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Arrival and departure windows of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in Chesapeake Bay in Virginia

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Abstract—The Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) has been listed under the Endangered Species Act since 2012, with the Chesapeake Bay distinct population segment listed as endangered. We tracked the timing of occupancy and movement in Chesapeake Bay of adult Atlantic sturgeon from the York River to best identify when Atlantic sturgeon are likely to interact with anthropogenic threats. We monitored 84 adult (40 male and 44 female) Atlantic sturgeon from August 2013 through January 2020 by using acoustic telemetry. Both spawning and non-spawning fish regularly utilized Chesapeake Bay, with females and males arriving as early as 27 February (when the mean water temperature was 7.7°C) and 4 March (6.5°C) and departing as late as 24 January (6.3°C) and 27 January (6.5°C), respectively. Peak occupation of the bay by Atlantic sturgeon occurred from 1 April to 31 August and again from 15 October to 1 December. Females of above average size (>1880 mm in fork length) spent significantly longer in the bay (>113 d) than smaller females and all males before spawning; therefore, the females capable of producing the most eggs were disproportionately exposed to anthropogenic threats. Although changes in arrival and departure dates are not statistically significant, during the 7 years of this study, both males and females generally arrived earlier and departed later each year than the previous year, increasing residency in Chesapeake Bay by a month in that time.

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The National Marine Fisheries Service listed 5 distinct population segments (DPSs) of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) under the Endangered Species Act in 2012 (Federal Register, 2012a 2012b). Since this listing, new spawning populations have been discovered (Hager et al., 2014; Balazik et al., 2017; Farrae et al., 2017; Savoy et al., 2017). It now appears that some rivers support 2 genetically different spawning populations and that rivers identified within the geographic area of a DPS may have a seasonal spawning group of sturgeon that are more closely related to sturgeon spawning in other rivers outside of the area of that DPS (White et al., 2021). Of the 5 DPSs in the United States, the Gulf of Maine DPS was listed as threatened under the Endangered Species Act, and the New York Bight, Chesapeake Bay, Carolina, and South Atlantic DPSs were listed as endangered. At the time of listing, the Chesapeake Bay DPS had one known spawning population: the population in the James River, which at the time had been confirmed to spawn after summer as temperatures decline (Balazik et al., 2012a). Like the York River, the James River is located in Virginia. Since the listing in 2012, adult Atlantic sturgeon have been confirmed to spawn in the York River (Hager et al., 2014); spawning is likely occurring in the Nanticoke River, located on the Delmarva Peninsula, and possibly in the Rappahannock River, located in eastern Virginia (ASMFC, 2017). Results of genetic analyses of the populations in the James and York Rivers indicate that these 2 populations are significantly differentiated (White et al., 2021).

Atlantic sturgeon are long-lived, wide-ranging, late-maturing, iteroparous, anadromous fish that spawn intermittently (Smith, 1985; Bemis and Kynard, 1997; Dadswell, 2006; NMFS, 2007; Peterson et al., 2008; Hager et al., 2020). Adult and migratory juvenile Atlantic sturgeon spend significant portions of each year along the East Coast for feeding, growing, overwintering, and migrating (Dovel and Berggren, 1983; Smith, 1985; Bain, 1997; Stevenson, 1997; Wirgin et al., 2015). These individuals undertake seasonal migrations to utilize inshore and offshore habitat (Ingram et al., 2019).

In Chesapeake Bay, there have been no peer-reviewed reports of the timing or windows of occupancy of Atlantic sturgeon. The objective of this study was to identify that timing and the movement of adult Atlantic sturgeon within Chesapeake Bay. We evaluated the migrations of males and females separately in terms of seasons, years, calendar days, photoperiod, and temperatures. Understanding the periods of occupancy is essential for the National Marine Fisheries Service to protect and ultimately recover this endangered species.

Materials and methods

We identified the entrance to Chesapeake Bay as an invisible line from Fort Story, Virginia, to Fisherman's Island National Wildlife Refuge near Cape Charles, Virginia, because this location was the most restricted point at the mouth of the bay (Fig. 1). We determined that a fish had left Chesapeake Bay if it was detected on receivers beyond the boundary denoted by this line or if it entered the mouth of the James, York, or Rappahannock River (Fig. 1). At locations where passive acoustic receivers (VR2W, Innovasea Systems Inc.[1], Boston, MA) were deployed to detect fish implanted with acoustic tags, water temperatures were collected with HOBO U12-015 data loggers (Onset Computer Corp., Bourne, MA) zip tied to the acoustic receivers or from the First Landing (near Cape Henry, Virginia) and York Spit (at the mouth of the York River near Perrin, Virginia) monitoring locations of the NOAA Chesapeake Bay Interpretive Buoy System (data available from website, accessed January 2022).

