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Abstract

Prompted by concerns about the status of Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*, in 2012 the National Oceanic and Atmospheric Administration listed one distinct population segment (DPS) as threatened (Gulf of Maine) and listed the remaining four DPSs as endangered (New York Bight, Chesapeake Bay, Carolina, and South Atlantic). To provide information for recovery planning, we estimated the survival of subadult and adult Atlantic Sturgeon in two river basins within the Carolina DPS (Roanoke and Cape Fear rivers, North Carolina) and two basins within the South Atlantic DPS (Ashepoo–Combahee–Edisto rivers [ACE], South Carolina; Altamaha River, Georgia). Estimated detection probability varied strongly by season but was similar among river basins, likely reflecting a winter migration into marine waters with minimal receiver coverage. Apparent monthly survival was very high and precisely estimated for the Roanoke River (0.985; 95% credible interval [CI] = 0.970–0.995), Cape Fear River (0.979; 95% CI = 0.971–0.986), ACE (0.989; 95% CI = 0.979–0.993), and Altamaha River (0.985; 95% CI = 0.973–0.994) basins. A pooled estimate for 87 adults from all four basins was 0.988 (95% CI = 0.982–0.992). The monthly rates implied annual apparent survival rates of 0.839 (Roanoke River basin), 0.778 (Cape Fear River basin), 0.871 (ACE basin), and 0.842 (Altamaha River basin); the pooled estimate for adults was 0.860. Our estimated survival rates were similar to other recent estimates for Atlantic Sturgeon but lower than recent estimates for several populations of Gulf Sturgeon *A. oxyrinchus desotoi*. Recovery of Atlantic Sturgeon in these southeastern rivers will occur more quickly if survival can be increased to a level that is consistent with published estimates of true natural mortality (0.03–0.07; annual survival ≥ 0.93).

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Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* occur along the East Coast of North America, with known spawning populations from the St. Lawrence River, Quebec, to the Altamaha River or Satilla River, Georgia (Smith 1985; Wirgin et al. 2000, 2007). Historically, this subspecies was an important component of coastal ecosystems and supported commercial fisheries, but it has declined dramatically in abundance due to a variety of factors, including overfishing and habitat loss (Smith 1985). The National Oceanic and Atmospheric Administration conducted a status review of the subspecies and classified it into five distinct population segments (DPSs): Gulf of Maine, New York Bight, Chesapeake Bay, Carolina, and South Atlantic (Atlantic Sturgeon Status Review Team 2007). In 2012, the Gulf of Maine DPS was listed as threatened and the remaining DPSs were listed as endangered under the Endangered Species Act of 1973 (NOAA 2012a, 2012b). Issues leading to the designation of southeastern U.S. DPSs (Carolina and South Atlantic) as endangered included low abundance and concerns about survival (e.g., commercial bycatch and poor habitat quality; NOAA 2012a). Reliable information on survival, including temporal and spatial variation, is important for monitoring Atlantic Sturgeon recovery and restoring populations within each DPS.

Relatively little is known about the survival of Atlantic Sturgeon, particularly those belonging to southeastern U.S. populations. Peterson et al. (2008) obtained annual survival estimates of 0.79–0.83 for adult Atlantic Sturgeon in the Altamaha River based on a catch curve analysis of age data. Apparent annual survival of juvenile Atlantic Sturgeon in the Altamaha River was low (0.03–0.34), but true survival was unknown due to the confounding effect of permanent emigration (Schueller and Peterson 2010). Kahnle et al. (2007) used length and age data for Hudson River Atlantic Sturgeon and obtained survival estimates of 0.76 for males (ages 15–31) and 0.92 for females (ages 22–40). Pine et al. (2001) developed population models for the Gulf Sturgeon *A. oxyrinchus desotoi*; based on capture–recapture data and prior studies, they used annual survival estimates of 0.75 for ages 1–3 and 0.84 for ages 4–25. Most recently, annual survival of Gulf Sturgeon was estimated to be 0.92 or higher in three of four geographic areas (Rudd et al. 2014).

