Transactions of the American Fisheries Society

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10241

ARTICLE

Spawning Drivers and Frequency of Endangered Atlantic Sturgeon in the York River System

Christian H. Hager*
Chesapeake Scientific, LLC, Williamsburg, Virginia 23185, USA

J. Carter Watterson
U.S. Department of the Navy, Naval Facilities Engineering Command, Atlantic, Norfolk, Virginia 23508, USA

Jason E. Kahn
National Marine Fisheries Service, Silver Spring, Maryland 20910, USA

Abstract
Despite over 100 years of commercial exploitation for their eggs, there is limited information about the spawning behavior of Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*. Spawning return intervals for males and females have been estimated in the most general of time spans, and researchers have established only in the last 25 years that Atlantic Sturgeon eggs and larvae are freshwater obligates, dispelling the notion that spawning occurred in estuaries. In this study, capture data from 2013 to 2019 for Atlantic Sturgeon were analyzed to estimate spawning return intervals to the York River system, a tributary to the Chesapeake Bay in Virginia. Then, using the data for female capture, we examined the abiotic influences that appear to drive egg deposition. Both males and females return to spawn at more frequent intervals than has been reported in the literature, with males returning once every 1.13 years and females returning once every 2.19 years. Three females were documented returning to spawn in consecutive years—one of them returning 5 out of 6 years. All of the females that were captured on the spawning grounds were gravid, with eggs at stage 5 or further progressed. In all of the years, 105 fall adult females were caught: 73 were at stage 5, 26 at stage 6, and 6 at stage 7. Of the 26 stage-6 females, 13 were actively releasing eggs when they were captured. Egg deposition was correlated with photoperiod, water temperature, and a drop in barometric pressure in the 24 h prior to capture. Ten of 13 females that were releasing eggs were caught during day lengths that were within 30 min of the autumn equinox. Females that were releasing eggs were only captured at water temperatures that were between 21.5°C and 25.1°C. This information should provide the foundation of predictive models that allow researchers and managers to understand how this endangered species is likely to respond to climate change.

Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* are long-lived, late maturing, iteroparous, anadromous fish (Smith 1985; Bemis and Kynard 1997; Dadswell 2006; NMFS 2007; Peterson et al. 2008). Sexual maturity varies latitudinally, with males maturing slightly younger than females do in all systems and fish in southern systems maturing as early as 4 years of age, while taking as long as 27 years in northern systems (Scott and Crossman 1973; Peterson et al. 2008). Sexual maturity appears to be more size-dependent than age-dependent (Caron et al. 2002). Spawning locations must be sufficiently far above the saltwater interface to allow larvae to drift downstream while remaining in freshwater (Bain 1997; Markin 2017).

*Corresponding author: christian.hager@chesapeakescientific.org
Received February 19, 2020; accepted April 10, 2020

The interval between spawning events has been reported broadly to span as many as 5 years, with females having more nonspawning years than males do (Smith 1985; Bain 1997; Caron et al. 2002; Peterson et al. 2008; Dadswell et al. 2017; Taylor and Litvak 2017). Within these broad ranges, northern populations skip spawning more frequently than southern populations (Hilton et al. 2016). Managers may interpret all upstream migrations as being motivated by spawning; however, subadults will also move into freshwater reaches for obviously nonsexual reasons (Hager 2016). The Atlantic States Marine Fisheries Commission (ASMFC 2017) and Kahn et al. (2019) have proposed metrics for confirming populations of spawning sturgeon. Van Eenennaam and Doroshov (1998) and Collins et al. (2000) provide detailed descriptions of the female egg maturation process, where some egg stages can be used to confirm spawning in that system.

Atlantic Sturgeon spawn in deep river sections (>7.6 m; Bain 1997; Caron et al. 2002) that are often in remote upriver regions, making it difficult to know when and where spawning is occurring or whether it is occurring at all. Because of this, the National Marine Fisheries Service (NMFS 2007) suspects that Atlantic Sturgeon historically spawned in 35 major rivers. Today it is estimated that between 19 and 27 river systems still support spawning (Hilton et al. 2016; ASMFC 2017). Much of what has been published on the reproductive behavior of this species was derived from fisheries-dependent data at a time when they were thought to reproduce in estuaries (Dovel and Berggren 1983; Smith et al. 1984). We now know that the Atlantic Sturgeon that occupy estuaries are a composition of mixed populations (Waldman et al. 1996; Wirgin et al. 2015), confounding previous conclusions about their spawning behavior or abundance (Smith 1985; Secor 2002; Kahnle et al. 2007).

By relying on fisheries-dependent data, all Atlantic Sturgeon were previously believed to spawn in the spring (Smith 1985). As fisheries-independent data has been collected, the spawning behaviors of Atlantic Sturgeon have appeared to be highly varied, employing a number of different reproductive strategies along the Atlantic coast. Recent research has documented fall spawning from Georgia to Virginia (Collins et al. 2000; Balazik et al. 2012; Hager et al. 2014; Smith et al. 2015; Ingram and Peterson 2016). Spring spawning occurs north of the Chesapeake Bay (Bain 1997; Hatin et al. 2002; Dadswell et al. 2017; Taylor and Litvak 2017). Dual spawning has been confirmed in the Edisto River in South Carolina (Collins et al. 2000). More recently, it was suggested that all rivers supported dual spawning (Balazik and Musick 2015), which was not ultimately supported with data (Kahn et al. 2019). However, it is possible, yet still unconfirmed, that dual spawning takes place in the James River, Virginia, the southernmost tributary of the Chesapeake Bay (Balazik and Musick 2015).

Spawning temperatures for Atlantic Sturgeon are generally discussed in a broad range from 13°C to 26°C, which can support spawning from Canada to Georgia (Smith 1985; Kahnle et al. 1998; Peterson et al. 2000; Caron et al. 2002; Hatin et al. 2007; Whippelhauser et al. 2017). In some rivers, spawning temperatures have been produced. Spawning typically occurs at water temperatures that are between 18°C and 20°C in the St. John River (Taylor and Litvak 2017; Mitchill et al. 2020). Larvae were captured in the Kennebec River when water temperatures were between 23°C and 24°C (Whippelhauser et al. 2017). Peak spawning occurs in the Hudson River when temperatures are between 13°C and 18°C (Kahnle et al. 1998). Post-spawn females were documented in the York and James rivers at temperatures that were between 24°C and 25°C (Balazik et al. 2012; Hager et al. 2014). Back-calculated spawning temperatures that were derived from captured larvae in the Roanoke River suggest that spawning occurs at temperatures that are between 24°C and 25°C (Smith et al. 2015). The Edisto River supports spawning in the spring and fall, with documented spawning temperatures between 13°C and 14°C in March and 17°C and 18°C in September and October (Collins et al. 2000).

This study used seasonal sampling to determine when spawning occurred and telemetry detections to measure spawning return intervals for Atlantic Sturgeon. We were able to combine the sexual stage of telemetered males and females with tracking data to calculate the spawning return intervals. Opportunistic captures of endangered adult Atlantic Sturgeon during the spawning season were also correlated with a number of abiotic conditions to infer the factors that induce spawning in females.

