolly-Seber model. In this study, 36 males and 24 females were telemetered and monitored between 2013 and 2019. We considered the fit of a variety of models, selecting the best fit using Akaike's information criterion. The optimal model estimated survival in seasonal increments and detection probability by sex in monthly increments. Five transmitters failed to leave the river and another 3 stopped being detected within 21 mo, but of those, recapturing fish confirmed 2 had been lost and 3 were technological failures (12.8% of 39 recaptured). Apparent adult annual survival was estimated to be 99.2% (95% CL: 97.9–99.7%). Addressing sex-specific detection probability and failed transmitters while including a length covariate for each individual produced higher survival estimates than previously reported studies of Atlantic sturgeon. Four males and one female appear to have died, with the location of last detection for 4 of the suspected mortalities in shipping channels near the mouth of the Chesapeake Bay, suggesting managers should focus on this area of increased risk. Such high survival estimates of the adult stage suggest Atlantic sturgeon survival may be more similar to other long-lived, late-maturing animal species than to most other short-lived fish species.

KEY WORDS: Telemetry · Atlantic sturgeon · Endangered species · Survival estimates · Tag loss · Male · Female

## 1. INTRODUCTION

Survival estimates of animal populations provide managers with critical information on productivity, population stability, and demography. Estimates of fish survival are used to develop reference points for fisheries or assess recovery status under the US Endangered Species Act (ESA). Generally, survival curves for fish begin with low survival early in life, followed by relatively predictable annual survival over the life span of the species (Dahlberg 1979, Hoenig 1983, Kahnle et al. 1998, Xiao 2001, Hewitt & Hoenig 2005). Theoretical annual survival rates can be calculated when we know the animal's maximum longevity (Hoenig 1983, Xiao 2001, Hewitt & Hoenig 2005).

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Acoustic telemetry technology has created a means of estimating survival using a variety of models (Hightower & Harris 2017, Brownscombe et al. 2019). Telemetry-derived estimates can be compared with catch curve analyses or longevity-derived theoretical estimates. These models use information on the pattern of detections of telemetered fish during discrete time intervals to estimate apparent survival ($\phi$) and detection probability ($p$). Survey designs that continuously collect acoustic data using stationary receivers throughout the study area, known as passive array designs, are less labor-intensive and thus more efficient for estimating survival than surveys that require capture or active relocation of telemetered individuals. This is particularly true when the population being studied is long-lived and wide-ranging.

In this study, we used passive telemetry data to estimate annual $\phi$ of adult Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*. Atlantic sturgeon are long-lived, wide-ranging, late-maturing, iteroparous, anadromous fish that spawn intermittently (Smith 1985, Bemis & Kynard 1997, Dadswell 2006, NMFS 2007, Peterson et al. 2008, Hager et al. 2020). The species has well-defined life stages (Bain 1997, Kahnle et al. 2007), including larvae (freshwater obligate), juveniles (non-reproductive, residing in their natal rivers), sub-adults (non-reproductive, migratory), and adults (reproductive and migratory). There are approximately 20 confirmed spawning populations along the Atlantic coast of the USA (ASMFC 2017, Kahn et al. 2019), and each population displays high fidelity to their natal river, with occasional straying to neighboring rivers (Grunwald et al. 2008, White et al. 2021). Determining survival rates of migratory Atlantic sturgeon populations is difficult because sub-adult and adult individuals from a single population are scattered broadly along the Atlantic coast, intermixed with individuals from other populations (Wirgin et al. 2012, 2015). During the spawning season, adults are not mixed with individuals from other populations, but males and females display different reproductive intervals, resulting in only a segment of the entire adult population returning to natal habitat each year (Hager et al. 2020). For these reasons, passive telemetry is the most efficient means to estimate survival of individuals from a certain population. Further, because Atlantic sturgeon longevity can exceed 60 yr (Kahnle et al. 2007, Dadswell et al. 2017), the more years of data there are, the greater the likelihood will be of documenting mortality as well as buffering anomalous events should they occur in a short data set.

Several Atlantic sturgeon survival estimates have been produced in the last decade. Annual survival estimates derived from telemetry data using Cormack-Jolly-Seber (CJS) and multi-state models produced estimates of annual $\phi$ ranging from 74 to 91% $\text{yr}^{-1}$ (Hightower et al. 2015, ASMFC 2017, Melnychuk et al. 2017), which are very similar to theoretical estimates using longevity (Table 1; Hoenig 1983, Xiao 2001, Hewitt & Hoenig 2005). Annual survival for Atlantic sturgeon in the Chesapeake Bay distinct population segment (DPS) has been estimated at approximately 88% (ASMFC 2017). There are no estimates of survival for unique reproductive populations within the Chesapeake Bay DPS even though preliminary genetic analyses suggest very little mixing between the James and York river populations (White et al. 2021). Genetic differentiation between 2 populations that are so geographically close suggests behavioral differences that limit the probability of straying between spawning locations, which may also affect the probability of encountering threats to survival.

