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Age structure and seasonal movement of Atlantic sturgeon (*Acipenser oxyrinchus*) aggregating in eastern Long Island Sound and the Connecticut River

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Abstract—Atlantic sturgeon (*Acipenser oxyrinchus*) seasonally aggregate in Long Island Sound and the Connecticut River, but their size and age structure and use of the river remain insufficiently understood. We analyzed all available length data from monitoring efforts (1988–2021: number of samples [*n*]=3544), estimated age from sections of pectoral-fin spines (*n*=296), and measured annuli widths for retrospective size-at-age analysis (*n*=166). Fish ranged from 21 to 218 cm in total length ([TL], mean: 105.2 cm TL), but 87% of them measured 50–130 cm TL. Ages ranged from 0 to 18 years (mean: 8.1 years), with 92% of all individuals estimated to be younger than 12 years. Annuli widths indicate that faster growing fish selectively disappeared from the study area over time. To reveal movement patterns, particularly for the upper Connecticut River (freshwater), we analyzed 3 years (2019–2021) of acoustic detections of 85 individuals. These fish occurred in the study area from March through November but stayed on average only 54–91 d. The majority of fish entering the receiver arrays in Long Island Sound also moved into the river but largely utilized its lower, brackish estuary. Still, a large proportion of individuals (35%–66%) made upriver excursions into freshwater, and the timing coincided with low flow and warm river temperatures in late summer. Therefore, both the brackish and freshwater portions of the Connecticut River serve as important seasonal feeding habitats for Atlantic sturgeon ≤130 cm TL.

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Sturgeon (Acipenseridae) are among the most endangered fish groups in the world, as historic overexploitation and habitat destruction have long decimated the populations of most of its extant 25 species (Pikitch et al., 2005). The Atlantic sturgeon (*Acipenser oxyrinchus*) is an anadromous species that occurs in waters along the Atlantic coast of North America from the Florida peninsula to the Gulf of St. Lawrence in Canada (a range approximately from 30°N to 52°N; Hilton et al., 2016). Juveniles remain in their natal rivers for 1–6 years before entering marine waters (Dovel and Berggren, 1983). Subadults, a group that includes fish 50–130 cm in total length [TL], then form aggregations and migrate along the coast, where they utilize natal and non-natal river estuaries to feed (Waldman et al., 2013). Overexploitation of this large, slow-growing, and late-maturing species during the 19th and 20th centuries caused severe population declines and triggered a coast-wide fishing moratorium in 1998 (Secor, 2002). River pollution, obstruction of freshwater spawning habitats by dams, vessel strikes, and dredging all acted to exacerbate negative abundance trends (Waldman et al., 2019). Today, all 5 genetically distinct population segments (DPSs) in the United States (i.e., the South Atlantic, Carolina, Chesapeake Bay, New York Bight, and Gulf of Maine DPSs) are listed as either endangered or threatened under the Endangered Species Act (Federal Register, 2012a, 2012b). Spawning populations are thought to have been lost from 13–19 of the 38 rivers across the Atlantic seaboard where they have historically been found (ASSRT, 2007; ASMFC, 2017; Waldman et al., 2019).

The Connecticut River is the largest river in New England (653 km long) and the main freshwater source to Long Island Sound (Koppelman et al., 1976). Historical records indicate that Atlantic sturgeon utilized and presumably spawned in several upstream locations in the Connecticut River (Galligan, 1960), but all spawning runs probably ceased in the early 20th century. Yet, both the Connecticut River and Long Island Sound still provide essential habitat for Atlantic sturgeon (Federal Register, 2017) because Atlantic sturgeon of all 5 DPSs are known to aggregate there from late spring to early fall presumably to feed or seek physiological refuge (Savoy and Pacileo, 2003; Waldman et al., 2013). The upper, freshwater portion of the Connecticut River (which begins at river kilometer [rkm] 22) could be of particular importance because Atlantic sturgeon appear to use it as either foraging ground or again as potential spawning habitat, the latter indicated by the recent discovery of pre-migratory juveniles in the river (Savoy et al., 2017).

The Connecticut Department of Energy and Environmental Protection (DEEP) has monitored Atlantic sturgeon in the area of Long Island Sound and the Connecticut River since 1988, by collecting samples of pectoral-fin spines for age determination and, more recently, by deploying receivers to detect acoustically tagged individuals (Savoy[1]). Fin spines of Atlantic sturgeon have been sampled nonlethally and can be used to determine age from annuli counts with acceptable precision (Stevenson and Secor, 1999). Furthermore, the proportionality of somatic and fin spine growth in sturgeons (Sunde, 1961; Kehler et al., 2018) is similar to the known coupling of somatic and otolith or scale growth in other fish species (Campana, 1990; Baumann et al., 2013), allowing back-calculation of lengths and growth characterization for individuals.

In this study, we analyzed the DEEP fin spine collection and recent DEEP telemetry data[2] because they both hold relevant, complementary information for conservation of Atlantic sturgeon in Long Island Sound and the Connecticut River. For example, size-at-age analyses allowed inferring whether the area is utilized only by juveniles and subadults or also to some extent by adults and how their respective length-at-age patterns compare to those of Atlantic sturgeon from other studied aggregations. In addition, the acoustic detections of tagged Atlantic sturgeon allowed us to develop detailed insights into what areas of Long Island Sound and the Connecticut River are of particular importance to Atlantic sturgeon and in what season, information that is critical for refining conservation measures.

The first objective of this study therefore was to quantify the length and age structure of Atlantic sturgeon by analyzing already existing samples of pectoral-fin spines. We hypothesized that the aggregation of Atlantic sturgeon in Long Island Sound and the Connecticut River consists predominantly of subadults and that their length-at-age patterns are similar to those recently compiled for Atlantic sturgeon in the New York Bight (Dunton et al., 2016). Back-calculation of the lengths of individuals specifically allowed us to test for changes in the variability of growth phenotypes with increasing age at capture. Our second objective was to analyze 3 years (2019–2021) of existing telemetry records for Atlantic sturgeon to determine their habitat utilization and areas of seasonal occupancy in the sound and the estuarine and freshwater portions of the river. We were particularly interested in the sizes of Atlantic sturgeon that make freshwater excursions into the upper Connecticut River to infer whether such behavior could be related to spawning. Lastly, we correlated the seasonal occupancy patterns to 2 environmental parameters, temperature and discharge volume in the Connecticut River, to identify signals for upriver movements.

Materials and methods

Fin spine samples: age and growth

Atlantic sturgeon were caught with gill nets or skiff trawls in the Connecticut River (rkm 0–52) and in adjacent eastern Long Island Sound (Fig. 1) from April through November in 1988–2021 by using procedures detailed in Damon-Randall et al. (2010). Gill nets had 100.0-by-2.3-m panels of different mesh sizes (7.6–25.4-cm stretched mesh) to maximize catchability across the expected size spectrum for Atlantic sturgeon (20–200 cm TL) (Moser et al., 2000; Damon-Randall et al., 2010). Gill nets were deployed for ≤2 h, and trawl nets (9.7 by 7.0 m, 2-cm codend mesh) were towed for ≤12 min at 1.5 kt. All captured Atlantic sturgeon were measured for TL and operationally classified as juveniles (<50 cm TL), subadults (50–130 cm TL), and adults (>130 cm TL) on the basis of permitting definitions of the National Marine Fisheries Service (NMFS[3]; Ingram et al., 2019). Because their sex and spatial origin were not known, we purposefully defined adults as broadly as possible, potentially including fish from southern DPSs (the South Atlantic and Carolina DPSs) that can be mature at 130 cm TL (Collins et al., 2000; Balazik et al., 2012). Samples for aging were taken from a subset of 50 individuals per year (25 fish that were <100 cm TL and 25 fish that were >100 cm TL) by clipping off a roughly 2-cm section of the right pectoral-fin spine (Suppl. Fig. 1). Immediately following these procedures, individuals were released. All methods used for capture and sampling of Atlantic sturgeon were approved and permitted by NOAA permits 16323 (prior to 2017) and 19641 (beginning in 2017).