In the present study, we used telemetry to estimate the survival rates of Atlantic Sturgeon within several southeastern U.S. rivers. Similar approaches have been used to estimate survival rates for Green Sturgeon *A. medirostris* along the Pacific coast of North America and for Gulf Sturgeon in the Gulf of Mexico and tributary rivers (Lindley et al. 2008; Rudd et al. 2014). Adult and subadult survival rates are key population parameters, so the availability of comparable but independent estimates from multiple rivers should be very useful in the planning of Atlantic Sturgeon recovery efforts. Our methods should also be useful for application to other species with telemetry detections from marine and riverine receiver arrays.

METHODS

Atlantic Sturgeon were captured primarily with set gill nets, and acoustic transmitters were surgically implanted into the fish by using methods similar to those of Fox et al. (2000). Transmitters were VEMCO V16-4H acoustic tags (nominal life span = 1,157 d) or VEMCO V16-6H tags (nominal life span = 1,633 d). The transmitters were detected by using fixed arrays of VEMCO VR2W submersible receivers that were deployed in riverine and estuarine waters of four basins: the Roanoke River, North Carolina; Cape Fear River, North Carolina; Ashepoo–Combahee–Edisto rivers (ACE), South Carolina; and Altamaha River, Georgia. Our transmitters also had the potential to be detected at other receiver arrays deployed from Florida to Maine by 35 research groups participating in the Atlantic Coast Telemetry Network (www.theactnetwork.com) based at Delaware State University.

We analyzed data separately for each basin to detect spatial variation in survival, and we also produced a pooled survival estimate for adult-sized Atlantic Sturgeon (>150 cm TL at tagging; Bain 1997). Each analysis was based on a capture history matrix with rows for individual fish and columns for months. The matrix contained a zero when no detections occurred in a particular month and a 1 if there were one or more detections. To minimize concerns about mortality due to capture, handling, and tag implantation, the analysis period for each individual began 1 month after tagging. We censored a few individuals at the expected end of transmitter battery life. The period of analysis was 46 months (October 2010–July 2014) for the Roanoke River basin (fish tagged in the Roanoke River and Albemarle Sound), 39 months (May 2011–July 2014) for the Cape Fear River basin, 47 months (September 2010–July 2014) for the ACE basin and for the pooled analysis, and 34 months (May 2011–February 2014) for the Altamaha River basin. An additional three fish from the Roanoke River basin, four fish from the Altamaha River basin, and seven fish from the ACE basin were excluded from our analysis because they either were not detected during our period of analysis or were detected only during a single period after tagging.

Capture histories were analyzed using a Cormack–Jolly–Seber model, which is an open capture–recapture model that provides estimates of detection probability (probability that a live fish will be detected on one or more receivers) and survival (Kéry and Schaub 2012). Parameter estimates were obtained through a Bayesian state-space modeling framework (Kéry and Schaub 2012) by using OpenBUGS software (Spiegelhalter et al. 2010). The Cormack–Jolly–Seber model provides estimates of apparent (or "local") survival—that is, a fish's probability of surviving and being in the study area (in this instance, the areas covered by receivers; Kéry and Schaub 2012). Given the short (monthly) interval for detections relative to the period of analysis, we assumed that the bias in estimated survival due to the timing of tagging or detections was

negligible. To examine variation in survival among individuals, we also calculated a simple indicator of survival for Atlantic Sturgeon in the Roanoke River basin: the range of months from release to final detection, expressed as a proportion of the number of possible months (from release to the end of battery life or to the end of the study).

Selection of the best model is a difficult and subjective process, and inferences are conditional on the model that is chosen (Link and Barker 2010; Kéry and Schaub 2012). Preliminary modeling indicated (1) little variation in apparent survival among periods but (2) strong seasonality in detection probability. Therefore, our base model for each basin or for the pooled analysis was defined as including time-dependent detection probability and constant survival. Our alternative model added fish TL as a covariate for survival. We chose the preferred model based on whether the 95% credible interval (CI) for the TL slope parameter contained zero. Following Kéry and Schaub (2012), we used uninformative prior distributions for mean survival (uniform, 0–1) and the logit-scale slope for the TL covariate (normal, mean = 0, variance = 1,000; bounds = −10 to 10). Example OpenBUGS code for modeling Atlantic Sturgeon in the Roanoke River basin is provided in the Appendix.