There are 3 possibly important considerations of Atlantic sturgeon survival that are not addressed in the recent survival estimates. Tag loss or failure is assumed to be non-existent, but many studies suggest that this is not a safe assumption (Cowen 2005, Cowen & Schwarz 2005, Rechisky & Welch 2010, Kieffer & Kynard 2012, Boone et al. 2013, Crossman

Table 1. Maximum reported life expectancy for Atlantic sturgeon populations, organized from north to south, along with estimates of telemetry-derived apparent annual survival and theoretical survival converted from Hoenig's (1983) equation for instantaneous mortality rates ($Z = e^{(1.44 - 0.984 \times \ln(t_{\max}))}$). CJS: Cormack-Jolly-Seber, NA: not applicable

| Region | Maximum life expectancy (yr) | Hoenig (1983) theoretical survival | CJS apparent annual survival | Citation |
|---|---|---|---|---|
| Canada | 60–64 | 0.937 | NA | Mangin (1964), Dadswell et al. (2017) |
| New York | 45 | 0.912 | 0.914 | Van Eenennaam et al. (1996), ASMFC (2017) |
| Virginia | 40 | 0.901 | 0.878 | Balazik et al. (2010), ASMFC (2017) |
| South Carolina | 25–30 | 0.881 | 0.778 | Smith (1985), ASMFC (2017) |

et al. 2013, Rudd et al. 2014, Secor et al. 2022). Differences in *p* between sexes have not been considered in previous modeling efforts despite adult females returning less frequently to nearshore locations where passive receiver arrays make transmitters more likely to be detected. And finally, length was not found to be an important consideration in the modeling design (Hightower et al. 2015), but because sturgeon adults are sexually dimorphic, length must be considered relative to the sex of the individual to understand its importance to survival estimates. Further, length of adult male and female Atlantic sturgeon is roughly correlated with age, allowing for a more detailed assessment of the adult segment of the population when accurate age data does not exist (Dunton et al. 2016).

The objective of this study was to use telemetry detection data to estimate annual $\phi$ for the York River Atlantic sturgeon population and then to compare that with other recent survival estimates relying on telemetry or longevity. Our modeling considers sex, sex-specific lengths, and sex-specific *p*. By monitoring passive telemetry coupled with mark–recapture methodology (Kahn et al. 2019) over 7 spawning seasons, we produced survival estimates that take into account tag loss or failure, sex-specific parameters, and the length of each individual.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The York River, Virginia, is located along the western edge of the Chesapeake Bay, north of the James River, south of the Rappahannock River. Fig. 1 shows detections of every fish in this study along the Atlantic coast; the dense receiver aggregation in Virginia is the York River, where these adults returned to spawn. The York River is formed by the confluence of the Pamunkey River, 150 km long, and the Mattaponi River, 166 km long. It is a 55 km long river that ranges from oligohaline at the confluence of its 2 main tributaries in West Point, Virginia, to polyhaline at its mouth just east of Gloucester Point, Virginia. Most of the lengths of both the Mattaponi and Pamunkey rivers are spring-fed and tidal freshwater.

### 2.2. Collection and detection methods

When collected and telemetered, all Atlantic sturgeon were in the adult size range (between 1250 and 2272 mm fork length [FL]; Grunwald et al. 2008, Kahn et al. 2019, Waldman et al. 2019) and in upstream freshwater locations on confirmed spawning grounds (Kahn et al. 2019, Hager et al. 2020); therefore, estimates produced are specific to York River adults. Average length of telemetered males was 1520 mm FL, ranging from 1218 to 1709 mm FL, while mean telemetered female length was 1887 mm FL, ranging from 1592 to 2188 mm FL. All capture and handling techniques followed ESA permit requirements and protocols (Kahn & Mohead 2010), and therefore results should be comparable to other studies on Atlantic sturgeon in the USA. Collections occurred from 2013 to 2016 using 23–36 cm stretch mesh gill nets during the spawning season from late July through mid-October (see Kahn et al. 2019). Individuals were sexed by applying pressure to the ventral surface, moving from anterior to posterior, ending at the vent, where males typically produce milt and females (on occasion) produce eggs. More often, gravid females did not produce gametes but were confirmed to be female when transmitters were implanted, as described in Kahn et al. (2021). Every captured fish received a passive integrated transponder (PIT) tag and had a genetic sample removed to identify the individual in the event the PIT tag or transmitter was lost. For 7 fish that were not sexually identified in the field, sex was determined through molecular analysis (N. Sard pers. comm.). When a fish was captured but not detected by the passive array, a metal detector was used to determine if the dysfunctional transmitter was lost (no metal) or failed (metal detected).