METHODS

Study area.— The York River, Virginia, is located along the western edge of the Chesapeake Bay, north of the James River and south of the Rappahannock River (Figure 1). The York River is formed by the confluence of the Pamunkey River, 150 km long, and the Mattaponi River, 166 km long. The York River is 55 km long and ranges from oligohaline at the confluence of its two main tributaries in West Point, Virginia, to polyhaline at its mouth just east of Gloucester Point, Virginia. Atlantic Sturgeon have been confirmed spawning in the Pamunkey River (Hager et al. 2014) and young-of-year fish have been incidentally captured in the lower Mattaponi River where it meets the Pamunkey River (Tuckey and Fabrizio 2012). However the confluence is low salinity and allows movement of young of year between the two. The York River has no freshwater reaches and does not support spawning of Atlantic Sturgeon. Though most of the length of both the Mattaponi and Pamunkey rivers are spring-fed and tidal freshwater, their lower reaches are oligohaline.

Collection methods.— Sampling occurred at river kilometer 74 from late July through mid-October each year between 2013 and 2019 (see Kahn et al. 2019). Gill-net sampling for Atlantic Sturgeon was conducted in the spring and fall, but the York River system only supports fall spawning (Kahn et al. 2019). The gill nets were custom made, with stretch mesh ranging in size from 23 to 36 cm. They were 91 m long but anchored on each bank, sized to extend from surface to river bottom, and set three in sequence in a 0.35-km section of river. Because Atlantic Sturgeon are endangered, many were cut out of the nets, resulting in many nets being used over the seven seasons. The shortest net was 6.5 m tall, fished in 4.9 m of water, and the tallest was 7.3 m tall, fished in 6.7 m of water. The three nets were always made of different mesh sizes to have an equal likelihood of catching adult Atlantic Sturgeon of all sizes, with the largest mesh downstream and smallest mesh in the middle. The temperatures from late July to October ranged from 30.3°C to 16.7°C, but sampling was restricted to times when the temperatures were below 28°C (Kahn and Mohead 2010).

Sex determination and staging.— Individuals were sexed during surgery or by applying pressure to the ventral surface, moving from the anterior to posterior ends and ending at the vent. Van Eenennaam and Doroshov (1998) and Collins et al. (2000) produced clear descriptions of the sexual stages of males and females. The males were noninvasively sexed as "milting" or remained sexually unidentified. Female egg stage was defined by Van Eenennaam

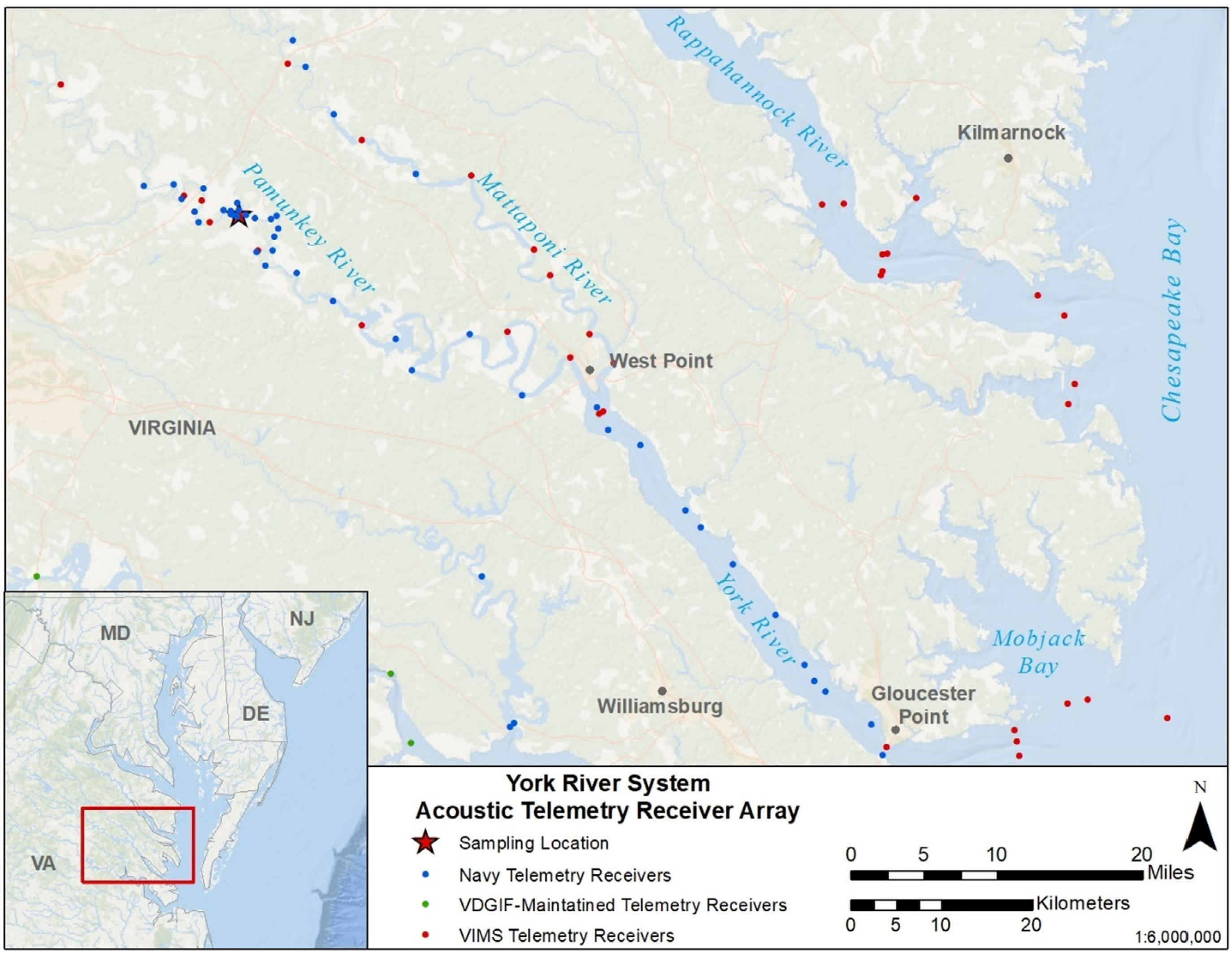

FIGURE 1. The York River and its tributaries, the Pamunkey and Mattaponi rivers. The dots along the map represent telemetry receivers and the star represents the upstream sampling station where the females were collected.

and Doroshov (1998:627–628), and the stages that were observed during this study were as follows:

- Stage 5: migratory nucleus. The ovarian folds are filled with fully grown (diameter 2.61 ± 0.12 mm), darkly pigmented oocytes possessing a thick three-layered envelope with micropyles. The germinal vesicle is displaced to the animal pole, and the oocyte has a distinct polarized structure, with a higher concentration of large yolk platelets and oil droplets in the vegetal hemisphere.
- Stage 6: oocyte maturation. Ovulated (or approaching ovulation) oocytes have undergone germinal vesicle breakdown and nuclear material is mixed with the cytoplasm.
- Stage 7: postovulatory. The ovaries contain numerous empty postovulatory follicles.