An Atlantic Sturgeon stock-rebuilding target of at least 20 protected mature age-classes for each spawning stock was established by the Atlantic States Marine Fisheries Commission (ASMFC 1990). The equilibrium production of mature females given our (combined-sex) estimates of annual survival was compared with production at an annual survival rate of 0.93 (based on an assumed rate of natural mortality $M = 0.07$; Kahnle et al. 2007). Maturation was assumed to follow the schedule reported by Kahnle et al. (2007). We also estimated the probability that Atlantic Sturgeon in our study rivers had annual survival rates greater than 0.93 (step function in the Appendix), which is a potential target level based on the M of 0.07 (Kahnle et al. 2007).

RESULTS

Sample sizes, the size range of tagged fish, and the analysis period varied among river basins (Table 1; Figure 1). Detection probability varied strongly among seasons, but the patterns were quite similar among river basins (Figure 2). Detection probability was generally low in December–February but rebounded sharply by April. Estimates of detection probability for April–October were relatively high in most cases, although there were occasional low values during summer (e.g., Roanoke River, ACE, and Altamaha River basins in July 2011). Mean monthly detection probability values were relatively similar among basins and were unaffected by inclusion of the TL covariate for survival (Table 1).

Mean monthly estimates of apparent survival were high, precise, and similar among basins (Table 1). The monthly values implied annual apparent survival rates of 0.839 (95% CI = 0.692–0.938) for the Roanoke River basin, 0.778 (95% CI = 0.699–0.846) for the Cape Fear River basin, 0.871 (95%

TABLE 1. Cormack–Jolly–Seber models fitted to capture history matrices for Atlantic Sturgeon that were tagged with acoustic transmitters in four river basins (Roanoke River, Cape Fear River, Ashepoo–Combahee–Edisto rivers [ACE], and Altamaha River) and for all adult-sized individuals (>150 cm TL at tagging) pooled across basins. Preferred models (shown in bold italics) were chosen based on whether the 95% credible interval (CI) for the slope of the TL effect on survival contained zero. Reported estimates are medians. Subadults (<150 cm TL at tagging) comprised 65% of tagged fish in the Roanoke River basin, 93% in the Cape Fear River basin, 12% in the ACE basin, and 5% in the Altamaha River basin (log$L$ = log likelihood).