Atlantic sturgeon were captured, implanted with acoustic transmitters (or tags), and released while on spawning runs in the Pamunkey and Mattaponi Rivers, the 2 main tributaries to the York River. For our analysis, individuals were considered to be on spawning runs if they met a 2-part test: 1) the fish moved a minimum of 20 km above the saltwater interface, and 2) it spent at least 2 weeks in fresh water (Kahn et al., 2019; Hager et al., 2020; Kahn et al., 2021). All tagged Atlantic sturgeon were in the adult size range (1250–2272 mm in fork length [FL]; Grunwald et al., 2008; Waldman et al., 2019; Kahn et al., 2019, 2021) and were captured in upstream freshwater locations on confirmed spawning grounds (Kahn et al., 2019; Hager et al., 2020).

Atlantic sturgeon were captured by using gill nets made of mesh with stretch measures of 23–36 cm from late July through mid-October during 2013–2019 (see Kahn et al., 2019) in the Pamunkey and Mattaponi Rivers. Our research methods followed the permit requirements

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

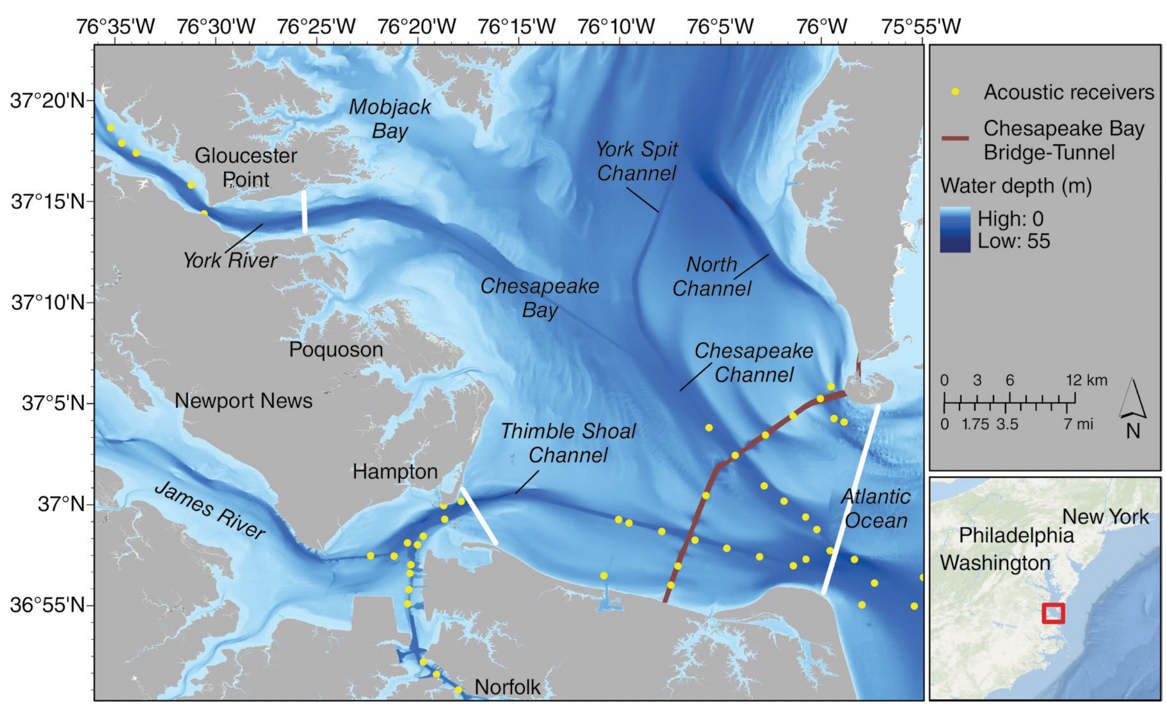

Figure 1

Map of the mouth of Chesapeake Bay showing the locations of passive acoustic receivers and the boundaries (white lines) identified to define the extent of Chesapeake Bay for documenting arrival, departure, and residency of tagged Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the bay. Fish were monitored with acoustic telemetry from August 2013 through January 2020.

and protocols of the Endangered Species Act (Kahn and Mohead, 2010).

Results of the genetic analysis of a previous study (White et al., 2021) indicate that fish from the York River are distinct from fish from other populations along the East Coast. However, some of the fish implanted with transmitters by our team and used in this study were fish natal to the James, Hudson, and Savannah Rivers, as well as to Albemarle Sound (Kazyak et al., 2021). Therefore, the occupancy timing presented herein is weighted toward adults of the population of the York River but is representative of movements of fish natal to 3 different DPSs.

The sex of individuals was determined by applying pressure to the ventral surface, moving from the anterior to posterior ends, ending at the vent. This technique typically produced milt from males (>90% of the time), and females on occasion produced eggs (<20% of the time). Gravid females were usually confirmed to be female when transmitters were implanted. Sex was routinely confirmed upon recapture (Kahn et al., 2021). Ultimately, sex was confirmed for every fish tagged and recaptured in this study.

During this study, 84 adult Atlantic sturgeon (40 males and 44 females) were implanted with V16P-4H, V16P-6x, or V16-6x acoustic transmitters (Innovasea Systems Inc.), with each tag weighing no more than 17.3 g. Transmitters produced a 69 kHz signal every 70–150 s and had a minimum life span of 6 years (11 transmitters) and a maximum life span of 10 years (73 transmitters). Transmitters were placed into incisions of 3–4 cm that were made most often between the 3rd and 4th ventral scutes anterior to the anal fins. The incisions were closed by using Vicryl dissolvable sutures (Ethicon Inc., Raritan, NJ).