Only these final three stages are explicitly defined or referenced because this study is specific to a freshwater location that is approximately 39 km upstream of the saltwater interface during the spawning season; no earlier egg stages were observed. Stage 6 is discussed later and specifically identified either as above or as two phases: eggs that are being released from the ovaries and loose in the body but not being released into the water and eggs that are actively being deposited. Most commonly, the gravid females did not produce gametes with pressure but were confirmed female when the transmitters were implanted and the egg samples were taken at that time. One or two eggs were removed from each female for staging. The female reproductive tissue was not biopsied, so when no eggs were found, either because the fish was spent or male, sex remained unidentified. Sex was occasionally confirmed upon recapture.

Calculation of spawning return frequency and detections.— To calculate return the rates of males and females between 2014 and 2019, we relied on telemetry data. Between 2013 and 2017, 54 acoustic transmitters (Vemco V16P-4H, V16P-6x, or V16-6x) were implanted in Atlantic Sturgeon. The incisions into which a transmitter was inserted were 2–4 cm in length, made most often between the third and fourth ventral scutes anterior to the anal fins. The incisions were closed by using Vicryl dissolvable sutures. After the surgery was complete, the fish were released approximately 1.5 km from the capture site to avoid multiple captures in one day. If a fish was captured twice in the same day ($n = 47$), the nets were removed for the rest of the day to avoid harassing the fish that were attempting to use the sampling location. The deployed transmitters were programmed to transmit a 69-kHz signal every 70–150 s and had a life span of at least 6 years. When the tags ceased being detected, they were no longer used to estimate return frequencies.

The implanted transmitters were passively tracked within the freshwater and saline reaches of the York River system year-round from 2014 through 2019. Figure 1 shows the passive Vemco VR2W-69-kHz receiver stations within the York River and the Chesapeake Bay. Seventy receivers that are maintained by Chesapeake Scientific and the U.S. Department of the Navy remained in place for the duration of this study. From July to November, additional receivers were placed in the Mattaponi and Pamunkey rivers. Because of the narrow width (most locations are <25 m wide) of the Pamunkey and Mattaponi rivers, the receivers acted as gates such that every fish that passed a receiver would be within a detectable range, verified through range studies presented by Hager (2016). The receivers were placed near the surface, faced downward, and they were serviced and downloaded monthly.

Atlantic Sturgeon were determined to be on a spawning run if they moved at least 20 km upriver of the saltwater interface (Van Eenennaam et al. 1996; Kynard and Horgan 2002) and spent at least 17 consecutive days in freshwater based on ad-hoc observations. Relying on the detections of individuals returning to spawning grounds each year, we used a ratio estimator:

$$\overline{p}_{\mathrm{r}} = \frac{\Sigma T_{\mathrm{return}}}{\Sigma T_{(t)}},$$

where $\overline{p}_{\mathrm{r}}$ is the mean proportion of telemetered fish (of each sex separately) to return over the duration of the estimate, while T_{return} and $T_{(t)}$ represent the total number of individuals of each sex that returned to spawn in each year and the total number of individuals of each sex that could have returned to spawn in those years, respectively. When transmitters were lost or failed, they were removed from this estimate following their final detection. Likewise, fish that were detected in another river system were not counted in T_{return} and $T_{(t)}$ for that year. The Vysochanskij–Petunin inequality (Vysochanskij and Petunin 1989; Andrushkiw et al. 2005) was used to calculate the 95% confidence limits (CLs) of the return intervals.

Calculation of factors contributing to egg deposition.— The correlation between abiotic factors and female reproductive stage were made qualitatively. For this analysis, we recorded the date of capture, photoperiod (sunrise to sunset), water temperature at the sampling location, egg stage of the females that were captured, FL (mm), flow rate, 24-h change in flow rate, 24-h proportional change in flow rate, barometric pressure, and 24-, 48-, 72-, and 96-h temperature and pressure changes before capture. To understand the factors that are associated with spawning, we primarily considered stage-6 females, with a real focus on the females that were releasing eggs at the time of capture.

Data for the abiotic conditions were collected onsite when possible, but when measurements could not be made at the sampling location we relied on the nearest location. All of the captured Atlantic Sturgeon were measured to the nearest millimeter FL. Water temperatures were recorded using a HOBO Onset U12-015 temperature logger that was tethered to the river bank and suspended at a depth of 1.5 m at low tide. While temperatures were recorded every 3 h, we relied on the midday temperature measurement for that day. The sunrise and sunset times corresponding to each sampling date were downloaded from the Web site "timeanddate.com," using the Pamunkey Indian Reservation (approximately 17 km east) as the location. Flow data was obtained from the U.S. Geological Survey gauge 01673000 from the Pamunkey River near Hanover, Virginia (approximately 20 km west). Barometric pressure was obtained from the National Oceanic and Atmospheric Administration, National Centers for Environmental Information, from Doswell, Virginia (approximately 24 km west).

RESULTS

Between 2013 and 2019, 283 male and 105 female Atlantic Sturgeon were captured during the fall spawning season; many of these were captured multiple times during the study. Of the 105 adult females, 73 were at stage 5, 26 at stage 6, and 6 at stage 7 (Figure 2). Of the stage-6 females, 13 had released eggs into their abdominal cavities without physically expressing eggs, while 13 were captured that were releasing eggs in the act of spawning. All six of the stage-7 females expressed eggs with pressure, but in 66% of those cases the eggs were gray and nonviable.