A total of 301 pectoral-fin spines from Atlantic sturgeon were available in the DEEP collection for age analysis. Samples were air dried for at least 2 months prior to

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[1] Savoy, T. 2017. Assessing reproduction of Atlantic and shortnose sturgeon in the Connecticut River, 15 p. Annual federal aid report for the State Wildlife Grant Program. [Available from Conn. Dep. Energy Environ. Prot., 333 Ferry Rd., Old Lyme, CT 06371.]

[2] Source data from this study are available upon request from the senior and contact authors.

[3] NMFS (National Marine Fisheries Service). 2024. Authorizations and permits for protected species (APPS): location/take information. [Web page available from website, last modified March 2024.]

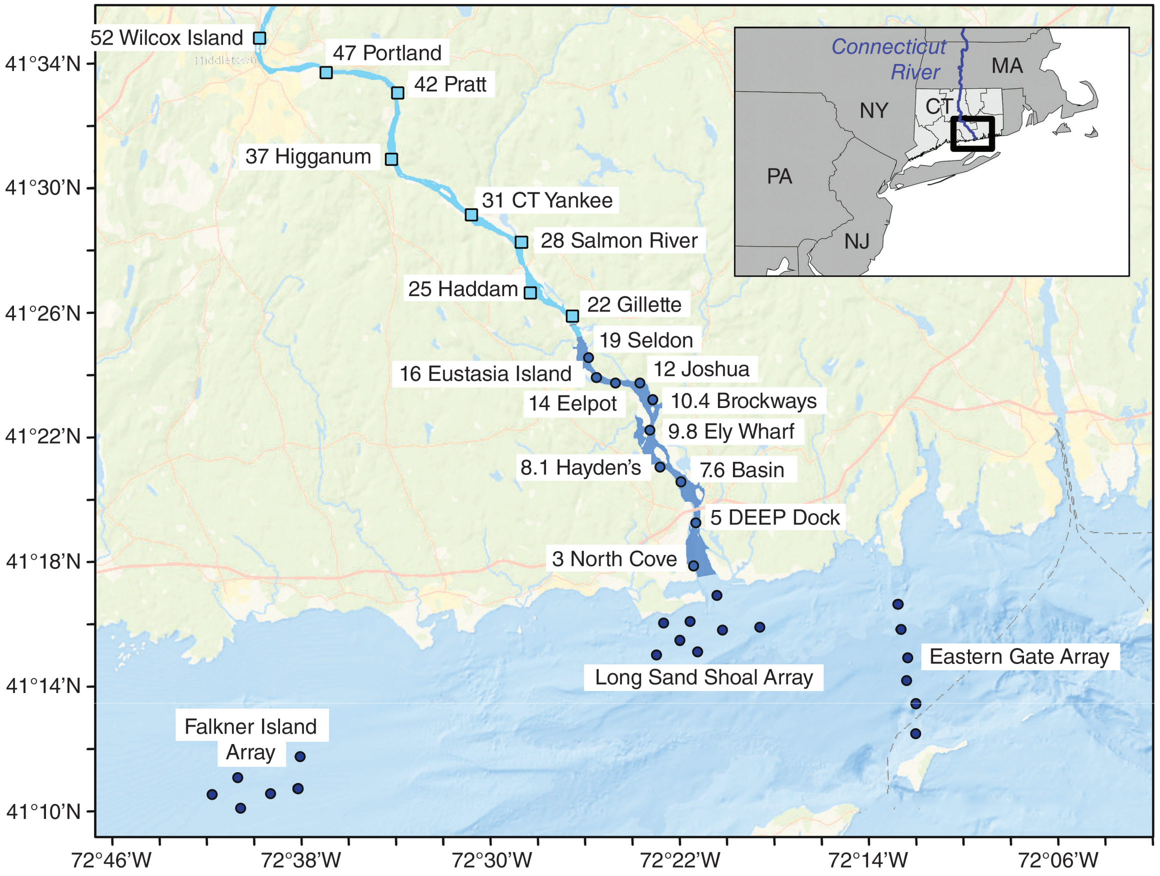

Figure 1

Map of the study area of eastern Long Island Sound and the Connecticut River in the northeastern United States, showing the locations where Atlantic sturgeon (*Acipenser oxyrinchus*) were captured and tagged from April through November during 2019–2021. Fish were tagged at the mouth of and all along the river, up to river kilometer (rkm) 52. Each receiver in the river is labeled with a numeral for the river kilometer of its location and the station name assigned to it by the Connecticut Department of Energy and Environmental Protection. For analysis and presentation of data from this study, receivers in the river are grouped into 2 areas: the brackish estuary (rkm 3–19; blue circles and river shading) and the freshwater upper section (rkm 22–52; cyan squares and river shading). Dark blue circles indicate the acoustic receivers that make up the 3 arrays in the sound, Long Sand Shoal, Eastern Gate, and Falkner Island. Data from receivers placed in the river beyond rkm 52 (at Wilcox Island) were omitted because those receivers recorded no detections of Atlantic sturgeon during the study period. Basemap data sources: NOAA OCS, Esri, DeLorme, and NaturalVue.

sectioning by using an IsoMet Low Speed Saw (Buehler Lake Bluff, IL) equipped with double diamond-dusted blades to produce sections approximately 0.4 mm thick. Calibrated images of each fin spine section on a dark background were taken with an Axiocam 105 digital camera (Zeiss, Oberkochen, Germany) connected to a Zeiss Discovery V8 stereomicroscope with transmitted light at 15× magnification. Analysis of these images was done with Image-Pro Premier software (vers. 9.0 and 10.0; Media Cybernetics, Rockville, MD). Each annulus was defined as an opaque zone paired with an adjacent translucent zone, except for the first annulus, which always takes the form of a star- or tree-shaped translucent ring (Kehler et al., 2018). We counted only annuli with translucent zones traceable around most of the spine (Baremore and Rosati, 2014) and measured interannular distances along a consistent straight axis (Suppl. Fig. 1). A considerable proportion of spine sections (n=130, 43%) contained inclusions, which are secondary fin rays that get absorbed into the lobes of the primary spine (Suppl. Fig. 1). Such samples could still be aged with confidence but precluded measurements of interannular distances for length back-calculation. Five samples were removed because of poor image quality, yielding 296 aged specimens, 90% of them caught after 2006.

Samples were examined blind 3 times by the primary age reader and 1 time by a second age reader, who did not know the age estimates of the primary reader. Aging precision was estimated within and between readers. We first computed the coefficient of variation (CV) for each fish *j*:

$$CV_{\mathrm{j}} = 100\frac{\sqrt{\sum_{i=1}^{N}\frac{\left(X_{\mathrm{ij}}-X_{\mathrm{j}}\right)^{2}}{N-1}}}{X_{\mathrm{j}}}, \qquad (1)$$

where N = the number of times the fish was aged;
X_{ij} = the *i*th age reading for fish *j*; and
X_{j} = the mean age for fish *j*.

Then, we averaged the CVs for individual fish to obtain the mean CV across all aged fish, resulting in a mean CV of 9.4% between the 3 age estimates of the primary age reader and a mean CV of 12.1% between the age estimates of the primary and secondary readers. For 36% and 27% of samples, respectively, the 3 readings by the primary reader and the estimates by both readers yielded the same age. An age discrepancy of ≤2 years was found between the estimates by the primary reader for 96% of samples and between readings by the 2 readers for 87% of samples. Importantly, between-reader deviations in age estimates were randomly distributed, as indicated by a nonsignificant result from Bowker's test of symmetry (P=0.17, Suppl. Fig. 2).

Because the 296 Atlantic sturgeon for which age was estimated represent a nonrandom, length-stratified subset of all individuals caught over time (n=3544), the age distribution was corrected for over- and underrepresentation of size classes relative to the total catch (Chih, 2009). The full sample of all captured fish and the subset of 296 samples used in age and growth analysis were binned into 5-cm-TL size classes, and the relative frequency of each size class was used to compute its weighting factor (proportion of full sample/proportion of subset) (Fig. 2). This factor was then used as a statistical weight for each aged individual in its corresponding size class. The aggregation of Atlantic sturgeon in Long Island Sound and the Connecticut River cannot be considered a population (mixed stock plus a few, if any, adults); therefore, we refrained from estimating the growth coefficient and asymptotic length with a population-based growth model. However, we visually compared our length-at-age data to a robust growth model compiled from published studies on age and growth of Atlantic sturgeon (Dunton et al., 2016).