The implanted transmitters were passively detected from August 2013 through January 2020. No females were tagged with acoustic transmitters in 2013; therefore, emigrations in 2013 and immigrations in 2014 were recorded for only males. Through January 2020, 100 acoustic receivers in the York River system, Chesapeake Bay, and Atlantic Ocean remained in place (Fig. 1). They were serviced and their data was downloaded either monthly or every other month depending on their location. Receivers in rivers, Chesapeake Bay, and nearshore waters of the Atlantic Ocean were downward-facing and deployed within 6 m of the surface, and offshore receivers were anchored to the seafloor and recovered with an acoustic release.

When monitoring movements of Atlantic sturgeon, we assumed acoustic transmitters were in fish that were behaving normally. We also performed range tests by using stationary transmitters and receivers at variable distances in Chesapeake Bay near the mouth of the James River. We used transmitters of the same size for the monitoring in this study and for the range tests to minimize error, but detection distances can also be affected by environmental conditions, such as tides and sea state (Mathies et al., 2014). A single stationary transmitter with a 10-s ping rate was deployed, and receivers were deployed every 100 m away from this transmitter. When receivers were placed at a depth of approximately 10 m, the distance at which over 90% of signals from the test transmitter were detected under optimal conditions was 1.3 km; in contrast, for receivers deployed at depths less than 2 m under rough conditions, this detection rate extended out only 200 m. Under various conditions over a 1-week period, receivers within 700 m of the transmitter detected at least 90% of transmissions. For the purposes of understanding when Atlantic sturgeon were present in Chesapeake Bay, we defined presence as multiple detections on 1 receiver or detections on 2 neighboring receivers on the same day. Therefore, any variability in detection distance would lead to underestimation of the timing of arrival and departure. Generally, we expected to detect fish within 700 m of a receiver.

Atlantic sturgeon belonging to the spawning population in the York River spawn only during the fall (August–October) of each year (Kahn et al., 2019; Hager et al., 2020). The times of first arrival to Chesapeake Bay from the Atlantic Ocean, of departure from Chesapeake Bay into tributary river systems, of entry into Chesapeake Bay from those same systems, and of departure from Chesapeake Bay to the Atlantic Ocean were recorded for each transmitter implanted in a fish as ordinal dates and as photoperiod in hours, minutes, and seconds from sunrise to sunset. We report the timing of these movements for each sex but considered mean, median, and timing for different proportions of transmitters (10%, 20%, etc.). In any given year, the general pattern of migration followed a normal distribution once it began; therefore, we report the earliest arrival and latest departure because 1) not all fish in the population are tagged with acoustic transmitters and not all tagged fish were acoustically detected, meaning that the timing is an approximation of actual first arrival or last departure, and 2) the purpose of this analysis was to identify periods of presence and absence from Chesapeake Bay. However, results from analyses of statistical differences are presented as mean values. We recorded the temperature from the nearest source (HOBO data logger, acoustic receiver, or buoy).

Most individuals left Chesapeake Bay in the summer by initiating a spawning run. Non-spawning fish generally remained near the mouth of the bay and were consistently detected throughout the summer, and spawning fish moved farther into the bay and had periods during which they were not detected as they moved through the areas without receiver coverage (Fig. 1). We conservatively calculated residency times in the bay from the date of first detection to the date of last detection, such that data for an animal detected leaving the mouth of the York River in the fall and not detected again were aggregated with data for other tagged fish leaving the river and used to calculate an average date of entry into the bay from the river, but we did not use that single data point to estimate bay residency. However, the dates of first or last detection, when used to calculate residency, were not necessarily representative of the beginning or end of occupancy because receiver coverage was incomplete. These periods of presence in Chesapeake Bay were analyzed by sex, by length and sex (because adult Atlantic sturgeon are sexually dimorphic), and by year.

Each Atlantic sturgeon was classified as either above or below the average length for its sex. Measurements were made by using a 2.44-m PVC T-board with a 3-m tailor's tape measure. The mean lengths of males and females were 1518 and 1880 mm FL (Kahn et al., 2019). Because fish generally grew through time, when adults were recaptured, they occasionally had moved from below average to above average length. For example, Fish 13-015, a male, was captured 6 times during the 7 years of this study (in 2013–2017 and 2019), ranging in size from 1490 to 1548 mm FL. This individual was categorized as *below average* the first 2 years and *above average* the last 5 years. In the event that a fish was not captured in the year of the analysis, its most recent measured length was used for categorization.

Differences in arrival and departure times (ordinal dates) and temperature were assessed by using analysis of variance in statistical software R (vers. 4.2.2; R Core Team, 2022). The significance level was 0.05. When significant differences were identified, Tukey's honestly significant difference test was used to identify significantly different variables. Data were organized in a table identifying sex, size category, year, bay entry, river entry, river departure and arrival, bay departure, photoperiod for each day of arrival and departure, and days spent in the bay before and after each spawning period for each tagged individual. Because photoperiod and day are correlated, only day of the year is discussed for ease in identifying when Atlantic sturgeon were present.