A total of 60 adult Atlantic sturgeon (36 males, 24 females) were implanted with internal Innovasea Systems V16P-4H, V16P-6x, or V16-6x acoustic telemetry transmitters, weighing no more than 17.3 g (see Table 2). These transmitters emitted a 69 kHz signal every 70–150 s and had a life span of a minimum of 6 yr (n = 11) and a maximum of 10 yr (n = 49). Surgeries were performed in accordance with Endangered Species Permit Number 19642, following the guidelines in Kahn & Mohead (2010). Transmitters were implanted into 3–4 cm incisions, made most often between the 3rd and 4th ventral scutes anterior to the anal fins. The incisions were closed using Vicryl® dissolvable sutures (Ethicon, Johnson and Johnson Surgical Technologies). Fish were released approximately 1.5 km from the capture site to avoid multiple captures in one day.

The implanted transmitters were passively detected from August 2013 through October 2019 by an array of Innovasea VR2W-69 kHz receiver stations within rivers, the Chesapeake Bay, and nearshore Atlantic

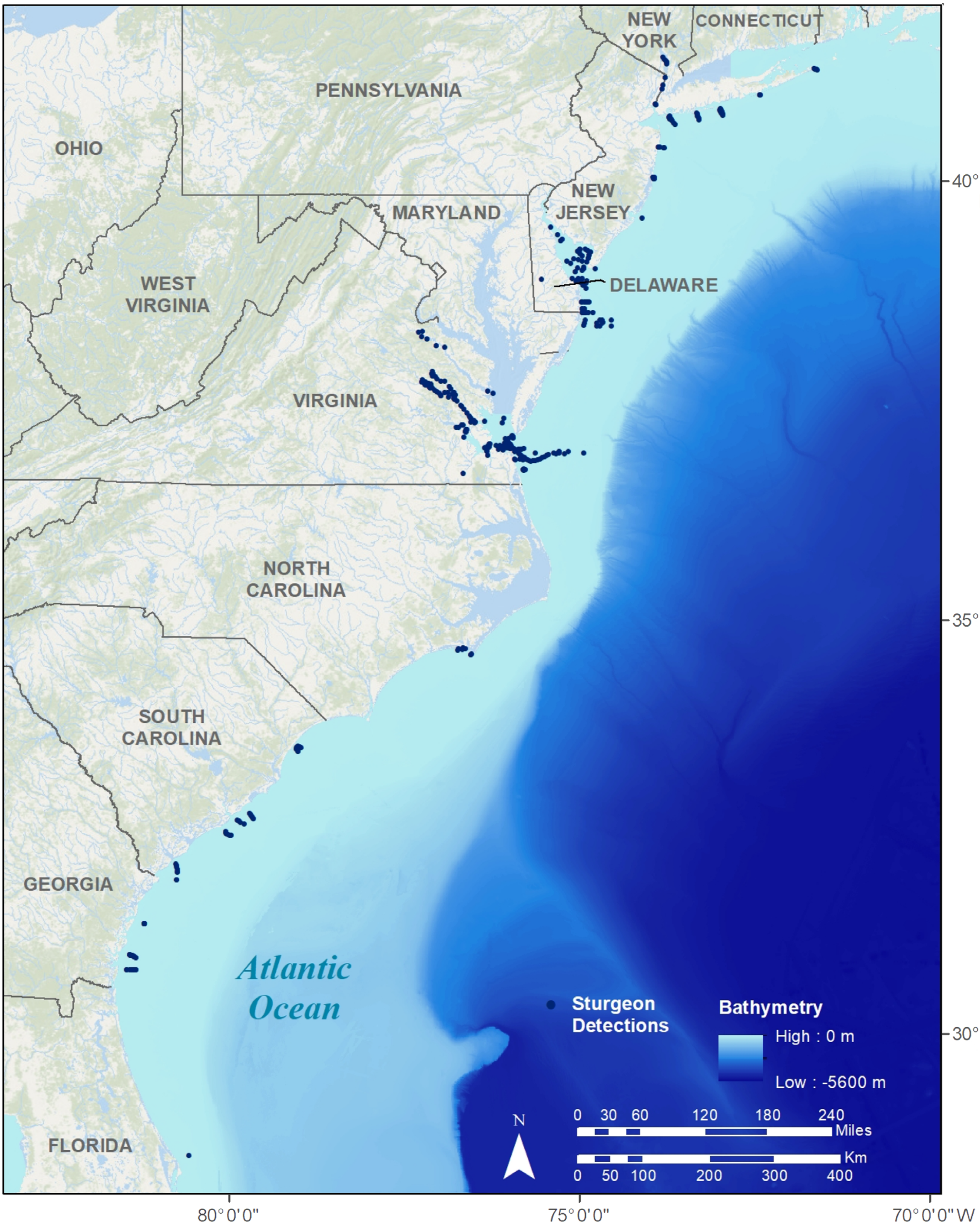

Fig. 1. Detections of adult York River Atlantic sturgeon, ranging from Florida to New York. All 100 receivers deployed and maintained as part of this study are shown

coastal waters and by Innovasea VR2AR receivers in offshore waters of the Atlantic Ocean. Detections were considered valid if they were picked up multiple times on the same receiver or at least a single time on adjacent receivers. A total of 100 receivers in the York River system, Chesapeake Bay, and Atlantic Ocean, maintained by Chesapeake Scientific and the US Department of the Navy, remained in place through January 2020. They were serviced and downloaded monthly. The VR2W receivers were downward-facing and deployed within 6 m of the surface while VR2AR receivers were deployed benthically and recovered with an acoustic release. Data sharing and collaboration with members of the Atlantic Cooperative Telemetry (ACT) Network and Florida Atlantic Coast Telemetry (FACT) Network provided detections of our transmitters from 2013 through 2019 between New York and Florida (Fig. 1). These shared detections account for less than 1% of the total detections in this study, and therefore variability in array deployment coastally should not significantly affect the modeling of survival probabilities.