Basin	Number tagged	TL (cm) range	Detection probability	Survival rate	Log$L$	Mean detection probability	Monthly survival Estimate	Monthly survival 95% CI	Fish TL slope Estimate	Fish TL slope 95% CI
Roanoke	20	72–178	*Time*	*Constant*	*−238.7*	*0.498*	*0.985*	*0.970–0.995*		
			Time	Size dependent	−240.2	0.498	0.988	0.972–0.998	0.02	−0.00 to 0.07
Cape Fear	81	67–175	*Time*	*Constant*	*−920.0*	*0.496*	*0.979*	*0.971–0.986*		
			Time	Size dependent	−922.5	0.495	0.980	0.972–0.989	−0.01	−0.02 to 0.01
ACE	42	141–202	*Time*	*Constant*	*−676.0*	*0.477*	*0.989*	*0.979–0.993*		
			Time	Size dependent	−677.0	0.477	0.989	0.982–0.994	−0.02	−0.06 to 0.01
Altamaha	41	144–231	*Time*	*Constant*	*−442.2*	*0.525*	*0.985*	*0.973–0.994*		
			Time	Size dependent	−444.7	0.525	0.988	0.977–0.995	−0.02	−0.05 to 0.02
Pooled	87	150–231	*Time*	*Constant*	*−1,252.5*	*0.464*	*0.988*	*0.982–0.992*		
			Time	Size dependent	−1,253.5	0.464	0.988	0.982–0.992	−0.00	−0.00 to 0.00
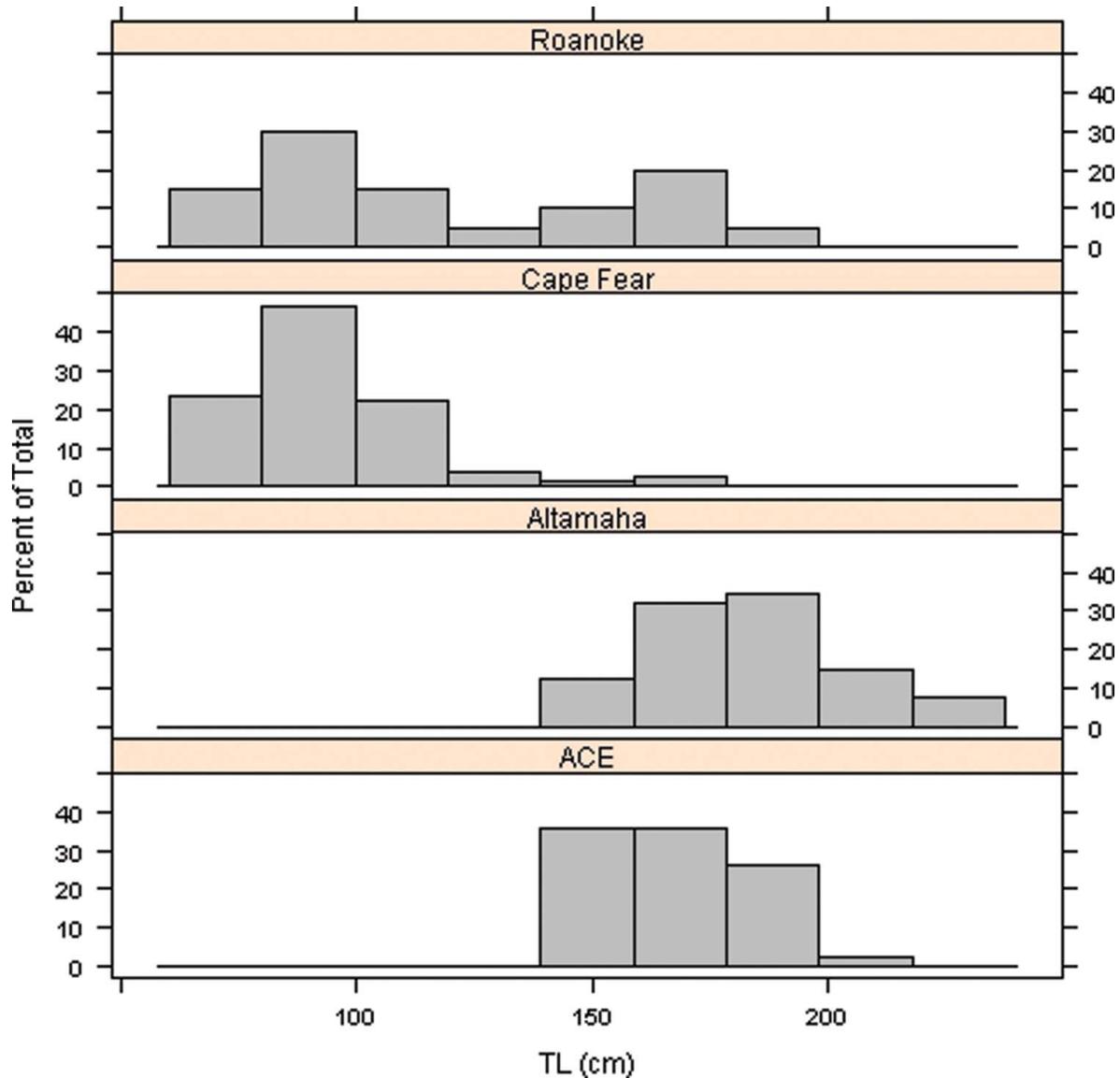
Figure 1.   Length frequency distribution (TL, cm) of Atlantic Sturgeon that were tagged with acoustic transmitters in four basins (2010–2014): Roanoke River ($N = 20$), Cape Fear River ($N = 81$), Ashepoo–Combahee–Edisto rivers (ACE; $N = 42$), and Altamaha River ($N = 41$).

CI = 0.796–0.928) for the ACE basin, and 0.842 (95% CI = 0.722–0.932) for the Altamaha River basin. The pooled estimate of annual apparent survival for adults was 0.860 (95% CI = 0.799–0.909). The probability that annual survival was greater than 0.93 ranged from 5.0×10^{-5} to 0.04 for the four basins and was 0.002 for the pooled analysis. A size effect (TL covariate) was not evident for any of the four basins or for the pooled model, although the lower bound of the 95% CI for the Roanoke River basin was close to zero. This result was probably due to four of the smaller Roanoke River fish (78–121 cm TL), which were detected for short periods relative to the total possible number of months at risk (Figure 3). Those four fish were last seen in April, August, September, and November, so

there was no obvious pattern in their timing of apparent mortality.