Sampling was conducted under permits from the Virginia Marine Resources Commission, the Virginia Department of Wildlife Resources (formerly the Virginia Department of Game and Inland Fisheries), and the National Marine Fisheries Service (permit nos, 16547 and 19642).

Results

Both spawning and non-spawning fish regularly utilized Chesapeake Bay, starting as the water began to warm in the spring and ending as it cooled in the fall. The earliest arrival of a tagged Atlantic sturgeon in Chesapeake Bay from the Atlantic Ocean was detected on 27 February for females and on 4 March for males, corresponding to daily mean water temperatures of 7.3°C and 6.5°C at the locations of first detection upon entry, respectively. Males and females generally did not arrive until water temperatures were above 6°C, except for 3 females, who arrived in water as cool as 2.9°C. The latest date of arrival of a fish implanted with an acoustic tag to the bay from the ocean, with the exception of the arrival of a male outlier on 22 August, was recorded on 17 July for males and on 11 July for females, corresponding to daily mean water temperatures of 27.9°C and 26.0°C at their locations of first detection upon entry, respectively. In all years, at least 1 Atlantic sturgeon remained in the bay after its arrival, even during the spawning event, until departure back to the ocean. The latest departure (last detection) from the bay to the ocean after spawning was recorded on 24 January for females and on 27 January for males, corresponding to daily mean water temperatures of 6.3°C and 6.5°C at the locations of last detection, respectively. Atlantic sturgeon generally left Chesapeake Bay for the ocean when water temperatures were approaching a minimum of 6°C, with the exception of a large male that left for the ocean when the daily mean water temperature at its location of last detection was 3.4°C.

The majority of fish were detected moving through Chesapeake Bay on spawning runs. Spawning males were detected in the bay during 78.7% (244 detections of the 310 times males are known to have moved through the bay to reach the river when they were detected) of their spawning runs, and spawning females were detected during 81.2% (108 detections of the 133 times females were known to be present) of theirs. Non-spawning fish did not always return to Chesapeake Bay, but when they did males were detected during 67.7% (23 detections of the 34 times males were known to be present) of their non-spawning years and females detected during 55.0% (61 detections of the 111 times females were known to be present) of theirs. The detection rate between years varied (Table 1), but the locations of the passive acoustic receivers we used to monitor migrations did not.

Males and females were detected in Chesapeake Bay during January or February 1.5% (5 of 344 males) and 1.2% (3 of 244 females) of the time, as both their arrival and departure between the bay and the ocean pushed into winter. There were no significant interannual differences in date of entry to the bay from the ocean in the spring or in date of departure from the bay to the ocean in the fall for males or females (Table 2). However, only 5 of 77 (6.5%) returning fish (male or female) were detected in the bay before 1 April in 2014 (0 fish), in 2015 (1 fish, when the mean daily temperature near the detection location was 10.2°C), and in 2016 (4 fish, when temperatures were 11–12.6°C), but in 2018 and 2019, the first fish were detected entering the bay in February.

Further illustrating this shift in arrival times, in 2018 and 2019, 30.8% of all adults (33 of 107 fish) had entered the bay by 10 April. The first detections in February of 2018 and 2019 were of the same female that arrived when the mean temperature in the bay was 2.9°C and 7.3°C. Likewise, in each of 2013, 2014, 2015, and 2016, cumulatively only 3 fish (of 161 individuals, 1.9%) were detected still out-migrating through the bay toward the ocean during December but, by 2019, 10 fish (of 47 individuals, 21.3%) were detected in the bay in December, with 2 fish remaining in the bay until January. Of those fish detected in December 2019 and January 2020, 9 individuals were tagged with acoustic transmitters in 2013 and 2014, with the other fish tagged with acoustic transmitters in 2015; therefore, the increase in sturgeon presence in December and January following the 2019 spawning season was not just a case of more Atlantic sturgeon being tagged with acoustic transmitters in later years. This apparent extension of the use of Chesapeake Bay was not significant, and only males had any significant differences in interannual behavior (Table 2).

Table 1

Numbers of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) of each sex tagged and the numbers and proportions of males and females that were detected within Chesapeake Bay at some point during a season, either before (pre) or after (post) spawning from 2013 through 2019. Atlantic sturgeon typically do not spawn every year; therefore, values are provided for both spawning and non-spawning fish. NA=not applicable because no tagged male or female Atlantic sturgeon were detected during the specified season.