For the subset of Atlantic sturgeon with longitudinal annuli measurements (n=166), we first ascertained that TL and fin spine size (radius at capture [R_{C}]) were linearly related (TL=11.3+19.7×R_{C}; coefficient of determination=0.70, P<0.001). Because that was the case, we then proceeded to estimate length at age of individuals with a commonly used, proportional back-calculation method (the "biological intercept" method; Campana, 1990):

$$TL_{\mathrm{i}} = TL_{\mathrm{c}} + \frac{\left(R_{\mathrm{i}}-R_{\mathrm{c}}\right)\left(TL_{\mathrm{c}}-TL_{0}\right)}{R_{\mathrm{c}}-R_{0}}, \qquad (2)$$

where TL_{i} = the fish TL at the *i*th annulus;
TL_{c} = the fish TL at capture;
R_{i} = the spine radius at the *i*th annulus;
R_{0} = the spine radius (set to 0); and
TL_{0} = the fish TL at the biological intercept (0.7 cm TL; Bain, 1997).

We then examined these data for the selective disappearance of fast or slow growth phenotypes from the aggregation with increasing age, using linear regressions of age at catch versus back-calculated TL at different previous ages.

Telemetry data: habitat utilization

Members of the DEEP staff used approved methods (Damon-Randall et al., 2010; Kahn and Mohead, 2010) to surgically implant acoustic transmitters (V7–V16 tags, InnovaSea Systems Inc., Boston, MA) in Atlantic sturgeon caught within the study area from 2014 through 2021 (Suppl. Table 1). Up to 35 subadult and adult Atlantic sturgeon were tagged per year, resulting in a total of 114 acoustic tags deployed by the DEEP since 2014. However, 84% of all tag deployments occurred in 2019–2021 (Suppl. Table 1); hence, data from only these 3 years were analyzed in our study for movement patterns and drivers. The DEEP also maintained several arrays of acoustic receivers (VR2W-69 kHz, VR2Tx, VR2AR monitoring receivers, InnovaSea Systems Inc.) in eastern Long Island Sound and the Connecticut River (Fig. 1). The array in the sound consisted of sub-arrays at Long Sand Shoal, Eastern Gate, and Falkner Island. The array in the river included up to 45 receivers placed linearly from the estuary to the Holyoke Dam (rkm 3–135). However, Atlantic sturgeon were detected only until rkm 52 (at Wilcox Island), and receivers were consistently deployed up to this point during the study period (Fig. 1). Receivers had a nominal detection radius of 1000 m to ensure coverage of the entire width of the Connecticut River (200–900 m). Receivers were retrieved monthly to download data and were immediately redeployed at consistent locations (±100 m).

Raw data for acoustic detections of tagged fish were compiled and analyzed by using the glatos package (vers. 0.4.0; Binder et al., 2018) in R (vers. 4.1.2; R Core Team, 2021). False detections (0.6%–1.0% of all detections) of Atlantic sturgeon were defined as those with an interval of >1 h between consecutive detections of any individual at any given receiver (Simpfendorfer et al., 2015). Data from 1 tag was excluded from analysis because the continuous detection of the fish with this tag over multiple years by a single receiver indicates that the fish either expelled the tag or expired near the receiver. Other extracted data were total number of detections, number of detecting receivers, and the date of first and last detection in the Connecticut River per year. As an additional step, we plotted the date of detection against its location (river kilometer) for each individual and visually inspected the derived abacus plots for plausibility and overall patterns (Suppl. Fig. 3). Finally, we used the recommended procedure in the glatos package to condense the millions of discrete detections into a series of year-, receiver-, and fish-specific "events," with a new event created in the following manner: 1) every

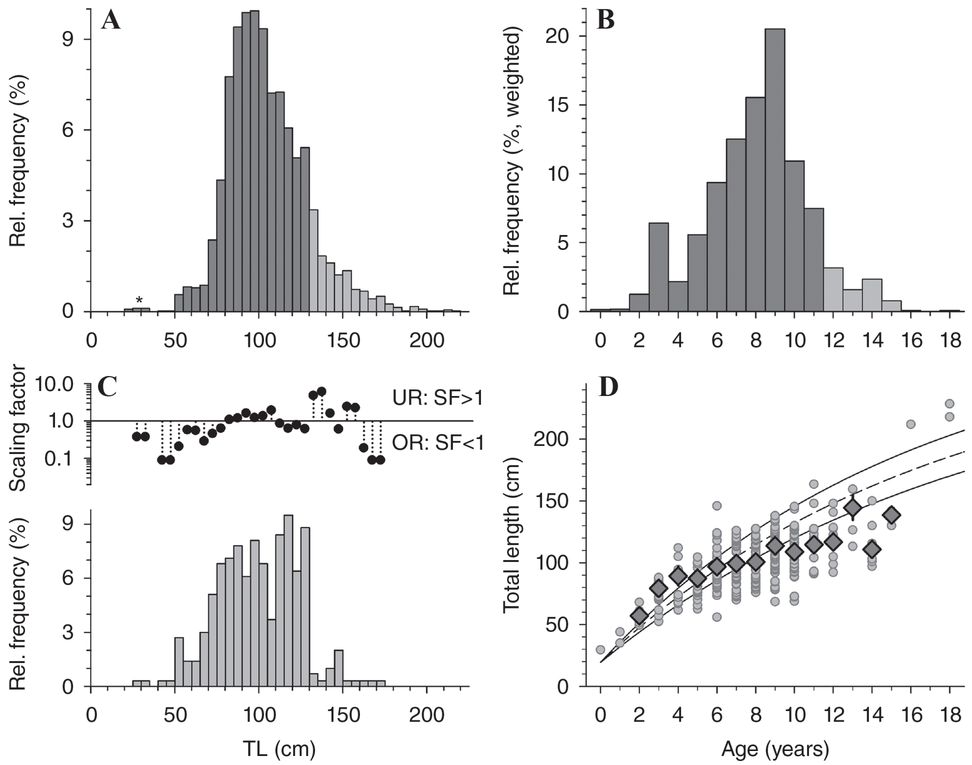

Figure 2

Length and age of the seasonal aggregation of Atlantic sturgeon (*Acipenser oxyrinchus*) in eastern Long Island Sound and the Connecticut River between 1988 and 2021. (**A**) Relative length distribution by size class (interval: 5 cm in total length [TL]) for all Atlantic sturgeon caught in the study period (number of samples [*n*]=3544), and (**B**) relative weighted age distribution based on analysis of sections of pectoral-fin spines from a subset of those fish (*n*=296). The asterisk in panel A denotes likely pre-migratory juveniles (20–35 cm TL). The light gray bars in panels A and B indicate distribution of adults, defined as those with sizes and ages greater than 130 cm TL and 12 years. (**C**) Relative length distribution of aged fish (*n*=296) (bottom graph) and statistical scaling factors (SF, black circles in top graph) derived for each size class, depending on whether age analysis overrepresented (OR) or underrepresented (UR) a given size class relative to the distribution for all captured fish in panel A. (**D**) Age–length relationship of Atlantic sturgeon (*n*=296). Circles represent age estimates for individuals, and diamonds represent weighted means for fish at ages 2–15. For the purpose of comparison, the dashed line and solid lines indicate the growth curve and 95% confidence interval from the model for Atlantic sturgeon compiled by Dunton et al. (2016).

6 h (approximately 0.5 of a tidal cycle) for fish “heard” consecutively at the same receiver, 2) if >6 h elapsed between consecutive detections on the same receiver, or 3) if a fish was detected at a new receiver. Using the start and end time of each event, we then calculated its duration and then summed up all event durations per year, receiver, and fish.