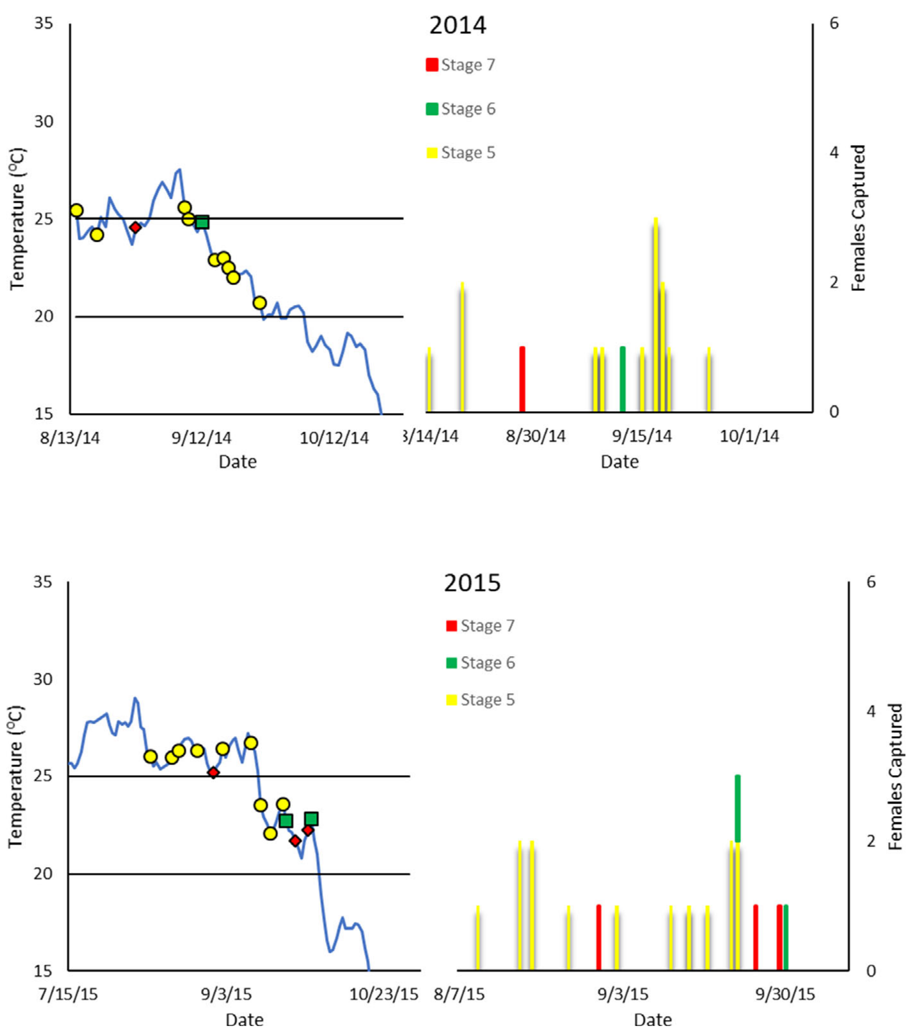

FIGURE 2. Correlation between females captured each year from 2014 to 2019 and the declining temperature from summer to fall. The lines at 25°C and 20°C depict the temperatures where spawning appears to be initiated and terminated.

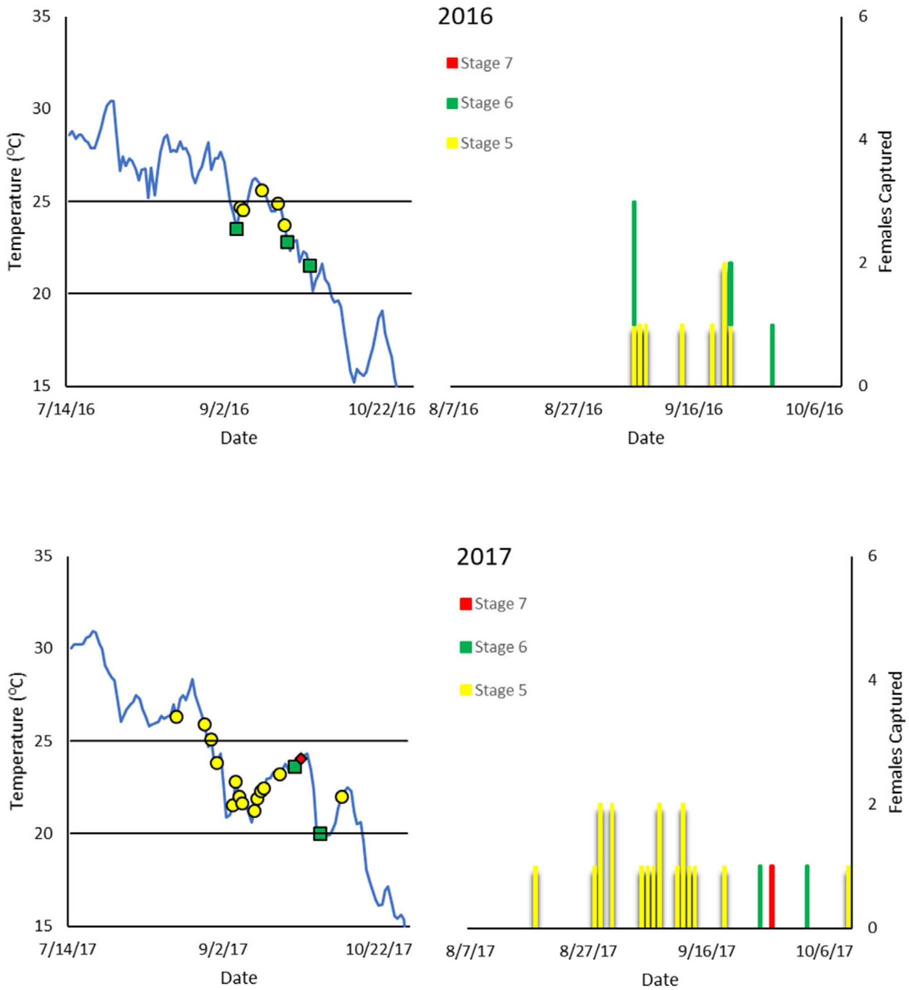

FIGURE 2. Continued.

Spawning frequency was estimated by using telemetry-tagged males ($n = 28$) and females ($n = 26$). When calculating the spawning return interval in the season following transmitter implantation, males returned 115 times out of a possible 130 spawning events between 2013 and 2019 (Table 1). Females returned 36 times out of a possible 79 spawning events. The mean spawning return rate for males was every 1.13 years (95% CL: 1.12, 1.14), with most of the males returning every year and only one male skipping two consecutive years. The females returned on average every 2.19 years (95% CL: 1.92, 2.56), with most spawning every other year. The females occasionally spawned in consecutive years, and only one female skipped three consecutive years (Table 1).

The actively spawning females ($n = 13$) provided the greatest insight into the conditions that resulted in spawning at the sampling site. There was no consistent correlation between fish length, time of capture, or the tidal conditions and capture during egg release (Table 2). Actively spawning females were always captured near the lead line of the gill net. Two females that were releasing eggs were captured at the downstream end of the deepest pool in the area (6.5 m), and most of the spawning fish were captured in water that was over 3 m in depth (measured from the location of capture) and not at the deepest location that was sampled by the net that captured them.

Three of the abiotic drivers that were considered were correlated with female egg release. First, temperature appears to have had an important influence on egg release. No females were captured that were releasing eggs outside of the thermal window ranging from 21.5°C to 25.1°C (Table 2). Photoperiod was also closely correlated with female egg stage. Ten of the 13 (77%) females that were releasing eggs were captured within 30 min of the autumn equinox. The majority of stage-6 and stage-7 females (13 of 19, 68.4%) were captured when day length was between 12 h and 12 h, 20 min, with a peak when sunrise was at 0656 hours and sunset was at 1900 hours.