		Spawning						Non-spawning					
		Males			Females			Males			Females		
			Detected in bay			Detected in bay			Detected in bay			Detected in bay	
Year	Season	No. tagged	No.	%	No. tagged	No.	%	No. tagged	No.	%	No. tagged	No.	%
2013	Post	12	10	0.83	NA	NA	–	NA	NA	–	NA	NA	–
2014	Pre	9	8	0.89	NA	NA	–	3	1	0.33	NA	NA	–
	Post	27	24	0.89	9	8	0.89	3	0	0.00	NA	NA	–
2015	Pre	24	23	0.96	2	2	1.00	4	4	1.00	6	4	0.67
	Post	24	13	0.54	4	3	0.75	4	3	0.75	6	2	0.33
2016	Pre	22	21	0.96	5	4	0.80	3	2	0.66	7	4	0.57
	Post	22	16	0.73	12	10	0.83	6	2	0.33	6	1	0.17
2017	Pre	28	25	0.89	4	4	1.00	3	3	1.00	13	11	0.85
	Post	29	21	0.72	17	15	0.88	2	2	1.00	13	7	0.54
2018	Pre	27	26	0.96	11	11	1.00	2	2	1.00	19	14	0.74
	Post	27	14	0.52	14	10	0.71	2	2	1.00	19	7	0.37
2019	Pre	28	24	0.86	22	18	0.82	1	1	1.00	11	8	0.73
	Post	31	19	0.61	33	23	0.70	1	1	1.00	11	3	0.27

The average date of arrival to Chesapeake Bay from the Atlantic Ocean for females was 12 April and for males was 22 April (P=0.005), correlating to mean temperatures at the locations of first detection upon entry into the bay of 11.8°C and 13.5°C (P=0.01), respectively. Fish of both sexes spent prolonged periods in Chesapeake Bay from entry to initiating a spawning run but took a quicker, more direct route out of the bay after spawning (Fig. 2). Females spent an average of 96.98 d (range: 27–184 d) in the bay before spawning, compared with 82.86 d (range: 3–160 d) for males (P=0.051). Males entered their spawning river from the bay on average on 13 July (when the mean temperature in the bay was 25.6°C; range: 11 April–3 September), and females entered on average on 15 July (24.8°C; range: 30 March–7 October). Females, on average, left the York River and reentered the bay on 24 October (19.4°C; range: 17 September–19 December), and males reentered on 25 October (18.8°C; range: 19 September–21 January). Males left the bay for the ocean after spawning on 13 November (15.4°C; range: 25 September–27 January), on average, and the average departure date for females was 9 November (16.6°C; range: 3 October–24 January). Arrival and departure dates relative to average length are provided in Table 3.

After spawning, males spent on average 20.51 d (range: 1–89 d) in Chesapeake Bay, compared with 14.79 d (range: 1–72 d) for females, as they out-migrated (P=0.022, for males versus females; P=0.11, when considering relative length of each sex). Results from assessment by period, either before or after spawning, indicate that females spent significantly longer in Chesapeake Bay only during the prespawning period in 2015 (P=0.02) and 2016 (P=0.038), spending 129.00 d (range: 116–142 d) and 115.30 d (range: 74–155 d) in the bay when males spent an average of 72.89 d (range: 26–134 d) and 71.92 d (range: 5–144 d) there. Differences between size groups and sexes were detected for bay entry day, river entry day, river entry temperature, and prespawning days (Table 4).

Discussion

The Atlantic sturgeon is an endangered species in Chesapeake Bay, and the best mitigation to promote its conservation is limiting potentially harmful interactions by identifying the times Atlantic sturgeon are present in Chesapeake Bay and by planning potentially harmful activities accordingly. Females were recorded in the bay during prespawning periods from 27 February to 7 October. Males entered the bay as early as 4 March and stayed during the spring and summer until as late as 3 September. With the lone exception of the spawning initiation on 7 October, the departure of Atlantic sturgeon from Chesapeake Bay to rivers and reentry into Chesapeake Bay from rivers did not overlap. In every year of this study, females were in the bay from 28 March to 26 November, and males were in the bay from 3 April to 23 November (Fig. 2). Females entered Chesapeake Bay from the Atlantic Ocean earlier than males, with the smallest

Table 2

Comparison of annual averages of the days of arrival and departure of tagged Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) into or out of Chesapeake Bay or a river, temperatures in the bay and river at arrival and departure, and number of days tagged fish spent in the bay before and after spawning, by sex. Atlantic sturgeon were monitored with acoustic telemetry from August 2013 through January 2020. Letters denote statistically significant differences ($P \leq 0.05$), with values having like letters not being significantly different from those within the compared group. Arrival and departure days are given as days of the year.