To broadly characterize habitat utilization by Atlantic sturgeon, we grouped DEEP receivers into 3 categories by habitat (Fig. 1): Long Island Sound (all sub-arrays) and the estuary (rkm 3–19) and upper section (≥rkm 22) of the Connecticut River. Distinguishing occupancy of the brackish estuarine waters of the lower section from that of the freshwater upper section of the Connecticut River was important because Atlantic sturgeon are anadromous and may migrate into freshwater for spawning. We delineated the 2 sections of the river following Meade (1966) and using long-term average salinity data from 2 monitoring stations of the U.S. Geological Survey (USGS) at Old Lyme and Essex (Connecticut water conditions, data available from website). For each fish and year, we aggregated the total time detected at receivers of each category and expressed it as the proportion of the overall time detected for each individual fish (Long Island Sound+estuary+upper section=100%). For each year, we also computed a weighted average of the number of days spent in each area, with the weight proportional to the total number of days detected for each individual. To visualize spatiotemporal clusters of occurrence of Atlantic sturgeon in the river, we computed kernel densities of aggregated detections per year and plotted them against date and river kilometer by using the R package ggplot2, vers. 3.3.5 (Wickham, 2016). We also extracted the annual dates of first and last detection in the Connecticut River for every fish (i.e., in both the estuary and upper section), but for computing averages, the tagging year was excluded to avoid bias in the mean date of first detection.

We hypothesized that larger Atlantic sturgeon 1) went farther upstream or 2) spent more time in the freshwater upper portion of the Connecticut River, which would support the notion that they utilized the upper section as spawning habitat. To test these hypotheses, we first adjusted the TL of each individual from the year of tagging to each year of detection (2019, 2020, and 2021) by applying a von Bertalanffy growth function using the values for growth coefficient, asymptotic maximum length, and theoretical age at which length is zero published by Dunton et al. (2016). For each fish and year, we then extracted the maximum river kilometer and the number of days spent in the upper section of the river, followed by year-specific and overall bivariate Pearson correlation analyses between TL at detection and 1) number of days in the upper section or 2) max river kilometer.

To analyze potential environmental cues for seasonal movement of Atlantic sturgeon into the Connecticut River, we used USGS data (USGS Current Water Data for Connecticut, available from website) to extract daily discharge volume for the Connecticut River (in cubic meters per second) from the nearest station in Thompsonville (USGS gauging station 01184000, at rkm 106). With this approach, we assumed that upriver flow patterns were also predictive of flow conditions farther downstream. Daily bottom temperatures (in degrees Celsius) were extracted and then averaged from 3 USGS gauging stations: Middle Haddam (01193050, at rkm 25), Essex (01194750, at rkm 9), and Old Lyme (01194796, at rkm 5) stations. For better visualization, we used nonparametric locally estimated scatterplot smoothing (20% bandwidth) on all daily values. River temperature and flow conditions both followed a strong seasonal pattern and were negatively correlated to each other (correlation coefficient [r]=–0.55, $P<0.001$, n=624). Hence, we first computed overall weekly averages (for the period 2019–2021) and then subtracted them from the annual weekly averages to obtain weekly temperature and discharge anomalies. These anomalies were then correlated to similarly derived weekly anomalies of the percentage of Atlantic sturgeon in the Connecticut River (estuary and upper section) relative to the total number of fish detected in a given year.

Given the migratory nature of Atlantic sturgeon (Waldman et al., 2013), some detections were likely of fish with acoustic tags implanted by research groups other than the DEEP. We therefore queried the databases of the Mid-Atlantic Telemetry Observation System (available from website) and the Atlantic Cooperative Telemetry Network (available from website) to determine which research institution implanted these tags and where the tagging was done. We then extracted summary statistics for these detections pooled over all 3 years, including the total number of detections by region and institution and the number of detected fish (n=114), for the entire study area and for only the upper section of the Connecticut River.

Results

Atlantic sturgeon caught since 1988 in Long Island Sound and the Connecticut River (n=3544) ranged in size from 21 to 218 cm TL, with a mean of 105.1 cm TL (standard deviation [SD] 23.4) (Fig. 2A). Juveniles (<50 cm TL) made up 0.4% (n=13) of Atlantic sturgeon collected in 1988–2021. The vast majority (86.6%, n=3087) of all the captured fish were subadults (50–130 cm TL), and 13% (n=444) of them were adults (>130 cm TL). Ages ranged from 0 to 18 years with a weighted mean of 8.1 years (SD 2.7) and a median of 8 years (n=296). In our study, 92% of the Atlantic sturgeon for which pectoral-fin spines were analyzed were 11 years or younger (Fig. 2B). Back-calculated TLs at ages 2–6 declined with increasing age at capture (linear regression: all $P\leq0.003$; Fig. 3), indicating that faster growing individuals selectively disappeared from the aggregation in Long Island Sound and the Connecticut River.

Between 2019 and 2021, acoustic receivers in our study area logged 1.38 million detections of a total of 85 unique Atlantic sturgeon tagged by the DEEP (mean: 8463 detections/fish; range: 2–30,384 detections/fish). At the time of tagging, fish ranged in size from 52.5 to 164.5 cm TL (mean: 109.6 cm), with 20% of them >130 cm TL. Tagging efforts continued throughout the study period; as a result, the number of detected Atlantic sturgeon more than doubled and annual detections quadrupled from 2019 to 2021 (Table 1, Fig. 4). Of all Atlantic sturgeon tagged in a given year, over 85% were redetected in the subsequent year or years. A total of 22 specimens were detected in all 3 years. We found that fish spent on average 2–3 months, maximally 4–6 months, in the study area (Fig. 1; Table 1). Once in Long Island Sound, over 90% of fish also entered the Connecticut River (estuary and upper section); only a small fraction remained exclusively in Long Island Sound each year (2%–8%, Fig. 4). The first fish entered the river between early March and early May, but it took from 2 weeks to 3 months for 50% of the fish detected in a given year to enter the river at least once (Table 1). Most fish utilized the Connecticut River, and 31%–57% of fish remained within the estuary (Fig. 4). Of the fewer Atlantic sturgeon that proceeded farther upstream and utilized the upper section of the river, half stayed there for fewer than 7 d, but 11 individuals in 2021 stayed 37–97 d. No Atlantic sturgeon were detected at receivers beyond rkm 52 in our 3-year study period. By 3–7 October, 50% of fish had exited the Connecticut River, and the last fish exited the river between 28 October and 29 November (Table 1).

Kernel density distributions similarly indicate substantial use of the estuary of the Connecticut River and a generally diminishing occupancy of areas farther upriver (Fig. 5). The densities of detections in Long Island Sound and the estuary at rkm 8–10 were high between late spring and the end of fall in all 3 years (Fig. 5). However,

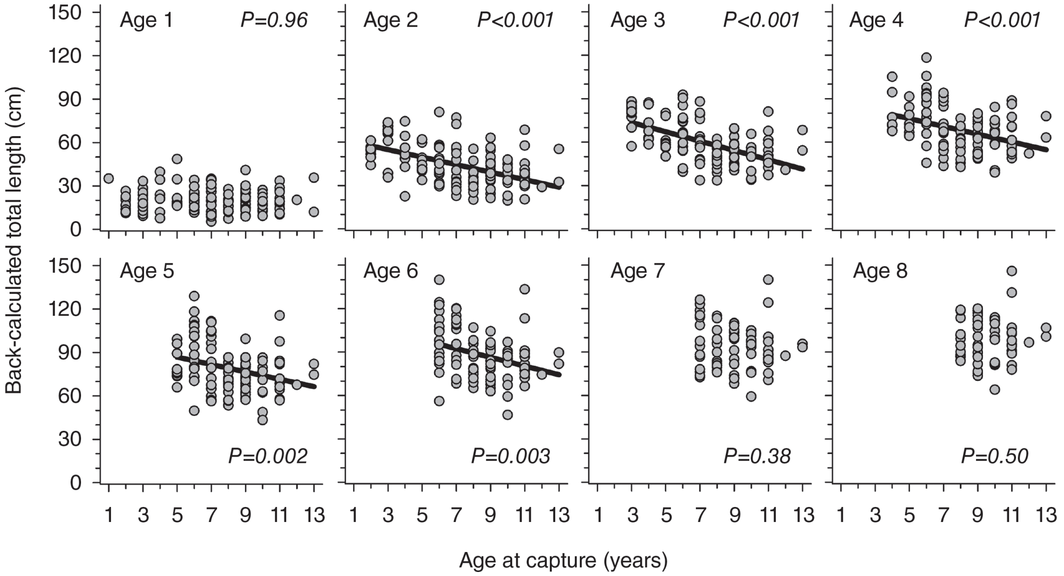

Figure 3

Relationship of back-calculated total lengths at ages 1–8 to ages at capture for Atlantic sturgeon (*Acipenser oxyrinchus*) caught from 1988 through 2021 in Long Island Sound and the Connecticut River. The thick lines in panels indicate the significant fits from linear regression. The 2 oldest individuals, with estimated ages of 16 and 18 years, were collected as mortalities and omitted from the dataset.