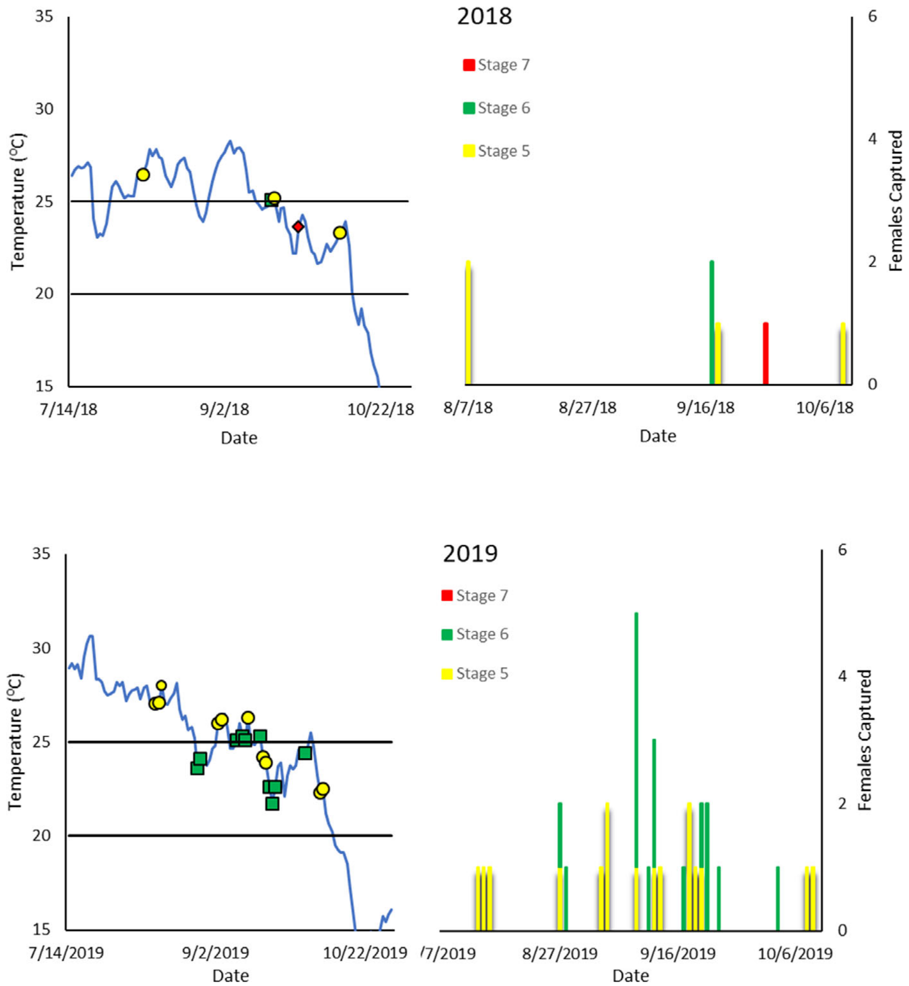

FIGURE 2. Continued.

Finally, for 70% (22 of 32) of the females that were at stage 6 or 7, 77% (10 of 13) of those that were releasing eggs, and 79% (15 of 19) of those that were either releasing eggs or spent, the barometric pressure had dropped in the 24 h prior to their capture by an average of −1.422, −2.133, and −2.404 millibars, respectively. There was no apparent correlation with female egg stage and FL, flow rate, 24-h change in flow rate, 24-h proportional change in flow rate, barometric pressure, and any other temporal changes in temperature or barometric pressure.

DISCUSSION

Atlantic Sturgeon spawning in the York River occurs in the fall as water temperatures decline from summer highs through optimal bioenergetic temperatures (Niklitschek 2001). Atlantic Sturgeon move upriver between July and August, and there is a closed spawning population through most of September (Kahn et al. 2019). The females in this study were captured throughout the fall spawning period, and every captured female was gravid with eggs that were staged as 5, 6, or 7. Similar developmental distribution was reported in the Hudson River, with females being at stage 5 or later when upriver (Van Eenennaam et al. 1996).

The analysis of the telemetry data from 2014 through 2019 revealed a narrower spawning return interval, with more frequent spawning events in more northern systems than has been reported by others (Bain 1997; Billard and Lecointre 2001; Dadswell 2006). Males from the York River returned to spawn every 1–3 years, with only one fish ever skipping two seasons, while females returned to spawn every 1–4 years, occasionally returning in consecutive years. In this study, the variables of T_{return} and $T_{(t)}$ were calculated from the year following transmitter implantation. Because the transmitters were implanted in the Atlantic Sturgeon while they were on spawning runs, those values could have been calculated to include the

TABLE 1. Telemetered fish identification numbers, sex, and seasons when a spawning run was made (X). The lengths and weights are reported from their initial capture. When an individual was believed to be dead, a "–" was used to note that no spawning run could be made and a "†" represents evidence of spawning in a different river. Not all of the rivers have receiver arrays, so it is also possible that some of these individuals spawned in unmonitored systems without being detected.

Fish ID	FL (mm)	Weight (kg)	Sex	2013	2014	2015	2016	2017	2018	2019
14-012	1,995	84.7	Female		X	–	–	–	–	–
14-023	1,773	56.8	Female		X		X		X	
14-034	1,988	83.6	Female		X	X	X		X	X
14-037	1,813	61.0	Female		X		X		X	
14-054	1,790	58.6	Female		X	X		X		X
15-003	1,820	61.8	Female					X		X
15-010	1,935	76.1	Female			X		X		X
15-011	1,899	71.3	Female			X			X	
15-020	1,855	65.8	Female					X		X
15-035	1,845	64.7	Female			X		X		X
15-048	2,188	119.9	Female			X		X		X
16-008	1,984	83.1	Female				X		X	
16-009	1,873	68.0	Female				X		X	
16-010	1,592	41.1	Female				X			
16-013	1,867	67.3	Female				X		X	
16-020	1,984	83.1	Female				X		X	
16-023	2,038	91.6	Female				X		X	X
16-027	1,881	69.0	Female				X		X	
17-003	1,663	46.6	Female					X		X
17-011	2,065	96.2	Female					X		X
17-016	1,978	79.6	Female					X		X
17-019	1,636	46.6	Female					X		X
17-031	1,890	70.1	Female					X		X
17-033	1,738	54.1	Female					X		X
17-036	1,858	66.2	Female					X		X
17-041	2,150	117.3	Female					X		X
17-053	2,004	86.1	Female					X		X
13-002	1,652	34.3	Male	X	X	X	X	X	X	X
13-003	1,503	30.7	Male	X	X	X	X	X	X	X
13-004	1,541	32.5	Male	X	X	X	X	X	X	X
13-005	1,298	20.8	Male	X		X	X	X	X	X
13-007	1,490	33.3	Male		X	X	X	X	X	X
13-009	1,382	24.9	Male	X	X	X	X	X	X	X
13-012	1,585	37.6	Male	X	X	X		X	X	X
13-013	1,653	37.9	Male	X	X	X	X	X	X	X
13-015	1,548	28.8	Male	X	X	X	X	X	X	X
14-002	1,593	34.0	Male		X		X	X	X	X
14-004	1,489	30.0	Male		X	X	X	X	X	X
14-007	1,502	30.7	Male		X	X	X	X	X	X
14-008	1,514	30.1	Male		X	X		X	X	X
14-009	1,572	34.0	Male		X		†		†	
14-013	1,624	36.6	Male		X	X	X	X	X	X
14-015	1,533	32.2	Male				X	X	X	X
14-020	1,481	30.0	Male		X	X		X	X	X
14-024	1,499	30.5	Male		X	X	X	X	X	X
14-026	1,709	40.7	Male		X	X	X	X	X	X
14-028	1,528	28.7	Male		X	X	X	X	X	X

TABLE 1. Continued.

Fish ID	FL (mm)	Weight (kg)	Sex	2013	2014	2015	2016	2017	2018	2019
14-029	1,367	24.9	Male		X	X	X	X		X
14-031	1,540	32.5	Male		X	X	X	X	–	–
14-032	1,666	38.6	Male		X	X	X		–	–
14-036	1,659	38.2	Male		X			X	X	X
14-043	1,634	42.9	Male		X	X		X		X
14-050	1,679	39.2	Male		X	–	–	–	–	–
16-039	1,647	37.7	Male				X	X		†
16-042	1,452	28.3	Male				X	X	X	X

TABLE 2. Physical description of females that were actively releasing eggs (late stage 6), along with relevant biotic and abiotic information.