DISCUSSION

Tagging of Atlantic Sturgeon in multiple rivers and monitoring the fish through a collaborative coastwide network of receiver arrays proved to be an effective approach for investigating apparent survival. Seasonal patterns of detection were quite similar among river basins. The low detection probabilities in winter likely reflected an offshore migration to areas with low receiver coverage. The timing was consistent with previous work conducted in two South Carolina rivers by
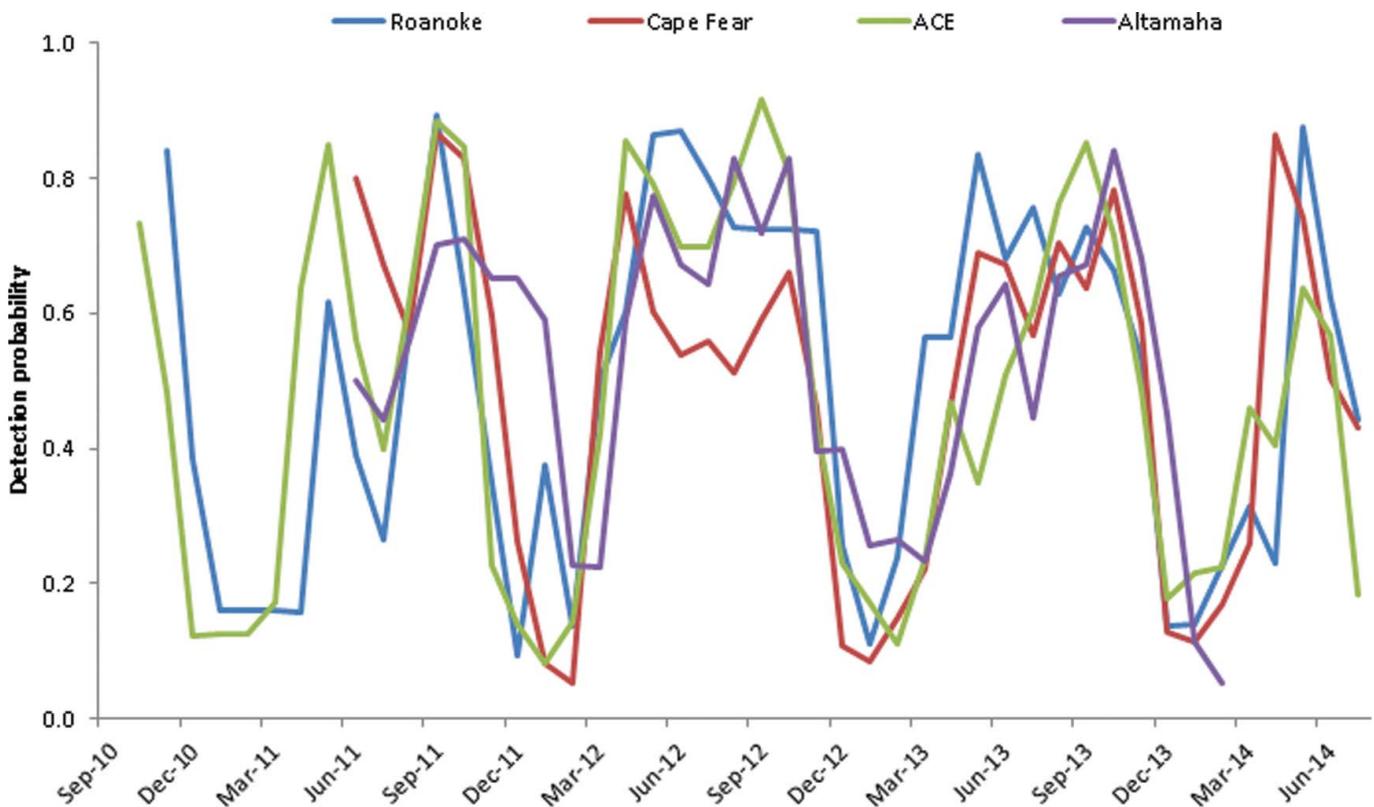
FIGURE 2.   Estimated detection probability (2010–2014) for Atlantic Sturgeon that were tagged with acoustic transmitters in four river basins (Roanoke River, Cape Fear River, Ashepoo–Combahee–Edisto rivers [ACE], and Altamaha River); values are based on the preferred model for each basin (see Table 1).