### 2.3. Model use and selection

Initial trials evaluated a variety of models (CJS, Pradel survival and recruitment, and Program RELEASE) estimating survival. Because estimates were not substantially different, we elected to report the results from the CJS model, performed in Program MARK v.8.2 (White et al. 1978, Rexstad & Burnham 1991, White & Burnham 1999). The CJS model is commonly used for survival estimation, and the incorporation of acoustic telemetry detections into the CJS model for estimating survival was recently recommended for survival studies of sturgeon species (Colborne et al. 2021). The encounter histories were entered for each month of the study in a binary fashion, where a '1' meant the transmitter was detected in that time interval and a '0' meant the transmitter was not detected. Therefore, an encounter history of '1001' meant that during 4 consecutive months, the transmitter was detected in the first, not detected during the second or third, and again detected in the fourth month. When a fish was recaptured with a non-functional or missing transmitter, the data was modified to reflect that the non-detections were due to missing transmitter data and not a true non-detection, where '.' was used to reflect missing data. In those cases, an encounter history may appear to be '101.1' showing a detection, followed by a month not being detected, then detected, then not detected, but the following month it was captured while still not being detected, revealing that the previous and subsequent months' non-detections were likely due to transmitter loss or failure, at which point the data entry was modified to reflect that situation (see Schwarz & Arnason 2007). Following the encounter history, the sex of each individual was identified as a group effect, where a terminal code of '1 0;' corresponded to a male and '0 1;' was a female. Individual fish length (FL, in m) was incorporated using an individual covariate following these terminal codes.

### 2.4. Model assumptions

The assumptions to ensure unbiased estimates were (1) detection periods were instantaneous, (2) all individuals had the same probability of being detected in each sampling period, (3) transmitters used for this survival estimate were neither lost nor overlooked and are recorded correctly, (4) all emigration from the study area was permanent, (5) every telemetered animal had the same probability of survival each month, (6) the fate of each animal with respect to detection and survival probability was independent of the fate of any other animal, and (7) sturgeon behavior was normal and representative of other sturgeon following release (Lindberg & Rexstad 2002, Chao & Huggins 2005).

We addressed each assumption as well as possible. The first 3 assumptions all deal with ensuring $p$ does not bias results. In reality, while the assumption is that detection periods are instantaneous (#1), they are discrete and as long as possible while still satisfying the equal detection assumption (#2), which we ensured by isolating sex as a group variable since individuals of different sexes had different detection probabilities as a result of their divergent spawning periodicity (Hager et al. 2020). There was no way to know every instance of transmitter loss or failure (#3), though we recaptured 65% of our telemetered individuals (Table S1 in the Supplement at www.int-res.com/articles/suppl/b032p001_supp.pdf) and addressed known transmitter loss/failure in the model. Transmitter numbers were recorded correctly. By working with the ACT and FACT Networks, which provide coverage from Florida and the Bahamas north through Maine, we were able to share detection data with other researchers throughout the Atlantic sturgeon range, ensuring no fish ever emigrated from the detection area (#4; Fig. 1), though a number of fish were not detected during a month where they were presumed to be between the last detected location and the next detected location. All adults in this study should have an equal chance of survival (#5), though slight differences in migratory distances may subject some fish to different risks than others. The final 2 assumptions are likely addressed because each fish is unique (#6), and internally telemetered fish displayed similar behavior to externally telemetered fish not included in this study (#7).

### 2.5. CJS model

Cormack (1964), Jolly (1965), and Seber (1965) modified a capture–recapture model proposed by Darroch (1959) that accounted for survival and capture probability to estimate abundance. Apparent survival can be estimated using a known abundance (number of transmitters released) and detection probability as a proxy for capture probability. An estimate of apparent survival acknowledges that the model, relying on telemetry data, still assumes no marks are lost and therefore produces an estimate that appears to be a value of survival but is actually survival minus transmitter loss/failure.

The CJS model used here was developed in a stepwise process to conform to model assumptions and produce the most reliable estimates. First, we identified individuals with known failed or lost transmitters, which were any individuals not detected leaving the river after surgery or individuals recaptured without being detected within the array. For those fish, we modified the matrix to show non-detections as missing data and captures as detections (the '.' described above to address assumption #3). The discrete time periods for the matrix were divided into 75 mo between August 2013 and October 2019; $\phi$ and $p$ were calculated for the intervals between each month. Individual transmitters were assigned to one of 2 groups: male or female, and each individual's length at first capture was recorded as a covariate. The assessed matrix was constant for all model variables tested.