ID	Fork length (mm)	Date	Time (24-h clock)	Temp (°C)	Tide	Slack tide (time)	Estimated progression	Estimated depth (m)	River morphology
14-033	1,880	9/12/14	1415	24.5	Flood	1500	½ spent	4–5	Main stem, confluence with large creek
15-048	2,225	9/22/15	0830	22.7	Flood	1120	Initiating, full of eggs	6.5	Center river, deep hole
15-029	1,867	9/30/15	1115	22.8	Ebb	1300	¾ spent	6.5	Center river, deep hole
16-009	1,921	9/6/16	1340	23.5	Ebb	1500	½ spent	4–5	Main stem, confluence with large creek
16-010	1,609	9/6/16	1625	23.5	Flood	1500	½ spent	3–4	Main stem, confluence with small creek
14-037	1,958	9/22/16	1700	22.8	Slack	1630	Initiating, full of eggs	3–4	Straight, thalweg
17-031	1,930	9/25/17	1140	23.5	Flood	0910	½ spent	3–4	Main stem, confluence with large creek
18-009	1,900	9/17/18	1230	25.1	Slack	1200	½ spent	2–3	Beside pool, along drop-off
18-010	2,051	9/17/18	1450	25.1	Ebb	1800	½ spent	2–3	North bank along drop-off
19-016	1,833	9/21/19	0900	21.7	Slack	0915	¼ spent	3	Upstream of small creek
17-041	2,200	9/23/19	1125	23.7	Slack	1155	¾ spent	3–4	Main stem, confluence with large creek
19-043	2,074	10/3/19	0850	24.8	Slack	0840	¾ spent	2–3	South bank along drop-off

year of implantation. As a result, the reported spawning return frequencies may slightly underestimate the true rate. The return rates for females, which usually skip a year between spawning events, are most likely underestimated because our calculations began counting their possible returns in the year that we would have expected them to remain at sea. In one exceptional instance, female 14-034 was present on spawning grounds during five out of six possible spawning events. She was captured on two of those returns and was at stage 5 at each time. Female 14-054 was also captured in 2014, 2015, and 2017 at stage 5 in each year. To our knowledge, these are the first documented female Atlantic Sturgeon that have been confirmed to be in gravid condition on spawning grounds in consecutive years. In captive White Sturgeon *Acipenser transmontanus*, it is possible for a female with stage-5 eggs to retain those eggs until the following spawning season (Joel Van Eenennaam, University of California, Davis, personal communication), so this may not be confirmation of a female spawning in consecutive years.

Female spawning condition changes relatively rapidly in the Pamunkey River. In 2019, female 17-041 was captured on September 18 and 23. On September 18, her eggs were at stage 5 and only 5 d later she had lost over 27.2 kg of eggs, continued to express eggs with pressure, and still appeared roughly ¼ full (Table 2). There is also a close temporal relationship between females at stage 6 and stage 7, often caught in the same year at roughly the same time. For this reason, it is interesting that four of the six stage-7 females had gray nonviable eggs. This suggests that the transition from viable, spawning eggs to nonviable, postspawn eggs may be very rapid, in some cases occurring while the female is still on the spawning grounds and prior to out-migration.

Spawning events are poorly documented for Atlantic Sturgeon, typically limited to evidence of a single spawning event (Collins et al. 2000; Smith et al. 2015). During this study, it appears that temperature, photoperiod, and a drop in barometric pressure in the 24 h prior to spawning are important drivers for egg release. Nineteen adult females were captured that were either releasing eggs or spent of which 13 were captured when the photoperiod was between 12.3 and 12.0 h. Research on other sturgeon has shown that photoperiod is also the primary driver for spawning in different systems and at different times of year (Papoulias et al. 2011; Kieffer and Kynard 2012). Likewise, spawning for many other teleost fish has been linked to photoperiod (Norberg et al. 2004; Migaud et al. 2006). Furthermore, of potential importance for sturgeon caviar production, artificially manipulating photoperiod has been shown to increase reproductive rates (Whitehead et al. 1978; Carrillo et al. 1989; Campos-Mendoza et al. 2004).

Water temperature during the fall spawning season (16.7–30°C is closely correlated with photoperiod but varies considerably between years. The 32 individuals who were at stage 6 or 7 in this study were all captured within the same 0.35-km stretch of river at temperatures between 20.6°C and 25.5°C (Figure 2). Twenty-six of those were caught in water that was cooler than 25°C: two that were actively releasing eggs (at 25.1°C) and four with eggs being released from the ovarian folds but not being expressed (at temperatures ranging from 25.1°C to 25.5°C). The 13 females that were captured while they were actively releasing eggs were captured at temperatures that were between 21.5°C and 25.1°C (Table 2). Temperatures above 25°C are associated with high egg mortality in sturgeon (Chapman and Carr 1995; Ingram and Peterson 2016). Thermal windows that are essential for spawning have been observed for Shortnose Sturgeon *Acipenser brevirostrum* as well (Kieffer and Kynard 2012).

The narrow temperature range when Atlantic Sturgeon were observed spawning correlates with the observed optimal growth rates for age-1 Atlantic Sturgeon in the Hudson River (Niklitschek 2001), and this may provide more insight into the reasons for egg deposition regardless of spring or fall spawning (Markin and Secor 2020). Niklitschek (2001) showed an optimal growth combination of temperature and dissolved oxygen for juvenile Atlantic Sturgeon of roughly 18–22°C at 70–100% dissolved oxygen saturation, which is the typical dissolved oxygen saturation in the Pamunkey River during spawning season. The data that were collected in this system suggest that females release their eggs in the temperature range between the upper threshold for optimal egg survival (Chapman and Carr 1995) and upper threshold for optimal juvenile growth (Niklitschek 2001). The drop in barometric pressure that was observed for every group of stage-6 and stage-7 combinations may indicate that timing is also influenced by the onset of fall storms, which would cause the water temperature to drop. In that way, female Atlantic Sturgeon may be able to release their eggs near the upper thermal limits for eggs and increase the likelihood of high survival.

Atlantic Sturgeon appear to time their spawning to maximize larval growth through the entire range of optimal temperatures. Baird et al. (2019) showed that predation risk for juvenile Green Sturgeon *Acipenser medirostris* from Largemouth Bass *Micropterus salmoides* and Striped Bass *Morone saxatilis* decreased with growth until nearing zero at 200–220 mm total length. Both of these predators are present in the Pamunkey River, and increasing growth rates at the most vulnerable size may increase the likelihood of year-class success. Further research will be necessary to understand the predation threat from these species in this system as well as from the introduction of the invasive Blue Catfish *Ictalurus furcatus*.

Identifying the parameters that drive spawning in a single system provides managers with justification for protective mitigation within that system. Improving our understanding of the factors that drive and thus may limit the reproductive potential of a species provides data that are crucial to its conservation. Given the shifts in local weather patterns due to climate change, the data that are presented here could be used to develop predictive models of spawning for Atlantic Sturgeon. Between 2013 and 2019, the preferred photoperiod for spawning did not fluctuate even though the proposed thermal window for spawning expanded by approximately 2 d each year, thus extending the potential spawning window by 2 weeks by 2019. Additional research is needed to address the population variability of genetics, bioenergetics, system-specific life histories, seasonality of egg release, and seasonally available larval food resources of Atlantic Sturgeon to understand how the species is likely to respond to climate change.