Collins et al. (2000b), who documented an ocean migration of Atlantic Sturgeon in October or November and a return to estuarine or riverine waters in approximately March. During the current study, Roanoke River Atlantic Sturgeon migrated into marine waters during November or December and returned to Albemarle Sound and the Roanoke River during late spring or summer (Flowers 2015). Laney et al. (2007) conducted winter trawl surveys of the North Carolina coast and showed that shallow, nearshore marine waters served as important overwintering habitat for Atlantic Sturgeon. The North Carolina coastal section represents one of several gaps in East Coast receiver coverage (Flowers 2015) that could account for our low number of winter detections. Furthermore, many receiver arrays to the north of Chesapeake Bay are removed during winter, so there were periods in which there was no receiver coverage of northern ocean waters. Another factor contributing to the low number of winter detections may have been a lack of movement. Riverine studies have shown that Shortnose Sturgeon *A. brevirostrum* are highly aggregated and exhibit little movement during winter (O'Herron et al. 1993; Fernandes et al. 2010). Our estimates of apparent survival are unlikely to have been biased by the low detection probabilities in winter, because the transmitters have long life spans and the status of a tagged individual is made clear upon its re-detection in spring or summer.

Monthly estimates of mean apparent survival were 0.979–0.989 for the four river basins, and the pooled adult estimate was 0.988. True survival in this case may be quite similar to apparent survival given the very high survival estimates and the widespread receiver coverage. Atlantic Sturgeon undoubtedly occupy areas without receiver coverage at times, but this temporary emigration should not have biased our long-term survival estimates (Williams et al. 2001). Other potential biases in our estimated survival rates could include transmitter failure or expulsion. We are unaware of any studies indicating that transmitter failure is likely. Tank studies of sturgeons have generally shown that tag expulsion is unlikely (Collins et al. 2002; Neely et al. 2009; although see Boone et al. 2013).