Using Program MARK's parameter index matrices, each monthly period could be coded to represent unique months or grouped to evaluate variable time periods of $\phi$ and $p$ corresponding to monthly (1, 2, 3, …), bi-monthly (1, 1, 2, 2, …), seasonal periods (1, 1, 1, 2, 2, 2, …; winter = December, January, and February and so on), pooled seasons (1, 2, 3, 4, 1, 2, …) or months (12 time parameters), or constant as has been considered by other researchers (Rudd et al. 2014, Hightower et al. 2015). Therefore, there were just over 200 possible models from the 10 different model combinations (5 time bins, considering both sexes; 5 × 2) for $\phi$ and $p$ and then either incorporating a length covariate or not for $\phi$ or $p$ by using the design function in Program MARK. Additionally, models were assessed that held $\phi$ and $p$ as constants. The objective of a good model is to identify the most parsimonious option that includes sufficient parameters to meaningfully fit the data (Browne & Cudeck 1993). Each of these models was assessed for goodness of fit using Akaike's information criterion corrected for small sample sizes (AICc; Akaike 1973, 1974). The model likelihood with the lowest AICc value was considered the optimal model, but only the 10 lowest AICc scores are presented in the results. We relied on the estimation of median c-hat in Program MARK to ensure the data were not over-dispersed. Using the optimal model, Program MARK produced point estimates of both $\phi$ and $p$ and 95% confidence intervals for each group at each discrete time period (Table S2).

Finally, for purposes of comparing results with other sturgeon survival estimates, we performed a series of sensitivity analyses. We analyzed a situation without identifying tag loss or failure but did consider differences in $p$ between sexes: the identical model but without using any coded '.' time periods, so known failed transmitters would be assessed as '0' and appear to be mortalities. Then we analyzed a model that did not identify tag loss or differences in $p$ between sexes: $\phi$ monthly and $p$ monthly, also replacing '.' with '0', which would be the same model as used in recent Atlantic sturgeon survival estimates (Hightower et al. 2015, ASMFC 2017). We then analyzed a situation with known tag loss or failure, but without considering differences in $p$ between sexes: a model containing '.'s but with no sex consideration (a higher AICc than the optimal model, but the same underlying data).

## 3. RESULTS

The 60 transmitters used in this study were detected 2 984 864 times along the Atlantic coast, with 2 970 773 detections occurring on the array we maintained in Virginia waters (99.5%). Of those, 2 295 108 (76.9%) detections were in the York River system during the fall spawning season. Each male was detected on average 619.7 times $\text{mo}^{-1}$ while each female was detected 328.1 times $\text{mo}^{-1}$. Acoustic detections were seasonally variable, with peak proportions of deployed transmitters detected in the spring and fall (Fig. 2). Females were typically detected further from the York River than males.

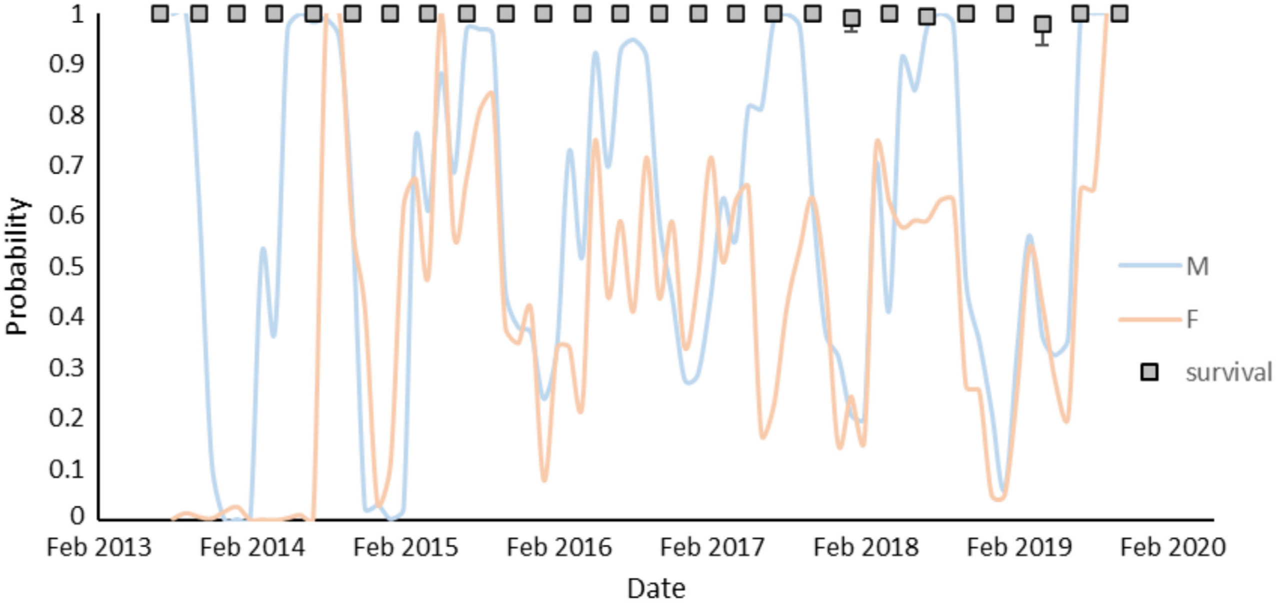

Fig. 2. Proportion of male and female telemetered Atlantic sturgeon detected each month between August 2013 and October 2019, with corresponding York River apparent seasonal survival (model: ϕ [season], *p* [monthly × sex] including a length covariate) and 95 % confidence intervals