Table 1

Summary statistics from telemetry data collected for tagged Atlantic sturgeon (*Acipenser oxyrinchus*) during 2019–2021 in the study area of Long Island Sound and the Connecticut River. The array of acoustic receivers in the sound consisted of 3 sub-arrays at Long Sand Shoal, Eastern Gate, and Falkner Island. A receiver array was deployed in each of 2 areas in the Connecticut River: the brackish estuary (river kilometer [rkm] 3–19) and the freshwater upper section (rkm 22–52).

Statistic	2019	2020	2021
Total number of fish detections	190,380	432,703	756,311
Total number of fish detected	30	61	72
Number of fish detected in previous years[1]	6	23	57
Days spent in study area Mean[2] | Maximum	80 | 122	77 | 120	83 | 170
Date first fish entered the river	10 May	31 March	11 March
Date 50% of fish had once entered the river[1]	25 May	9 July	19 June
Date 50% of fish exited the river	7 Oct.	3 Oct.	3 Oct.
Date last fish exited the river	10 Nov.	29 Nov.	28 Oct.
% fish detected only in the sound	3	2	8
% fish in sound and estuary (not upper river)	57	31	56
% fish in upper river			
– at least 1 d	43	66	35
– at least 14 d	13	28	17
– at least 30 d	0	18	7

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[1] The number of fish detected in all 3 years is 22.
[2] Includes only fish tagged in prior years.

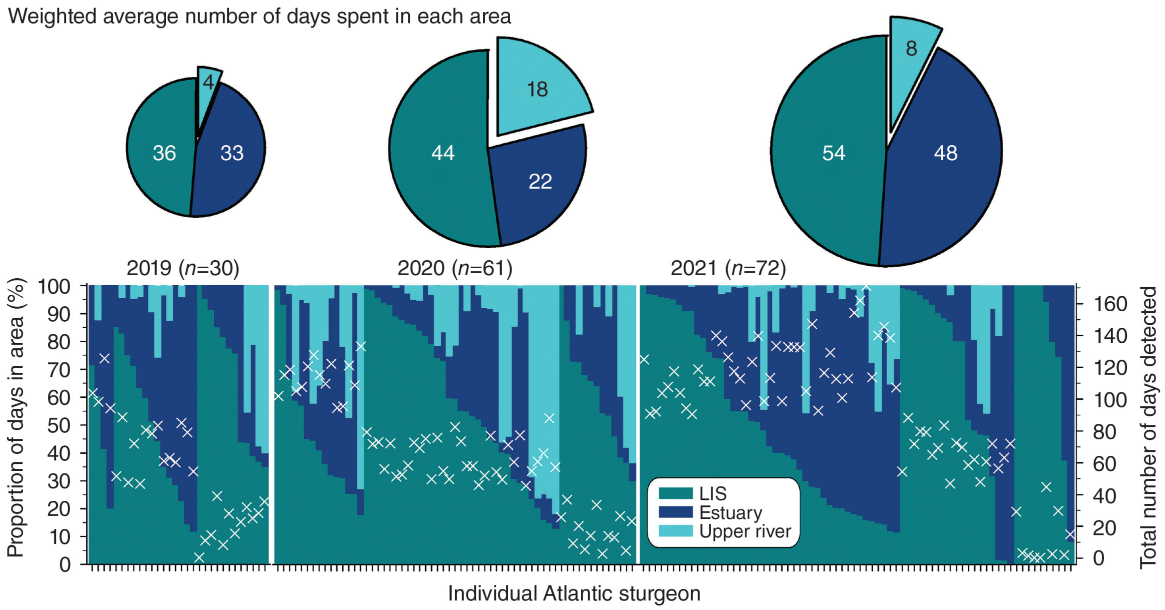

Figure 4

Overview of occupancy patterns of tagged Atlantic sturgeon (*Acipenser oxyrinchus*) in Long Island Sound (LIS) and the Connecticut River during 2019–2021, based on telemetry data. Pie charts depict a weighted average of the number of days that Atlantic sturgeon spent in each of 3 areas in each year: LIS (dark teal) and the estuary (dark blue) and upper section of the Connecticut River (cyan). In the bottom panels, the proportion of days each Atlantic sturgeon spent in each of the 3 areas in each year (colored columns) and the total number of days each individual was detected in the study area (white crosses) are represented. These numbers of days were used to weight the averages shown in the pie charts. *n*=number of fish detected in the given year.

in 2021, the highest relative density of detections was in the river mouth and Long Island Sound, unlike in 2019 and 2020, when relative densities were higher in the lower river (rkm 8–10) (Fig. 5). Intriguingly, although upstream detections were generally low, an area of increased densities occurred in August and September at rkm 47 (near Portland) in 2020. Of all the Atlantic sturgeon detected each year, 33% (2019), 30% (2020), and 10% (2021) visited rkm 47 for at least 1 d. Occupancy of the upper section of the Connecticut River by Atlantic sturgeon was independent of fish size: TL and the number of days spent in this section or the maximum upriver distance at which a fish was detected were statistically unrelated (Fig. 6; Pearson correlation: all $P \geq 0.06$).

The occurrence of Atlantic sturgeon in the Connecticut River (estuary and upper section) generally coincided with warm river temperatures (>21°C) and low river discharge (<500 m^3/s) (Fig. 7, top panels). The temperature pattern was season dependent. Atlantic sturgeon did not enter the Connecticut River in spring until river temperatures had at least exceeded approximately 20°C, and in fall occupancy of Atlantic sturgeon in the Connecticut River and temperature declined concomitantly (Fig. 7, bottom panels). Weekly temperature and discharge anomalies in the Connecticut River were negatively correlated to each other (Pearson correlation: $r=-0.69$, $P<0.001$, $n=98$), but neither category of anomalies was statistically related to the anomalies in occupancy of the river by Atlantic sturgeon (Pearson correlation: all $P>0.18$). Therefore, beyond coinciding with the general seasonal pattern, neither temperature nor river discharge further affected occupancy of the river by Atlantic sturgeon. However, in 2021, events of unusually high precipitation in summertime were associated with dips in river occupancy, followed by apparent reentry (Fig. 7, top-right panel).

Our database query returned an additional 324,764 detections of Atlantic sturgeon in our study area during 2019–2021 (Suppl. Table 2); these detections were for 114 individuals tagged by research groups other than the DEEP. Most individuals ($n=67$) were and most detections ($n=263{,}920$; mean: 3939 detections/fish) were for fish tagged in 2015–2018 by researchers from Stony Brook University in marine waters off the Rockaway Peninsula in New York (mean TL: 102.8 cm; TL range: 71–232 cm; 5% >130 cm TL; Suppl. Table 2). Most other detected individuals ($n=46$) were tagged by various institutions inside and outside of the Chesapeake Bay region. Notably, only 6 fish not tagged by the DEEP (5%, all tagged in New York) proceeded farther into the upper section of the Connecticut River (Suppl. Table 2).