Assuming that our estimates of apparent survival have negligible bias due to permanent emigration or transmitter failure, we obtained annual survival estimates of 0.839 for the Roanoke River basin, 0.778 for the Cape Fear River basin, 0.871 for the ACE basin, and 0.842 for the Altamaha River basin, and we generated a pooled estimate of 0.860 for adults. Given the overlapping marine distributions and shared threats among populations and DPSs, the pooled estimate of adult survival should be useful for large-scale recovery planning (Dunton et al. 2012; Waldman et al. 2013; Wirgin et al. 2015a, 2015b). The survival estimate for the ACE basin is probably low, as nine fish that were not detected during the final study
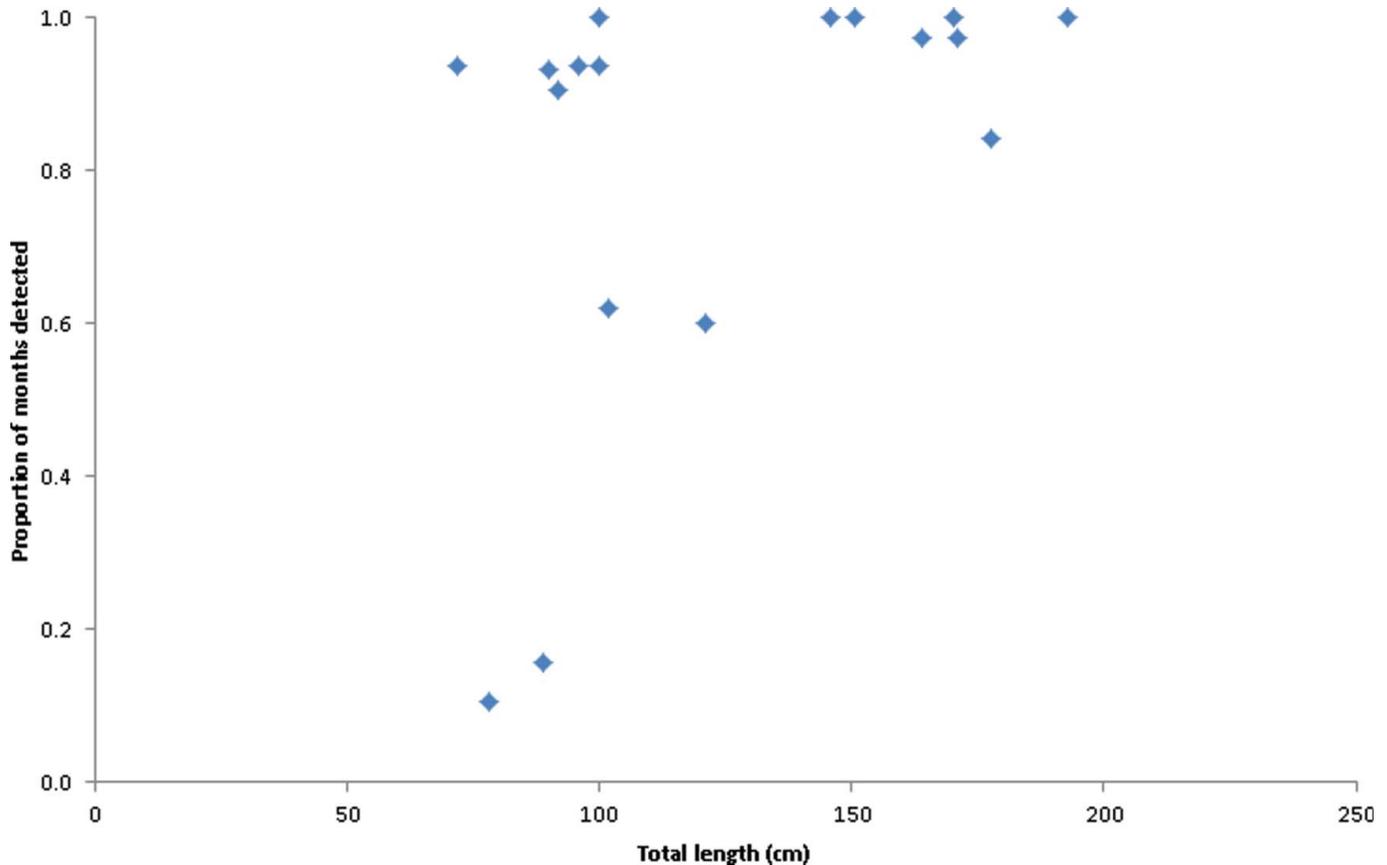
FIGURE 3. Range of months from release to final detection, expressed as a proportion of possible months at large (from release to the end of the study or to the end of transmitter battery life), presented in relation to TL (cm) at tagging for Roanoke River basin Atlantic Sturgeon.

period were detected later (between August and December 2014). Our survival estimates are consistent with other recent estimates for subadult and adult Atlantic Sturgeon (Kahnle et al. 2007; Peterson et al. 2008) but lower than estimates for Gulf Sturgeon in some eastern Gulf of Mexico rivers (Rudd et al. 2014). Our survival estimates imply a range of 0.14–0.25 for the total instantaneous mortality rate ($Z = -\log_e[\text{survival}]$). Given that there is no legal harvest of Atlantic Sturgeon, these Z-estimates likely reflect a combination of true M (e.g., due to predation, disease, or senescence) and mortality due to anthropogenic sources, such as degraded habitat, vessel strikes, or bycatch mortality in ocean, estuarine, or inland waters (Collins et al. 1996, 2000a; Secor and Waldman 1999; Stein et al. 2004; Oakley and Hightower 2007; Simpson and Fox 2009; Brown and Murphy 2010; Balazik et al. 2012). The Z-estimates could also be biased upward by permanent emigration from any of the areas with receiver coverage. The extent of this bias is unknown but should be lessened by the long periods of analysis and by the presence of offshore arrays, which can encounter fish that do not return to riverine waters.