After assessing 72 AICc values, the most parsimonious model relied on seasonal intervals to estimate ϕ, monthly intervals for each sex for optimal representation of *p*, and an individual covariate that accounted for the length of each fish. The top 10 full models suggest survival is best calculated either bimonthly or seasonally but that *p* is consistently reliant on sex (Table 2). Average seasonal survival for the York River population was 0.993 (0.972–0.998) in the winter, 0.981 (0.955–0.992) in the spring, 0.994 (0.985–0.997) in the summer, and 0.999 (0.999–0.999) in the fall, which can be extrapolated to an annual ϕ rate of 0.992 (0.979–0.997).

The comparison model of ϕ (monthly), *p* (monthly) with no group effects or length covariate and including known lost or failed transmitters estimated annual ϕ to be 0.950 (0.929–0.965). The same model, but incorporating '.' for known failed or lost transmitters assesses the impact of not including sex as a component of the survival estimate. In that case, estimated annual ϕ was 0.974 (0.964–0.981). These data are displayed in Table 3, also showing the results of the preferred model if failed transmitters or differences in *p* between sexes are not considered. Apparent mortality in each model was primarily affected by time of last detection within the array.

Table 2. The 10 best-fitting models from 202 analyzed. Atlantic sturgeon survival (ϕ) and detection probability (*p*) is shown for each model along with the presence (Y) or absence (N) of a covariate. Parameters and estimate of median c-hat also shown for each model

| ϕ | *p* | Covariate | AICc | ΔAICc | Parameters | c-hat |
|---|---|---|---|---|---|---|
| Seasonal | Monthly × sex | Y | 3088.414 | 0 | 174 | 1.0 |
| Bimonthly | Monthly × sex | Y | 3116.965 | 28.5508 | 186 | 1.0 |
| Seasonal | Monthly | Y | 3138.436 | 50.0221 | 100 | 1.0 |
| Seasonal × sex | Monthly × sex | Y | 3147.886 | 59.4724 | 200 | 1.0 |
| Seasonal | Bimonthly × sex | Y | 3170.261 | 81.8472 | 102 | 1.0 |
| Bimonthly | Bimonthly × sex | Y | 3194.973 | 106.5593 | 114 | 1.0 |
| Seasonal × sex | Bimonthly × sex | Y | 3222.816 | 134.4017 | 128 | 1.0 |
| Seasonal | Monthly × sex | N | 3260.35 | 171.9363 | 174 | 1.0 |
| Seasonal | Bimonthly × sex | N | 3269.533 | 181.1194 | 102 | 1.0 |
| Monthly | Bimonthly × sex | Y | 3271.866 | 183.4518 | 150 | 1.0 |

Table 3. Apparent annual survival (ϕ) estimates of the entire York River Atlantic sturgeon population, depicted as preferred model (top row) followed by other models for comparison. The other models were the preferred model without correcting failed transmitters (2nd row), preferred model without considering differences in detection probability (*p*) but including length relative to sex (3rd row), model design of previous Atlantic sturgeon survival estimates correcting for failed transmitters but not considering length relative to sex (4th row), and model design of previous Atlantic sturgeon survival estimates without correcting for failed transmitters or length (last row). The use of a covariate for length is noted as Y (yes) or N (no). Missing data code: known missing data entered in the matrix as '.' or '0'

| Model | Covariate | Missing data code | Apparent annual survival | Lower 95 % CI | Upper 95 % CI |
|---|---|---|---|---|---|
| ϕ Seasonal, *p* Monthly × sex | Y | . | 0.991893 | 0.978743 | 0.996779 |
| ϕ Seasonal, *p* Monthly × sex | Y | 0 | 0.984814 | 0.890069 | 0.994451 |
| ϕ Seasonal, *p* Monthly | Y | . | 0.991766 | 0.931831 | 0.998929 |
| ϕ Monthly, *p* Monthly | N | . | 0.973611 | 0.963706 | 0.980524 |
| ϕ Monthly, *p* Monthly | N | 0 | 0.950379 | 0.928911 | 0.964923 |

In total, 39 of the 60 telemetered sturgeon were recaptured (see Table S1). There were 8 transmitters that ceased being detected over the 7 yr period (13.3%), and 5 fish (13-010, 14-035, 14-042, 16-025, and 16-040) were not detected leaving the river either due to transmitter rejection, transmitter discharge during spawning, transmitter failure, or fish death. Fish 13-015, 14-017, 14-030, 14-035, and 14-042 (not detected leaving the river) were recaptured alive but without functional transmitters (5 of 39, 12.8%). One fish (13-015) was given a new transmitter upon recapture. Three others (14-017, 14-030, and 14-035, 7.7%) had metal detected in their abdomens, confirming transmitter failure and retention. One of those failures occurred after less than 24 h, and all failures occurred within 21 mo of implantation.