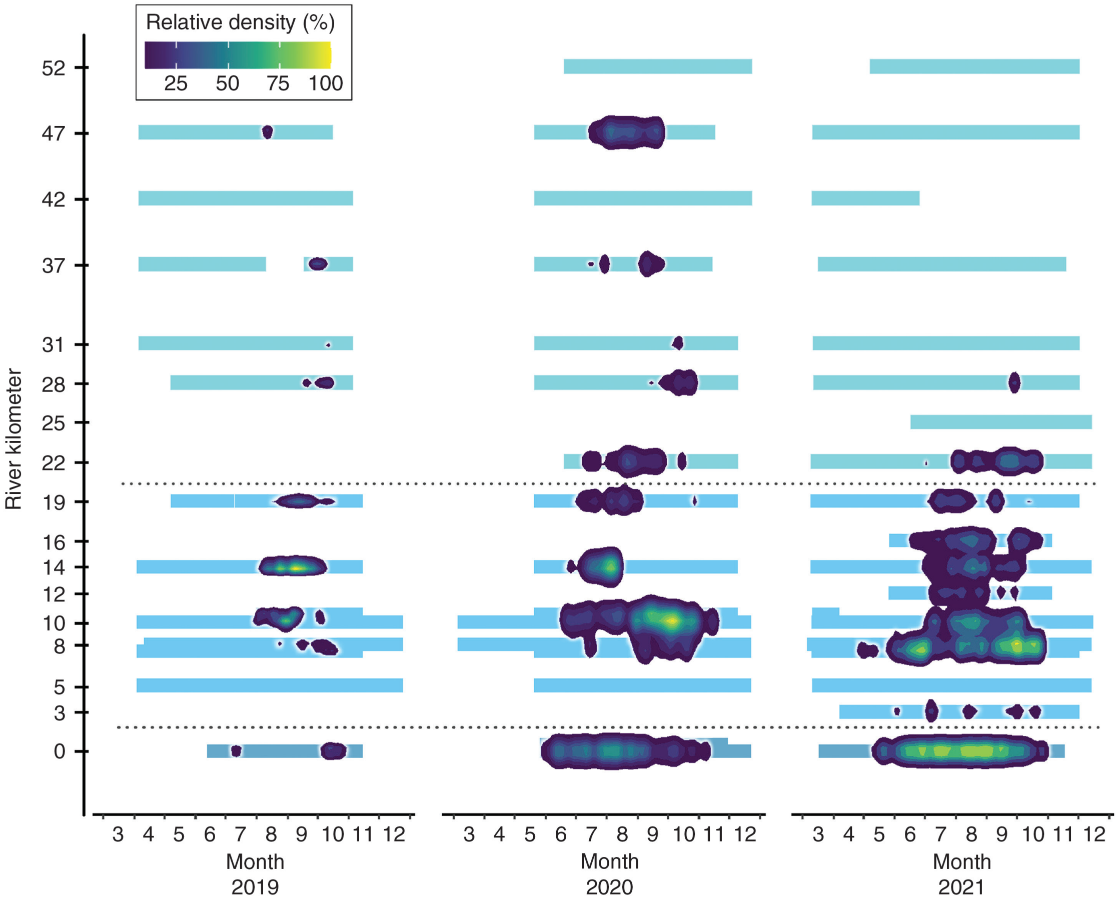

Figure 5

Spatiotemporal occupancy patterns of tagged Atlantic sturgeon (*Acipenser oxyrinchus*) in 2019–2021 in Long Island Sound (LIS) and the Connecticut River, based on telemetry data. Colored contours indicate kernel density distributions of all detections of Atlantic sturgeon relative to the total number of detections in each year. The blue horizontal bars depict the months of deployment during each year for each receiver (identified by the river kilometer of their location). Telemetry data were collected from 3 separate acoustic receiver arrays in LIS and the estuary and upper section of the Connecticut River.

Discussion

We analyzed archived pectoral-fin spines of Atlantic sturgeon and recent telemetry records to better characterize a seasonal aggregation of Atlantic sturgeon in eastern Long Island Sound and the Connecticut River. This aggregation consisted mostly of subadult, fast-growing individuals smaller than 130 cm TL and younger than 12 years; individuals we regarded as mature were rare. This relative lack of large adults was not surprising because the spawning population in the Connecticut River likely was extirpated many decades ago, and other contemporary aggregations of Atlantic sturgeon in the region have similarly truncated age structures. In a study in the New York Bight, for example, over 700 Atlantic sturgeon were assigned ages between 2 and 35 years, but only 4 specimens were older than 21 years, and the age distribution similarly consisted mostly of subadults (85% younger than 12 years) (Dunton et al., 2016).

Older individuals (≥7 years) were smaller than expected for their age, given predictions from the growth model that is currently the most robust for Atlantic sturgeon (Dunton et al., 2016; Fig. 2C). This observation is corroborated by the pattern in the lengths at age back-calculated from annuli widths in sections of pectoral-fin spines, a pattern that indicates a consistent decline in lengths at ages 2–6 with increasing age at capture. Such an apparent change in growth phenotype with age at capture, known as Lee's phenomenon (Lee, 1912; Ricker, 1969), could have a number of explanations that are not mutually exclusive, from general life history trade-offs between growth and longevity (Gerking, 1957; Ricker, 1975) to size-selective mortality (Carlander, 1945) or size-selective migration patterns (Stanley, 1980). Life history trade-offs appear unlikely to

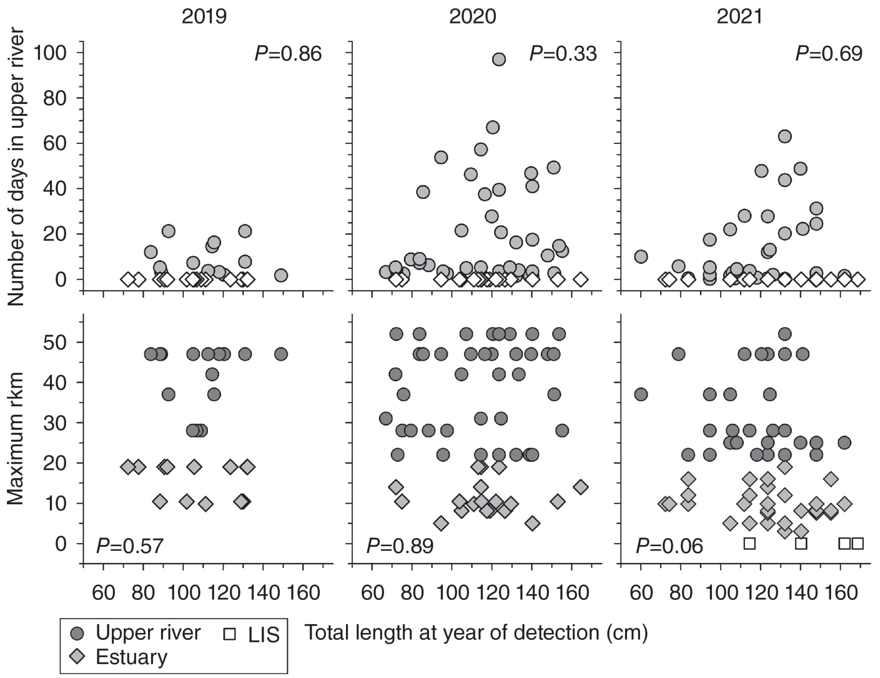

Figure 6

Occupancy of the Connecticut River by Atlantic sturgeon (*Acipenser oxyrinchus*) in relation to their size during 2019–2021. In the top panels, the number of days spent in the upper section of the river in relation to total length at the year of detection by an acoustic receiver is provided for tagged individuals. White diamonds indicate fish that spent 0 d in the upper river. In the bottom panels, the maximum river kilometer (rkm) at which each individual was detected in relation to total length at the year of detection is represented. Symbols indicate the habitat area where fish were detected: the freshwater upper section and brackish estuary of the Connecticut River and Long Island Sound (LIS). All metrics were length independent (Pearson correlation: $P \geq 0.06$).

have had an effect on growth in our study because the aggregation of Atlantic sturgeon that we focused on consisted predominantly of subadults.