Prior modeling studies for Atlantic Sturgeon have assumed an adult M of 0.07 (Boreman 1997; Kahnle et al. 2007), whereas Rudd et al. (2014) obtained a field-based M-estimate of 0.03 for

the largest population of Gulf Sturgeon (Suwannee River, Florida). Modeling studies focused on adult Atlantic Sturgeon have suggested a target Z of 0.10–0.12 for a sustainable fishery (Boreman 1997; Kahnle et al. 2007); Pine et al. (2001) suggested that at Z-values greater than 0.17–0.19, the rebuilding of Gulf Sturgeon populations would be unlikely. We would expect a more robust or rapid recovery of Atlantic Sturgeon in our study rivers if total mortality can be decreased to levels that are consistent with true M (0.03–0.07; i.e., an annual survival rate of 0.93 or higher). However, we also note that our survival estimates were similar among the four rivers, whereas Atlantic Sturgeon abundance is likely much higher for the Altamaha River (Peterson et al. 2008). Flowers and Hightower (2015) estimated that the abundance of riverine Atlantic Sturgeon was higher for the Edisto River than for the Cape Fear River, which in turn had substantially higher abundance than the Roanoke River. Thus, abundance differences among rivers may be attributable to other factors, such as survival at early life stages.

One measure of the difference between our current survival estimates and the target levels is the equilibrium production of mature females. Starting from an initial cohort of 100 females at age 11 (the first age with a non-zero proportion of mature individuals) and using a target survival rate of

0.93 ($M = 0.07$), we obtain 50 age-classes (through age 60) with at least one mature individual, resulting in a total of 1,020 mature females (see Supplementary Table S.1 and Figure S.1 online). Our highest annual survival rate (0.87) would result in 34 age-classes containing at least one individual (still exceeding the Atlantic States Marine Fisheries Commission's target) but would only yield 419 mature females—a 59% reduction in equilibrium spawning stock production. Clearly, moderate differences in survival have large impacts over the long life span of Atlantic Sturgeon.

Continued monitoring of these populations is warranted because many of the fish analyzed in this study have transmitter expiration dates of 2015 or later. Future detections will eliminate uncertainty about the status of fish that have not been detected recently and will provide a longer time frame for judging temporal variability in survival. Information about the locations where fish were last detected might prove beneficial in identifying threats to survival. These spatially explicit detections can also be used in multistate models (e.g., Flowers 2015) that allow for spatial and temporal variation in survival. Continued monitoring could also provide feedback about whether regulation changes (e.g., gear restrictions or seasonal closures) are improving survival. An increase in the tagging of subadult Atlantic Sturgeon would aid in judging the size dependence of survival, particularly in the ACE basin, where only large fish were tagged during the present study. Subadults would be expected to spend more time in estuarine waters and less time in the ocean than adults, so threats to survival would differ for the two groups. A larger sample size of subadults would also be beneficial for assessing the timing of apparent mortalities relative to potential risk factors in estuarine waters.

ACKNOWLEDGMENTS

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Appendix: OpenBUGS Code for the Cormack–Jolly–Seber model

Example of an OpenBUGS code for fitting a Cormack–Jolly–Seber model for Atlantic Sturgeon, with time-dependent detection probability and survival that varies as a function of the TL covariate.

```
model
{
    # Priors
    mean.S ~ dunif(0, 1)                          # Uninformative on probability scale (Kéry and Schaub 2012:186)
    mu_S <- log(mean.S/(1-mean.S))                # Logit transformation (Kéry and Schaub 2012:186)
    b_S ~ dnorm(0, 0.001) I(-10, 10)              # Prior for logit-scale slope for TL (Kéry and Schaub 2012:190)
    for (i in 1:NumInd)
    {
        for (j in 1:Periods-1)
        {
            logit(S[i,j]) <- mu_S + b_S * (TL[i] - mean_TL)
        }
    }
    mean_p <- mean(p[2:Periods])
    for (j in 1:Periods)
    {
        p[j] ~ dunif(0, 1)
    }
    mean_TL <- mean(TL[])
    # Likelihood
    for (i in 1:NumInd)
    {
        z[i,first[i]] ~ dbern(1)                           # Known to be alive at the time of entry into this analysis
        for (j in first[i]+1:last[i])
        {
            eff.S[i,j-1] <- z[i,j-1] * S[i, j-1]
            z[i,j] ~ dbern(eff.S[i,j-1])                   # Current state depends on state at previous occasion and survival probability
            eff.p[i,j] <- z[i,j] * p[j]
            y[i,j] ~ dbern(eff.p[i,j])                     # Detection probability for an individual depends on its state (must be alive) and estimated p
        }
    }
    Annual.S <- pow(mean.S, 12)
    Good.S <- step(Annual.S - 0.93)
}
```