## 4. DISCUSSION

Telemetry can be used to estimate survival rates of wide-ranging animals. Telemetry-derived survival estimates rely on detections as a proxy for survival and therefore require assumptions relating to *p* (Ricker 1975, Krebs 1999, Lindberg & Rexstad 2002, Chao & Huggins 2005). Transmitter failure can unknowingly negatively bias survival estimates. Siberian sturgeon *Acipenser baerii* were observed extruding 32% of Innovasea V16 transmitters in a laboratory setting within 12 wk of implantation, either through the surgical site or through the vent (Boone et al. 2013). Shortnose sturgeon *A. brevirostrum* transmitter expulsion rates have been observed between 6.7 and 21.4% (Kieffer & Kynard 2012) to as high as 75% (Crossman et al. 2013). Gulf sturgeon *A. oxyrinchus desotoi* are suspected to have shed tags, which was responsible for potential negative biases in survival estimates (Rudd et al. 2014). Atlantic sturgeon have been reported to shed 0% (Crossman et al. 2013), 6.8% (Secor et al. 2022), and up to 12.8% (this study) of their transmitters following tagging. Other studies on other fish families have estimated transmitter failure rates ranging from 5 to 45% (Cowen 2005, Cowen & Schwarz 2005, Rechisky & Welch 2010). In this study, 5 transmitters failed to leave the system (8.3% of 60 implanted) but 2 of those 5 fish that appeared to have died without leaving the system were later recaptured alive through congruent mark–recapture research (Kahn et al. 2019). We confirmed 5 transmitter losses or failures (12.8% of 39 recaptured fish). Other survival estimates that did not recapture telemetered individuals to verify transmitter function must assume their 'estimates of apparent survival have negligible bias due to permanent emigration or transmitter failure' (Hightower et al. 2015, p. 518).

Recapture rates (65.0%; 39 of 60) achieved in this study were likely only possible when a long-running mark–recapture effort is conducted in a small system such as the York River. Using only the individuals that we know had failed transmitters or had lost them, and assuming the other non-detections were mortalities, we see that being unable to account for lost or failed transmitters had more of a negative bias on our survival estimates than being unable to account for differences in *p* between sexes (Table 3). Heterogeneity in *p* has been modeled and shown to be the primary source of bias in survival estimates (Pledger & Efford 1998, Schwarz & Arnason 2007). Given that the transmitter loss rates presented above show sturgeon transmitter loss/failure to be within the range observed for other species, it is interesting that our sensitivity analyses suggested transmitter loss created the greatest bias, though the effects of each source of bias were similar. Our results suggested survival estimates can be roughly equally and additively affected by failing to account for differences in *p* between sexes and transmitter loss/failure (Table 3). While transmitter loss from sturgeon species has been well documented and no technology functions without occasional premature failure, how to account for it in telemetry-based studies needs to be resolved.

Detection probability was not only affected by transmitter loss or failure. Receiver placement and environmental conditions can influence *p* (Mathies et al. 2014). Most studies of aquatic species, including this one, focus on placing receivers in riverine and estuarine habitats (Kocik et al. 2009, Melnychuk 2009, Welch et al. 2009, Nelson et al. 2013). Many of the receivers managed by this study's authors as well as those in the ACT and FACT Networks were predominantly inshore. Receivers are typically placed to maximize detections or in specific habitat types, but individuals remaining further from shore or in poorly monitored locations are less likely to be detected. When in the Chesapeake Bay array, there was little difference in detection likelihood or movement rates between males and females moving towards or away from spawning habitat. Females generally spend more time undetected, but without better receiver coverage, it is impossible to say whether they remain offshore during non-spawning periods or travel to estuaries with poor receiver coverage. Anadromous York River Atlantic sturgeon males spawn approximately once every 1.13 yr while females spawn once every 2.19 yr (Hager et al. 2020), leaving more time for females to travel further from their natal rivers. For instance, 3 different females spent 25, 18, and 17 mo between detections, while the longest any male went without being detected was 8 mo. This caused differences in *p* that needed to be addressed by grouping our matrices by sex, and we suspect this detection difference would be similar for other adult Atlantic sturgeon populations, particularly farther north where spawning periodicity is more protracted (Dadswell et al. 2017).