There is some evidence for size-selective fishing mortality strengthening Lee's phenomenon in shovelnose sturgeon (*Scaphirhynchus platorynchus*), a freshwater sturgeon species from the upper Missouri River (Koch et al., 2009), but Atlantic sturgeon have now been protected from exploitation for over 2 decades (i.e., longer than the life of the oldest specimens in our sample). Although accidental catches of Atlantic sturgeon still occur and likely are a hindrance to the recovery of this species (Stein et al., 2004), it is doubtful that bycatch mortality could be size selective enough to cause the observed pattern. A more probable explanation therefore might be that larger, faster growing Atlantic sturgeon selectively disappear from the aggregation in Long Island Sound and the Connecticut River not because they die but because they already left to migrate back to their natal rivers.

Still, our interpretations remain speculative because of a few compounding sources of uncertainty. First, aging of Atlantic sturgeon and using measurements of annuli widths from fin spine sections are notoriously difficult, are less precise than desirable (i.e., CV >5%), and are poorly validated. However, potential underestimation of ages is largely a concern for older, adult Atlantic sturgeon, not in subadults that were the vast majority of Atlantic sturgeon included in this study. Second, we lacked information about the sex ratio and spatial origin of the aggregation of Atlantic sturgeon in our study area, and both sex and origin are known to affect overall growth patterns. For example, female Atlantic sturgeon grow more slowly and to larger maximum sizes than males (Van Eenennaam et al., 1996; Stevenson and Secor, 1999; Stewart et al., 2015), and Atlantic sturgeon from northern latitudes (>38°N) grow slower than fish originating from more southern systems (Smith, 1985; Dunton et al., 2016). Hence, potential changes in sex ratio or origin over time could confound the observed changes in growth.

Gear selectivity might have played a role, too, given that the majority of Atlantic sturgeon in this study were caught with gill nets (15–18-cm stretched mesh) that we suspect selected against the largest fish (>180 cm TL; Suppl. Fig. 4). However, we found that Lee's phenomenon

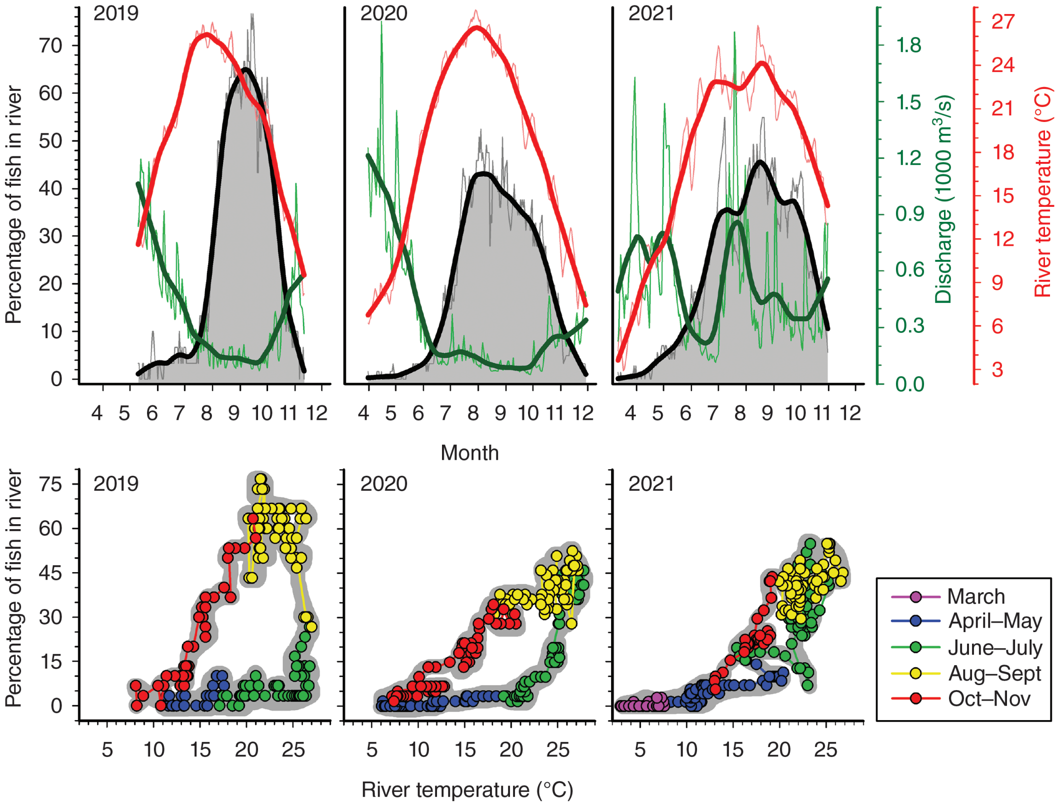

Figure 7

Seasonal occurrence of Atlantic sturgeon (*Acipenser oxyrinchus*) in the Connecticut River in relation to river discharge (green lines) and temperature (red lines) in 2019–2021. In the top panels, thin lines depict daily values, and thick lines represent values from locally estimated scatterplot smoothing (20% bandwidth). Black lines and gray shading indicate the percentage of fish present in the monitored part of the river (from North Cove in the estuary up to river kilometer 52 at Wilcox Island) relative to all fish detected in each year. In the bottom panels, the relationship between temperature and the percentage of fish present in the river in each year is represented, by month or pair of months. The gray area around the colored points in each panel was added to highlight the overall seasonal progression of the temperature–occupancy relationships.

remained detectable, even when we restricted the dataset to fish <100 cm TL (i.e., well below the presumed selectivity), indicating that this pattern was not just a sampling artifact. To better characterize the aggregation of Atlantic sturgeon in our study area and elucidate reasons for its growth changes over time, future studies should include sampling with larger mesh sizes and determination of the sex and origin of specimens (Waldman et al., 2013).

Analysis of the telemetry records revealed several intriguing patterns, aided by the dataset size (about 1.4 million detections of Atlantic sturgeon over 3 years) and the design of the receiver arrays that allowed inference of seasonal occupancy of Atlantic sturgeon in eastern Long Island Sound and both the estuary and upper section of the Connecticut River. Overall, Long Island Sound and the Connecticut River clearly provide important seasonal habitats for Atlantic sturgeon, supporting the emergent view that natal and non-natal rivers fulfill critical ontogenetic habitat requirements for Atlantic sturgeon (White et al., 2024). Despite the expected large variability between years, months, and individuals, we found that this aggregation of Atlantic sturgeon typically utilizes the study area between spring and fall. However, individual fish stayed there for only 2–3 months on average, either because movements within Long Island Sound took fish beyond the receiver arrays or because their stay was a transient part of a coastal migration (Dunton et al., 2010; Kazyak et al., 2021). During winter, Atlantic sturgeon largely emigrate out of Long Island Sound and the Connecticut River, likely to seek warmer waters (>9°C) on the continental shelf of the Northwest Atlantic Ocean (Rothermel et al., 2020).

Movement of Atlantic sturgeon into the estuary and upper section of the Connecticut River resembled the seasonal cycle of temperatures in the river, with peak temperature and peak occupancy co-occurring around late summer. However, the onset of the ingress into the Connecticut

River in spring and summer appears to be driven more by a temperature threshold (20°C–25°C). Episodes of high discharge negatively affected occurrence of Atlantic sturgeon in the Connecticut River, likely because of the preference of Atlantic sturgeon for energetically more favorable conditions of low flow. This response to changes in discharge volume is consistent with the selective tidal transport behavior of green sturgeon (*Acipenser medirostris*) in San Francisco Bay (Kelly et al., 2020) and the synchronization of upriver movements with flood tides by Atlantic sturgeon in the Hudson River (Dovel and Berggren, 1983). Climate change is predicted to increase extreme weather events; therefore, extreme rainfall and discharge events, such as those observed in July 2021 (when flow peaked for the year at 1855 m^3/s; USGS Current Water Data for Connecticut), are likely to become more frequent (Runkle et al., 2022). In a recent assessment, diadromous fish and benthic invertebrates were found to be highly vulnerable to climate change and decadal variability (Hare et al., 2016), due in part to such changes in discharge patterns. Given the complex effect of river discharge on the distribution of Atlantic sturgeon in this study, increased frequency of flooding in the summer could disrupt utilization of the Connecticut River by this species.