ACKNOWLEDGMENTS

This research was aided by the support and assistance of the following contributors. Ramsey Noble, Gabriel Irigaray, Jay Russo, Tracy Massey, Craig Marcusson, Kirk Moore, and Carter Griggs were senior technicians. We are also grateful to April Deacy, Desiree Nuckols, Kirk Moore, and Kevin Brown from the Pamunkey Tribe and to William Tyler for river access. We thank Albert Spells of the U.S. Fish and Wildlife Service and Dave MacDuffee, Dave Noble, Brittany Bartlett, and Jessica Bassi and Laura Busch of the U.S. Department of the Navy. Additionally, we thank the U.S. Department of the Navy for providing personnel and funding through Contract N62470-09-D-2003 for the telemetry tags and receivers; the National Marine Fisheries Service for providing personnel and issuing the Endangered Species Act sampling permits, and the Virginia Department of Game and Inland Fisheries and the Virginia Marine Resources Commission for issuing the state sampling permits. Sampling was conducted under Virginia Marine Resources Commission Permits 13-059, 14-016, 15-023, and 16-036 for 2013, 2014, 2015, and 2016, respectively; Virginia Department of Game and Inland Fisheries Permits 047061, 051600, 053337, 055949, 060198, 061577, and 065154 for 2013, 2014, 2015, 2016, 2017, 2018, and 2019, respectively; and National Marine Fisheries Service Permits 16547 and 19642.

ORCID

Jason E. Kahn https://orcid.org/0000-0001-6426-9189

REFERENCES

Andrushkiw, R. I., D. A. Klyushin, Y. I. Petunin, and M. Y. Savkina. 2005. The “exact” confidence limits for unknown probabilities in Bernoulli models. Center for Applied Mathematics and Statistics, Report 0405-25, Newark, New Jersey.

ASMFC (Atlantic States Marine Fisheries Commission). 2017. Atlantic Sturgeon benchmark stock assessment and peer review report. ASMFC, Alexandria, Virginia.

Bain, M. B. 1997. Atlantic and Shortnose sturgeons of the Hudson River: common and divergent life history attributes. Environmental Biology of Fishes 48:347–358.

Baird, S. E., A. E. Steel, D. E. Cocherell, J. B. Poletto, R. Follenfont, and N. A. Nang. 2019. Experimental assessment of predation risk for juvenile Green Sturgeon, *Acipenser medirostris*, by two predatory fishes. Journal of Applied Ichthyology 36:14–24.

Balazik, M. T., G. C. Garman, J. P. Van Eenennaam, J. Mohler, and L. C. Woods III. 2012. Empirical evidence of fall spawning of Atlantic Sturgeon in the James River, Virginia. Transactions of the American Fisheries Society 141:1465–1471.

Balazik, M. T., and J. A. Musick. 2015. Dual annual spawning races in Atlantic Sturgeon. PLOS (Public Library of Science) ONE [online serial] 10:e0128234.

Bemis, W. E., and B. Kynard. 1997. Sturgeon rivers: an introduction to Acipenseriform biogeography and life history. Environmental Biology of Fishes 48:167–183.

Billard, R., and G. Lecointre. 2001. Biology and conservation of sturgeon and Paddlefish. Reviews in Fish Biology and Fisheries 10:355–392.

Campos-Mendoza, A., B. J. McAndrew, K. Coward, and N. Bromage. 2004. Reproductive response of Nile Tilapia (*Oreochromis niloticus*) to photoperiodic manipulation; effects on spawning periodicity, fecundity and eggs size. Aquaculture 231:299–314.

Caron, F., D. Hatin, and R. Fortin. 2002. Biological characteristics of adult Atlantic Sturgeon in the St Lawrence River estuary and the effectiveness of management rules. Journal of Applied Ichthyology 18:580–585.

Carrillo, M., N. Bromage, S. Zanuy, R. Serrano, and F. Prat. 1989. The effect of modifications in photoperiod on spawning time, ovarian development and egg quality in the Sea Bass (*Dicentrarchus labrax* L.). Aquaculture 81:351–365.

Chapman, F. A., and S. H. Carr. 1995. Implications of early life stages in the natural history of the Gulf of Mexico Sturgeon, *Acipenser oxyrinchus desotoi*. Environmental Biology of Fishes 43:407–413.

Collins, M. R., T. I. J. Smith, W. C. Post, and O. Pashuk. 2000. Habitat utilization and biological characteristics of adult Atlantic Sturgeon in two South Carolina rivers. Transactions of the American Fisheries Society 129:982–988.

Dadswell, M. 2006. A review of the status of Atlantic Sturgeon in Canada, with comparisons to populations in the United States and Europe. Fisheries 31:218–229.

Dadswell, M. J., C. Caepa, A. D. Spares, N. D. Stewart, R. A. Curry, R. G. Bradford, and M. J. W. Stokesbury. 2017. Population characteristics of adult Atlantic Sturgeon captured by the commercial fishery in the Saint John River estuary, New Brunswick. Transactions of the American Fisheries Society 146:318–330.

Dovel, W. L., and T. J. Berggren. 1983. Atlantic Sturgeon of the Hudson River estuary, New York. New England Fish and Game Journal 30:140–172.

Hager, C. 2016. Operation of the Navy’s telemetry array in the lower Chesapeake Bay. Annual Report to U.S. Navy, Contract N62470–10-D-3011, Task Order CTO 53, Norfolk, Virginia.

Hager, C., J. Kahn, C. Watterson, J. Russo, and K. Hartman. 2014. Evidence of Atlantic Sturgeon (*Acipenser oxyrinchus*) spawning in the York River system. Transactions of the American Fisheries Society 143:1217–1219.

Hatin, D., R. Fortin, and F. Caron. 2002. Movements and aggregation areas of adult Atlantic Sturgeon (*Acipenser oxyrinchus*) in the St. Lawrence River estuary, Quebec, Canada. Journal of Applied Ichthyology 18:586–594.

Hatin, D., J. Munro, F. Caron, and R. D. Simons. 2007. Movements, home range size, and habitat use and selection of early juvenile Atlantic Sturgeon in the St. Lawrence estuarine transition zone. Pages 129–155 *in* J. Munro, D. Hatin, J. E. Hightower, K. McKown, K. J. Sulak, A. W. Kahnle, and F. Caron, editors. Anadromous sturgeons: habitats, threats, and management. American Fisheries Society, Symposium 56, Bethesda, Maryland.

Hilton, E. J., B. Kynard, M. T. Balazik, A. Horodysky, and C. B. Dillman. 2016. Review of the biology, fisheries, and conservation status of the Atlantic Sturgeon, (*Acipenser oxyrinchus, oxyrhinchus* Mitchell, 1815). Journal of Applied Ichthyology 32(supp 1):30–66.

Ingram, E. C., and D. L. Peterson. 2016. Annual spawning migration of adult Atlantic Sturgeon in the Altamaha River, Georgia. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 8:595–606.

Kahn, J. E., C. Hager, J. C. Watterson, N. Mathies, and K. Hartman. 2019. Comparing abundance estimates from closed population mark recapture models of endangered adult Atlantic Sturgeon. Endangered Species Research 39:63–76.