Apparent mortalities for this York River population typically occur during migrations into (May and June) or out of (November and December) Chesapeake Bay. Four of the suspected 5 mortalities were last detected near the mouth of the Chesapeake Bay in an area of heavy vessel traffic and seasonal fishing effort, which may indicate an area of increased risk to this endangered species and could be an area of emphasis for management actions in the future to improve survival. This part of the Chesapeake Bay was previously noted as an area of concern (ASMFC 2007). Appropriate conservation actions could be timing and area closures to limit vessel traffic or intercept fishing gear during migratory periods.

In this study, we assessed each model variation with a covariate for the length of each individual as well as without any consideration of length. Results from our modeling suggest that Atlantic sturgeon survival is associated with fish length (Table 2). This contradicts the findings reported in Hightower et al. (2015), but the difference may be because that study focused on both sub-adults and adults or because it did not differentiate sizes by their sexes. For the telemetered fish in our study, there was very little overlap in size ranges between sexes, with males averaging 1520 mm FL and females averaging 1887 mm FL. The 5 suspected mortalities all exceeded the mean lengths for their sexes. Fish 14-024, 14-031, 14-032, and 14-050 were 1581, 1575, 1702, and 1715 mm FL males, respectively and 14-012 was a 2057 mm FL female (Table S1). It is possible that longer fish of each sex could have been older and near the end of their lives. Larger fish also have a greater likelihood than smaller fish of being hit when passing through a propeller or encountering a dredge, supporting our hypothesis for causes of mortality (Brown & Murphy 2010, Hondorp et al. 2017, Demetras et al. 2020). Males spawn nearly twice as often and therefore encounter vessels and commercial nets twice as often, which may explain why more males were lost despite being smaller than almost all females.

This study produced higher survival rates than previous estimates for Atlantic sturgeon. Using longevity to estimate survival (Table 1) produced a range of survival estimates between 86 and 93.5 % (Hoenig 1983). A recent Atlantic sturgeon stock assessment (ASMFC 2017) used a CJS model to calculate finite $\phi$ rates for each US DPS of 74.0, 91.4, 87.8, 77.8, and 86.0 % for the Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic DPSs, respectively. Hightower et al. (2015) estimated $\phi$ rates of approximately 86 % annually in the southeast USA. Melnychuk et al. (2017) estimated $\phi$ of subadult Atlantic sturgeon captured and telemetered along Long Island, New York, to be approximately 88 %. Because length of fish in this study appears to be a significant influence on probability of mortality, differences in survival rates between other studies and this one could be due to monitoring different-sized fish, which are facing different threats at those times of their lives. Each of these previous studies assumed no transmitter loss, but none validated that assumption (Hightower et al. 2015, ASMFC 2017, Melnychuk et al. 2017). Furthermore, in our study, most transmitters that were lost or failed did so within the first 9 mo of tagging and all were lost or failed within the first 21 mo, which is similar to that observed by Boone et al. (2013). While this study spanned 7 yr, most studies, even on long-lived species, are no more than 4 yr (Hightower et al. 2015, Melnychuk et al. 2017). The effect of not being able to account for tag loss would be even greater because transmitter losses generally occur early in a study and most studies are of relatively short duration.

The point estimate and 95% confidence limits of York River sturgeon survival suggest a differently shaped survival curve than is typically used to model fish. Our survival estimates show strong agreement with those presented for lake sturgeon *A. fulvescens* when survival estimates can continue monitoring long-lived species for years after being tagged (Colborne et al. 2021). Other long-lived, late-maturing species have stage-variable survival (Brault & Caswell 1993, Fujiwara & Caswell 2001, Lee et al. 2013, Zedrosser et al. 2013, Lockwood & Mann 2019, Verborgh et al. 2020, Colborne et al. 2021), as has been suggested for Atlantic sturgeon (Kahnle et al. 2007). Mammals exhibit relatively high first-year mortality, with improved survival as juveniles, peak survival as adults, and then lower survival post-senescence (Brault & Caswell 1993). We believe Atlantic sturgeon demography should be modeled similarly because larval sturgeon experience high mortality, followed by a refuge size from indigenous predators as juveniles grow in freshwater, followed by another likely period of reduced survival when sub-adult sturgeon first move offshore, but again a refuge size as they outgrow most natural predators as adults (Bain 1997, Kahnle et al. 2007). To date, there is no evidence of senescence in sturgeon or reason to predict an age when mortality probability would increase. We did not attempt to estimate survival by ages, but in the Hudson River, the maximum age of observed spawning males was 19–31 yr, while in females it was 36–64 yr (Van Eenennaam et al. 1996, Bain 1997, Kahnle et al. 2007). The difference in ages suggests sex-related differentiation in longevity that may not be seen during a 7 yr study of survival rates in a species that lives for over 60 yr. However, it was noteworthy that 80% of suspected mortalities in this study were males, and a larger sample size or longer monitoring period may provide insight into sex-differentiated survival. Considering sturgeon survival using age-specific or stage-specific survival parameters as has been done for other species with similar life histories (Pollock 1991, Loison et al. 1999, Pletcher 1999) with considerations of behaviors that make populations genetically unique would assist managers in understanding the consequences of human-mediated mortalities at different life stages or affecting different populations.

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