The density of acoustic detections of tagged fish in the study area indicate that Atlantic sturgeon spent most of their time within Long Island Sound and the brackish estuary of the Connecticut River. We interpret this pattern in where fish spent their time as related to feeding behavior, given that estuaries are particularly rich in prey organisms for Atlantic sturgeon, such as benthic mollusks, polychaetes, arthropods, and in rare cases even fish (Johnson et al., 1997; Haley, 1999; Guilbard et al., 2007; McLean et al., 2013; Novak et al., 2017). Specifically for the estuary of the Connecticut River, Savoy (2007) found that Atlantic sturgeon preyed almost exclusively on polychaetes. The area is also a known summer feeding ground for shortnose sturgeon (*Acipenser brevirostrum*), the only other native sturgeon species in the area (Savoy and Benway, 2004).

A considerable proportion of individuals (35%–66%) each year proceeded farther upriver from the estuary into freshwater for periods ranging from a single day to a few weeks. These fish were no larger or smaller than those remaining farther downstream. Most fish made fast, linear movements far into the upper section of the Connecticut River, as has previously been observed for Atlantic sturgeon in Minas Bay (an inlet of Bay of Fundy in Canada), with these movements interpreted as extensive searching for or movement between food patches (McLean et al., 2013). We suspect that migrating Atlantic sturgeon were searching for alternative prey sources in the upper section of the Connecticut River, perhaps driven by intra- or interspecific seasonal competition for benthic prey in the estuary of the river (Savoy and Benway, 2004).

Interspecific competition with shortnose sturgeon may influence movements of Atlantic sturgeon. Shortnose sturgeon are generally more common in freshwater areas, and Atlantic sturgeon are often concentrated in deeper, more saline waters of the estuary (Haley, 1999). However, the distributions and, therefore, the prey of both species likely overlap. A previous analysis for the estuary of the Connecticut River revealed that shortnose sturgeon mostly eat amphipods and polychaetes (Savoy and Benway, 2004) and Atlantic sturgeon almost exclusively prey on polychaetes there (Savoy, 2007). Given that shortnose sturgeon migrate to the estuarine portion of the river in late spring to late summer (Benway, 2002; Buckley and Kynard, 1985), the 2 sturgeon species are likely to occupy the same area and share a common, primary food source. Such overlap may engender exploitative competition and prompt Atlantic sturgeon to explore potential new foraging grounds in the upper portion of the Connecticut River. There, shortnose sturgeon are known to prey on mayflies (Ephemeroptera), midges (Chironomidae), and freshwater clams (*Pisidium* spp.), but comparable diet data for Atlantic sturgeon are lacking (Savoy and Benway, 2004).

The seasonal use of freshwater habitat by anadromous Atlantic sturgeon is more commonly associated with spawning behavior, and Atlantic sturgeon historically spawned in the Connecticut River before spawning runs ceased likely many decades ago (Van Eenennaam et al., 1996). Intriguingly, in 2019 and particularly in 2020, we discerned a hotspot of seasonal occupancy near the receiver at Portland (rkm 47), which is sufficiently upstream from the historic salt-wedge maximum (rkm 26) (Meade, 1966) and features deep sections (>10 m) with cobble or gravel substrate that Atlantic sturgeon prefer for spawning (Smith and Clugston, 1997; Bain et al., 2000; Hatin et al., 2002). However, most fish that swam upriver were subadults. Although the largest individuals in each year (141–154 cm) were technically adults, only males or Atlantic sturgeon from southern populations (the Carolina and South Atlantic DPSs) have been found to be already mature at this size (Smith et al., 1984; Van Eenennaam et al., 1996).

Moreover, the timing of these freshwater excursions was inconsistent with known spring spawning runs of Atlantic sturgeon in other northern rivers. In the Hudson River, most Atlantic sturgeon are already spent from early to mid-June (Van Eenennaam et al., 1996), and it has been reported from another study that Atlantic sturgeon move into freshwater from the end of May to mid-July (Breece et al., 2021). In the Saint John River (in New Brunswick, Canada), estimated spawning dates for Atlantic sturgeon are in early July, on the basis of larval growth models (Taylor and Litvak, 2017). Atlantic sturgeon in the Savannah River in Georgia initiate their spring runs from February to March (Vine et al., 2019). In contrast, the Atlantic sturgeon in our study arrived at the Portland area in mid- to late August (Suppl. Table 3), too late for a spring spawning run as expected for Atlantic sturgeon of the New York Bight DPS. Only southern populations of Atlantic sturgeon make additional spawning runs in fall (Smith et al., 1984; Collins et al., 2000; Ingram and Peterson, 2016). In light of all evidence, we therefore believe that feeding-related explorations are the most parsimonious reason for Atlantic sturgeon to make freshwater excursions as we observed them in this study. This assertion does not exclude the possibility of rare, ephemeral spawning events by Atlantic sturgeon that continue to elude detection in the upper section of the Connecticut River (Coleman et al., 2024).

Conclusions

Long Island Sound and the Connecticut River serve as much-used habitat for a dynamic, seasonal aggregation of mostly subadult Atlantic sturgeon with ecologically intriguing age and growth patterns. Many of the tagged Atlantic sturgeon returned to this area year after year (DEEP[4]), indicating that the area is an important feeding ground. Although Atlantic sturgeon are known to utilize estuaries to feed (Haley, 1999; Dunton et al., 2010; McLean et al., 2013), we found that juveniles and subadults also commonly spent time and energy to travel upriver into freshwater habitats—a behavior that had previously been associated only with spawning. The Connecticut River is likely not the only system where non-natal juvenile and subadult fish utilize freshwater; therefore, future studies should continue exploration of the importance of upriver areas for juvenile and subadult Atlantic sturgeon in other rivers on the East Coast of the United States.

Given that Atlantic sturgeon from all 5 DPSs likely contribute to the aggregation in Long Island Sound and the Connecticut River (Waldman et al., 2013), its conservation and restoration in the face of anthropogenic change could positively affect other Atlantic sturgeon stocks. This is especially true for smaller stocks like those in the James and Delaware Rivers, which are not as robust as the Hudson River stock but still contribute 6%–12% of the fish in the aggregation in the Connecticut River (Waldman et al., 2013). Continued survey and research efforts are clearly warranted to improve understanding of the growth, movements, and genetic makeup of this aggregation of Atlantic sturgeon, and this work should include targeting of large individuals (>130 cm TL) and further investigations of subadult use of the upriver environments.

Resumen

El esturión del Atlántico (*Acipenser oxyrinchus*) se agrega estacionalmente en la Sonda de Long Island y el río Connecticut, pero aún no se conoce lo suficiente de la estructura de tallas y edades ni del uso del río. Analizamos todos los datos de longitud disponibles de monitoreos (1988–2021: número de muestras [n]=3544), estimamos la edad a partir de secciones de las espinas de las aletas pectorales (n=296) y medimos la anchura de los anillos para realizar un análisis retrospectivo de la talla a la edad (n=166). Los peces tuvieron entre 21 y 218 cm de longitud total ([LT], media: 105.2 cm LT), pero el 87% de ellos medían entre 50 y 130 cm LT. Las edades variaron entre 0 y 18 años (media: 8.1 años), estimándose que el 92% de todos los individuos eran menores de 12 años. La anchura de los anillos indicó que los peces de crecimiento más rápido desaparecieron selectivamente de la zona de estudio a lo largo del tiempo. Para revelar los patrones de movimiento, particularmente para la parte superior el río Connecticut (agua dulce), analizamos 3 años (2019–2021) de detecciones acústicas de 85 individuos. Estos peces ocurrieron en el área de estudio de marzo a noviembre, pero permanecieron en promedio solo 54–91 d. La mayoría de los peces que entraron en las estaciones receptoras en la Sonda de Long Island también se desplazaron al río, pero utilizaron principalmente su estuario salobre inferior. Una gran proporción de individuos (35%–66%) realizó incursiones río arriba hacia el agua dulce, coincidiendo con el bajo caudal y las temperaturas cálidas del río a finales del verano. Por lo tanto, tanto las porciones salobres como de agua dulce del río Connecticut sirven como importantes hábitats estacionales de alimentación para el esturión del Atlántico ≤130 cm TL.

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