	Males before spawning				
Year	Bay entry day	River entry day	Bay entry temp (°C)	River entry temp (°C)	No. of days in bay
2015	115.85	189.10[ab]	14.9	25.6[ab]	72.89[a]
2016	115.11	187.15[a]	13.8	24.9[ab]	71.92[a]
2017	104.00	186.22[a]	12.5	24.5[a]	83.21[ab]
2018	114.85	194.09[ab]	12.4	26.1[ab]	81.58[ab]
2019	107.41	212.09[b]	13.7	26.7[b]	106.46[b]
	Males after spawning				
Year	River exit day	Bay exit day	River exit temp (°C)	Bay exit temp (°C)	No. of days in bay
2014	289.00[a]	309.14	20.1[a]	15.4	20.75
2015	296.25[abc]	311.00	18.1[ab]	17.0	20.06
2016	300.45[bc]	322.36	18.2[ab]	14.9	21.09
2017	295.53[ab]	320.00	20.2[a]	15.0	27.59
2018	300.66[bc]	319.72	18.6[ab]	13.6	19.44
2019	306.44[c]	319.70	17.1[b]	14.9	12.27
	Females before spawning				
Year	Bay entry day	River entry day	Bay entry temp (°C)	River entry temp (°C)	No. of days in bay
2015	104.67	222.00	13.2	27.7	129.00
2016	104.14	197.20	13.1	22.9	115.25
2017	88.47	176.25	9.4	24.2	86.50
2018	108.16	202.82	10.9	26.8	89.18
2019	103.15	192.59	13.1	23.0	96.47
	Females after spawning				
Year	River exit day	Bay exit day	River exit temp (°C)	Bay exit temp (°C)	No. of days in bay
2014	297.25	313.71	18.0	14.5	14.71
2015	287.67	310.67	19.9	17.0	20.50
2016	289.67	307.18	20.8	16.9	18.70
2017	295.28	310.41	20.1	17.2	16.69
2018	292.93	311.35	21.4	16.7	12.00
2019	302.85	317.96	18.0	15.2	12.13

females returning the earliest (Table 4). When spawning, females of below average size (<1880 mm FL) entered the York River the earliest, all males entered roughly at a similar intermediary time, and then significantly later, females of above average size moved into the river (Table 4). The largest females with the most reproductive potential (Mitchell et al. 2020) spent significantly more time each summer in the bay (over 113 d on average) than smaller females or all males. Therefore, the threats faced by Atlantic sturgeon in Chesapeake Bay are disproportionately affecting the largest females of the population, those most critical to the recovery of this population of Atlantic sturgeon.

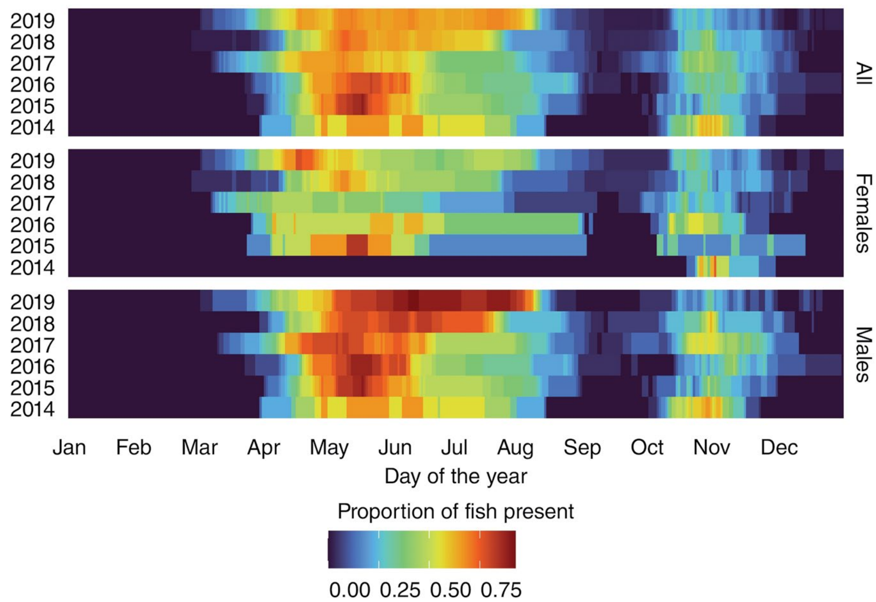

Figure 2

Proportion of all tagged Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) present in Chesapeake Bay during the periods before and after spawning from August 2013 through January 2020. Presence of females and males are also shown separately. No females were tagged or available for detection until the fall of 2014. Passive acoustic telemetry was used to monitor tagged fish.

One of the threats in Chesapeake Bay is vessel strike, with the tendency of Atlantic sturgeon to drift along with water flow (Poletto et al., 2014) making them particularly vulnerable to being pulled through the propellers of vessels (Brown and Murphy, 2010; Balazik et al., 2012b; Demetras et al., 2020). In modeling efforts, this suction of propellers is great enough to pull a whale up from a depth equivalent to 2 full ship drafts and into contact with propellers (Silber et al., 2010). When fish are pulled up to propellers, there is a direct linear relationship between length and probability of being struck such that smaller fish have a better chance than longer fish of moving through without contacting a blade. We recommend that vessel operation and movement be timed to avoid, to the extent possible, the periods from 1 April through 31 August and from 15 October through 1 December. Although this timing would avoid interactions with most tagged adult individuals, adult presence between 2013 and 2019, at its extremes, was documented between 27 February and 24 January; therefore, Atlantic sturgeon will face threats in Chesapeake Bay even if those protection periods are established.