Kahn, J., and M. Mohead. 2010. A protocol for use of Shortnose, Atlantic, Gulf, and Green sturgeons. NOAA Technical Memorandum NMFS-OPR-45.

Kahnle, A. W., K. A. Hattala, and K. A. McKown. 2007. Status of Atlantic Sturgeon of the Hudson River Estuary, New York, USA. American Fisheries Society Symposium 56:347–363.

Kahnle, A. W., K. A. Hattala, K. A. McKown, C. A. Shirey, M. R. Collins, T. S. Squiers, T. Savoy, D. H. Secor, and J. A. Musick. 1998. Stock status of Atlantic Sturgeon of Atlantic coast estuaries. Report to the Atlantic States Marine Fisheries Commission, Alexandria, Virginia.

Kieffer, M., and B. Kynard. 2012. Spawning and non-spawning migrations, spawning, and the effect of river regulation on spawning success of Connecticut River Shortnose Sturgeon. Pages 73–113 *in* B. Kynard, P. Bronzi, and H. Rosenthal, editors. Life history and behavior of Connecticut River Shortnose Sturgeon and other sturgeons. World Sturgeon Conservation Society, Publication 4, Norderstedt, Germany.

Kynard, B., and M. Horgan. 2002. Ontogenetic behavior and migration of Atlantic Sturgeon, *Acipenser oxyrinchus oxyrinchus*, and Shortnose Sturgeon, *A. brevirostrum*, with notes on social behavior. Environmental Biology of Fishes 63:137–150.

Markin, E. L. 2017. Atlantic Sturgeon *Acipenser oxyrinchus* growth responses to dual seasonal spawning, latitudinal thermal regimes, and Chesapeake Bay environmental stressors. Doctoral dissertation. University of Maryland Center for Environmental Science, Cambridge.

Markin, E. L., and D. H. Secor. 2020. Growth of juvenile Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) in response to dual-season spawning and latitudinal thermal regimes. U.S. National Marine Fisheries Service Fishery Bulletin 118:74–86.

Migaud, H., N. Wang, J.-N. Gardeur, and P. Fontaine. 2006. Influence of photoperiod on reproductive performances in Eurasian Perch *Perca fluviatilis*. Aquaculture 252:385–393.

Mitchill, S. M. J., M. J. Dadswell, C. Ceapa, and M. J. W. Stokesbury. 2020. Fecundity of Atlantic Sturgeon (*Acipenser oxyrinchus* Mitchill, 1815) captured by the commercial fishery in the Saint John River, New Brunswick, Canada. Journal of Applied Ichthyology 36:142–150.

Niklitschek, E. J. 2001. Bioenergetics modeling and assessment of suitable habitat for juvenile Atlantic and Shortnose sturgeons in the Chesapeake Bay. Doctoral dissertation. University of Maryland, College Park.

NMFS (National Marine Fisheries Service). 2007. Status review of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*). Report to NMFS/NOAA (National Oceanic and Atmospheric Administration), Silver Spring, Maryland.

Norberg, B., C. L. Brown, O. Halldorsson, K. Stensland, and B. T. Björnsson. 2004. Photoperiod regulates the timing of sexual maturation, spawning, sex steroid and thyroid hormone profiles in Atlantic Cod (*Gadus morhua*). Aquaculture 229:451–467.

Papoulias, D. M., A. J. DeLonay, M. L. Wildhaber, and D. E. Tillitt. 2011. Characterization of environmental cues for initiation of reproductive cycling and spawning in Shovelnose Sturgeon *Scaphirhynchus platorynchus* in the lower Missouri River, USA. Journal of Applied Ichthyology 27:335–342.

Peterson, D. L., M. B. Bain, and N. Haley. 2000. Evidence of declining recruitment of Atlantic Sturgeon in the Hudson River. North American Journal of Fisheries Management 20:231–238.

Peterson, D. L., P. Schueller, R. DeVries, J. Fleming, C. Grunwald, and I. Wirgin. 2008. Annual run size and genetic characteristics of Atlantic Sturgeon in the Altamaha River. Transactions of the American Fisheries Society 137:393–401.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.

Secor, D. H. 2002. Atlantic Sturgeon fisheries and stock abundances during the late nineteenth century. Pages 89–98 *in* W. Van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, editors. Biology, management, and protection of North American sturgeon. American Fisheries Society, Symposium 28, Bethesda, Maryland.

Smith, J. A., H. J. Flowers, and J. E. Hightower. 2015. Fall spawning of Atlantic Sturgeon in the Roanoke River, North Carolina. Transactions of the American Fisheries Society 144:48–54.

Smith, T. I. J. 1985. The fishery, biology, and management of Atlantic Sturgeon, *Acipenser oxyrhynchus*, in North America. Environmental Biology of Fishes 14:61–72.

Smith, T. I. J., D. E. Marchette, and G. F. Ulrich. 1984. The Atlantic Sturgeon fishery in South Carolina. North American Journal of Fisheries Management 4:164–176.

Taylor, A. D., and M. K. Litvak. 2017. Timing and location of spawning based on larval capture and ultrasonic telemetry of Atlantic Sturgeon in the Saint John River, New Brunswick. Transactions of the American Fisheries Society 146:283–290.

Tuckey, T. D., and M. C. Fabrizio. 2012. Estimating relative juvenile abundance of ecologically important finfish in the Virginia portion of the Chesapeake Bay. Annual Report submitted to the Virginia Marine Resources Commission, Project F-104-R-16, Newport News, Virginia.

Van Eenennaam, J. P., and S. I. Doroshov. 1998. Effects of age and body size on gonadal development of Atlantic Sturgeon. Journal of Fish Biology 53:624–637.

Van Eenennaam, J. P., S. I. Doroshov, G. P. Moberg, J. G. Watson, D. S. Moore, and J. Linares. 1996. Reproductive conditions of the Atlantic Sturgeon (*Acipenser oxyrinchus*) in the Hudson River. Estuaries 19:769–777.

Vysochanskij, D. F., and Y. I. Petunin. 1989. Justification of the 3σ rule for unimodal distribution. Theory of Probability and Mathematical Statistics 21:25–36.

Waldman, J. R., J. T. Hart, and I. I. Wirgin. 1996. Stock composition of the New York Bight Atlantic Sturgeon fishery based on analysis of mitochondrial DNA. Transactions of the American Fisheries Society 125:364–371.

Whippelhauser, G. S., J. Sulikowski, G. B. Zydlewski, M. A. Altenritter, M. Kieffer, and M. T. Kinnison. 2017. Movements of Atlantic Sturgeon of the Gulf of Maine inside and outside of the geographically defined distinct population segment. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 9:93–107.

Whitehead, C., N. R. Bromage, J. R. M. Forster, and A. J. Matty. 1978. The effects of alterations in photoperiod on ovarian development and spawning time in the Rainbow Trout. Annales de Biologie Animale Biochimie Biophysique 18:1035–1043.

Wirgin, I., M. W. Breece, D. A. Fox, L. Maceda, K. W. Wark, and T. King. 2015. Origin of Atlantic Sturgeon collected off the Delaware coast during spring months. North American Journal of Fisheries Management 35:20–30.