Adult Atlantic sturgeon use Chesapeake Bay seasonally, as has been reported for this species in other systems (Dovel and Berggren, 1983; Smith, 1985; Bain, 1997; Dunton et al., 2010; Ingram and Peterson, 2016; Ingram et al., 2019). Atlantic sturgeon overwinter in the Atlantic Ocean, and they move into Chesapeake Bay as waters begin to warm. Males and females generally do not arrive until water temperatures are above 6°C. In general, both males and females have been arriving to the bay earlier and earlier each year (Table 2, Fig. 2). This trend of earlier arrival times is consistent with temperature data (from buoys of the Chesapeake Bay Interpretive Buoy System) that indicate that the warming of Chesapeake Bay begins earlier each year, affecting migratory timing and species distributions in the bay and other areas along the Atlantic coast of the United States (Richardson et al., 2018; Crear et al., 2020; Pinsky et al., 2020). Our observations support the conclusion of Ingram et al. (2019) that use of offshore habitat was influenced primarily by inshore drivers.

Departure of tagged fish from Chesapeake Bay and back into the Atlantic Ocean occurred relatively quickly after spawning (Table 4). On average, females took approximately 2 weeks and males took approximately 3 weeks to move through the bay to the ocean. Females generally left the York River after spawning, and males remained until all females had left. Because the timing of the spawning season of Atlantic sturgeon is driven by temperature and photoperiod (Hager et al., 2020), male out-migration into the bay was significantly later in 2016 and 2018, and the late movement from river to bay became even more extreme in 2019 (Table 2). Despite the change in the day that males reentered the bay from rivers, there was no corresponding change in the day males left the bay for the ocean. Given that nearly every male spawns every year (Hager et al., 2020), acoustic

Table 3

Range of ordinal dates of occupancy in Chesapeake Bay for each size class of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) monitored with acoustic telemetry from August 2013 through January 2020, by sex and season, before (pre) and after (post) spawning. The size classes are below or above average size, which was 1518 and 1880 mm in fork length [FL] for males and females, respectively. The year 2016 was a leap year. A day of the year exceeds 365 or 366 for a particular year because at least 1 fish from that size class remained in Chesapeake Bay into the following calendar year. NA=not available because no females of that size class were detected in that year.

		Below average (mm FL)	Above average (mm FL)
Year	Season	Males	
2013	Post	276–327	275–312
2014	Pre	106–224	91–225
	Post	280–327	271–326
2015	Pre	101–242	93–239
	Post	279–333	271–370
2016	Pre	69–241	91–240
	Post	283–392	285–359
2017	Pre	71–245	67–243
	Post	262–369	276–356
2018	Pre	91–246	91–243
	Post	287–335	279–374
2019	Pre	85–239	63–230
	Post	284–351	285–373

		Below average (mm FL)	Above average (mm FL)
Year	Season	Females	
2013	Post	NA	NA
2014	Pre	NA	NA
	Post	293–326	278
2015	Pre	85–200	103–244
	Post	278–349	273–287
2016	Pre	87–247	88–242
	Post	275–330	284–309
2017	Pre	68–210	90–205
	Post	270–347	260–320
2018	Pre	59–243	87–235
	Post	277–335	282–374
2019	Pre	58–252	64–280
	Post	272–365	270–389

detections of tagged males in Chesapeake Bay in the fall were generally a result of them leaving the York River. However, because fewer than half of all females spawn each year, detections of tagged females from September until they left the bay for the ocean were not necessarily a result of them leaving a river. Atlantic sturgeon continued to leave the bay at similar temperatures each year regardless of spawning status, size, or sex (Tables 2 and 4), indicating that the cue for exiting the bay is either day or temperature and not simply a rapid migration from spawning river to ocean once spawning is complete.

Conclusions

Atlantic sturgeon face the greatest risk of interacting with anthropogenic threats when in estuarine and fresh water. Virginia and Maryland both support a variety of fisheries in Chesapeake Bay that have bycatch of Atlantic sturgeon (Welsh et al., 2002; Stein et al., 2004; ASSRT, 2007; Trice[2]). Water quality in Chesapeake Bay has improved somewhat in the past 50 years, but large areas are still hypoxic or anoxic (Scavia et al., 2021; Tian et al., 2022). Vessel strikes are the most frequently observed source of mortality of Atlantic sturgeon in Chesapeake Bay (in records of Atlantic sturgeon salvaged and reported under National Marine Fisheries Service permit no. 21858), despite very low reporting rates (Brown and Murphy, 2010; Balazik et al., 2012b; Fox et al.[3]).

The results of our research indicate that Atlantic sturgeon use Chesapeake Bay primarily when water temperatures exceed 6°C. When Chesapeake Bay is cooler, Atlantic sturgeon in coastal waters off mid-Atlantic states seek thermal refuge in offshore waters (Ingram et al., 2019; Rothermel et al., 2020; Hager and Breault[4]). The amount of the year during which water temperatures are higher than 6°C in Chesapeake Bay is increasing relatively rapidly. When this study began in 2013, the period of offshore overwintering by Atlantic sturgeon was 2–4 months, but the length of that period has fallen to approximately 35 d in 2019. Waters along the Atlantic coast of the United States are expected to continue warming through the 21st century (IPCC, 2023), affecting the timing of arrivals and departures of Atlantic sturgeon into and from Chesapeake Bay. As waters in Chesapeake Bay provide more days of hospitable temperatures for Atlantic sturgeon, we anticipate and have observed a corresponding increase in their use of Chesapeake Bay, particularly by the largest females (>1880 mm FL), who currently spend significantly longer in Chesapeake Bay than fish of any other sizes (Table 4). All adult Atlantic sturgeon in Chesapeake Bay are subject to the threats of vessel strike, poor water quality, and bycatch. Vessel strikes appear to pose the greatest threat

[2] Trice, G. E., IV. 2014. Observing striped bass and Atlantic sturgeon bycatch in a striped bass fishery using raised footlines in the Chesapeake Bay, 9 p. Fishery Resource Grant FRG 2014-02. Va. Inst. Mar. Sci., William Mary, Gloucester Point, Va. [Available from website.]

[3] Fox, D. A., E. A. Hale, and J. A. Sweka. 2020. Examination of Atlantic sturgeon vessel strikes in the Delaware River estuary, 36 p. Final report for NMFS award no. NA16NMF4720357. [Available from Agric. Annex Rm. 123, Del. State Univ., 1200 N. DuPont Hwy., Dover, DE 19901.]

[4] Hager, C., and D. K. Breault. 2023. Spatiotemporal distributions of species detected within Virginia's offshore lease areas. Volume 2: The Virginia Wind Energy Lease Area A-0483, 141 p. Report to Bureau of Ocean Energy Management for contract no. 140M0122P0023. [Available from Chesapeake Scientific LLC, 100 Sixpence Ct., Williamsburg, VA 23185.]

Table 4

Comparison of average seasonal residency in Chesapeake Bay and its rivers for tagged Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) monitored with acoustic telemetry from August 2013 through January 2020, by sex and size class. Average days of arrival in the bay and then in a river, days of departure from that river and then from the bay, temperatures in the bay and river at entry and exit, and number of days tagged fish spent in the bay each season, before and after spawning, are provided. The size classes are below or above average size (BA or AA), which was 1518 and 1880 mm in fork length for males and females, respectively. Letters denote statistically significant differences ($P \leq 0.05$), with values having like letters not being significantly different from values in each column for arrivals and departures separately. Days of entry and exit are given as days of the year.

		Before spawning				
Sex	Size class	Bay entry day	River entry day	Bay entry temp (°C)	River entry temp (°C)	No. of days
Female	AA	104.77[ab]	218.88[b]	12.22	27.02[b]	113.61[a]
	BA	100.51[a]	179.35[a]	11.46	23.18[a]	83.36[b]
Male	AA	111.56[b]	196.09[c]	13.78	26.10[b]	86.15[b]
	BA	112.18[b]	191.04[ac]	13.13	24.82[a]	77.45[b]

		After spawning				
Sex	Size class	River exit day	Bay exit day	River exit temp (°C)	Bay exit temp (°C)	No. of days
Female	AA	294.33	311.31	20.25	16.69	14.84
	BA	298.07	313.44	18.86	16.01	14.76
Male	AA	297.19	316.04	18.96	15.08	21.44
	BA	298.60	316.92	18.46	15.42	19.04

to populations of this species, and the larger the fish, the less likely it is to pass through a propeller without being struck, disproportionately threatening large females who also have the greatest fecundity. The U.S. Congress established the Endangered Species Act to require federal agencies and encourage states to protect endangered species like the Atlantic sturgeon. The data provided herein should allow managers to establish appropriate avoidance periods to protect Atlantic sturgeon and prevent the extirpation of populations of Chesapeake Bay.

Resumen

El esturión del Atlántico (*Acipenser oxyrinchus oxyrinchus*) está incluido la Ley de Especies Amenazadas desde 2012, con una fracción de la población de la bahía de Chesapeake listada como en peligro. Rastreamos los lapsos de ocupación y movimiento de esturiones adultos en la bahía de Chesapeake del Atlántico procedentes del río York para identificar cuándo es probable que el esturión del Atlántico interactúe con las amenazas antropogénicas. Monitoreamos 84 esturiones del Atlántico adultos (40 machos y 44 hembras) desde agosto de 2013 hasta enero de 2020 mediante telemetría acústica. Tanto los peces desovantes como los no-desovantes utilizaron regularmente la bahía de Chesapeake, con hembras y machos llegando desde el 27 de febrero (cuando la temperatura media del agua fue de 7.7°C) y el 4 de marzo (6.5°C) y partiendo el 24 de enero (6.3°C) y el 27 de enero (6.5°C), respectivamente. La mayor ocupación en la bahía por el esturión del Atlántico fue del 1 de abril al 31 de agosto y de nuevo del 15 de octubre al 1 de diciembre. Antes de desovar, las hembras de tamaño mayor al promedio (>1880 mm de longitud furcal) pasaron significativamente más tiempo en la bahía (>113 d) que las hembras más pequeñas y todos los machos. Por lo tanto, las hembras capaces de producir la mayor cantidad de huevos estuvieron desproporcionadamente expuestas a las amenazas antropogénicas. Aunque los cambios en las fechas de llegada y salida no son estadísticamente significativos, durante los 7 años de este estudio, tanto los machos como las hembras generalmente llegaron antes y se marcharon más tarde cada año que el anterior, aumentando en un mes la residencia en la Bahía de Chesapeake.

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