

RESEARCH

Open Access



Spatiotemporal patterns in habitat use of natal and non-natal adult Atlantic sturgeon in two spawning rivers

Shannon White^{1*}, Matthew Breece², Dewayne Fox³, David Kazyak¹, Amanda Higgs⁴, Ian Park⁵, Cassia Busch⁶, Barbara Lubinski¹, Robin Johnson¹ and Amy Welsh⁶

Abstract

Background Monitoring movement across an organism's ontogeny is often challenging, particularly for long-lived or wide-ranging species. When empirical data are unavailable, general knowledge about species' ecology may be used to make assumptions about habitat use across space or time. However, inferences about habitat use based on population-level ecology may overlook important eco-evolutionary contributions from individuals with heterogeneous ethologies and could diminish the efficacy of conservation and management.

Methods We analyzed over a decade of acoustic telemetry data to understand individual differences in habitat use of federally endangered adult Atlantic sturgeon (*Acipenser o. oxyrinchus*) in the Delaware and Hudson rivers during spawning season. In particular, we sought to understand whether sex or natal origin could predict patterns in habitat use, as there is a long-held assumption that adult Atlantic sturgeon seldom stray into non-natal rivers.

Results In both rivers, migration timing, spawning habitat occupancy, and maximum upstream migration distance were similar between natal and non-natal individuals. While non-natal individuals represented only 13% of fish detected in the Hudson River, nearly half of all tagged fish detected in the Delaware River were non-natal and generally occupied freshwater habitats longer than natal individuals. In both systems males had more heterogeneous patterns of habitat use and longer duration of occupancy than did females.

Conclusions This study demonstrates the importance of non-natal rivers for fulfilling ontogenetic habitat requirements in Atlantic sturgeon. Our results may also highlight an opportunity to improve conservation and management by extending habitat designations to account for more heterogeneous patterns in individual habitat use in non-natal freshwater environments.

Keywords Atlantic sturgeon, Natal origin, Sex, Acoustic telemetry, Habitat use, Straying, Philopatry

*Correspondence:

Shannon White
slwhite@usgs.gov

Full list of author information is available at the end of the article



This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2024. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

Background

Ontogenetic changes in habitat requirements may necessitate organisms to move through complex habitat mosaics that occur across temporal and spatial scales. It is often not feasible to track individuals throughout their entire life cycle [27, 42], and so general knowledge about species' life history and behavioral meta-analyses may be used to infer patterns of movement and habitat use across ontogeny [38]. While assumptions about movement are generally accurate for describing broad ethological patterns, they may overlook contributions from individuals with rare or alternative behavioral phenotypes [8]. Individual functional diversity is increasingly recognized as an important driver of eco-evolutionary processes, and failure to account for such variation risks an incomplete understanding of the processes shaping contemporary demography [22, 25, 28]. Consideration for individual-level traits may be particularly important under current regimes of environment change, where rapid shifts in habitat quality can elicit novel behaviors that result in range expansion or evolutionary change [45].

Assumptions about movement and habitat use can also determine how we manage and conserve species, particularly taxa of heightened conservation concern that may lack data due to low abundance or monitoring constraints. For example, Atlantic sturgeon (*Acipenser o. oxyrinchus*) is an anadromous species that is broadly distributed across the east coast of North America [1]. Although the timing of stage-specific habitat use varies considerably between sexes and across the species' range, larval and juvenile Atlantic sturgeon are generally stenohaline and spend up to 6 years in their natal river before migrating to the ocean [26]. Throughout subadult and adult life stages, individuals perform extensive coastwide migrations, where they may move over 1500 km in the open ocean while also temporarily occupying habitats in tidal sections of non-natal rivers and estuaries [17, 31]. As a highly philopatric and iteroparous species, Atlantic sturgeon generally return to their natal river to spawn at approximately 5–20 years of age, with 1–5 years separating consecutive spawning migrations [11, 26]. This life history produces genetically distinct spawning populations within each river, including some rivers with genetically distinct spring- and fall-run populations [58].

Historic overharvest collapsed most Atlantic sturgeon populations in the early 1900s, and the species was listed under the United States Endangered Species Act (ESA) in 2012 [40, 41]. As part of this listing decision, populations in United States' waterways were divided into five distinct population segments (DPSs), each representing populations that are genetically and physiologically similar [2, 20, 56]. The two known spawning populations in Canada are separately protected as threatened under

the Committee of the Status of Endangered Wildlife in Canada [14], although harvest is still allowed at reduced levels. Stock assessments and species management plans have recognized a need for quantitative estimates of population size and a better understanding of spatiotemporal habitat use among populations [1]. However, these goals remain difficult to realize because adults spend most of their lives broadly distributed in marine habitats where capture efficiency is low [31, 61]. Although thousands of Atlantic sturgeon have been acoustically telemetered throughout the species' range [1], the natal origin of tagged individuals is often unknown or overlooked which obfuscates our understanding of population- and DPS-specific movement and habitat use.

Given the difficulty of sampling Atlantic sturgeon outside of riverine environments, population demographic and genetic data are often collected during spawning season when adults congregate in relatively discrete freshwater habitats for several weeks in spring or fall [e.g., 29, 30, 44, 58]. When conducting spawning surveys, there is generally an underlying assumption that all adults captured near putative spawning habitats are natal to the population of interest [23]. This assumption has thus far been supported by the species' philopatric life history and limited evidence of straying into non-natal rivers [26, 32]. However, the absence of long-term, fine-scale individual movement data has limited the ability to make empirical inferences about Atlantic sturgeon habitat use in non-natal rivers. In addition, although significant genetic differentiation among populations suggests limited admixture [20, 58, 63], genetic data alone may not accurately characterize the natal composition of adults present at the time of spawning. For example, if non-natal individuals are present but represent a small proportion of all adults, then they may not be detected in population genetic analyses. In addition, for many populations of Atlantic sturgeon, genetic analyses are based only on juveniles captured prior to ocean migration [58]. Therefore, while observed levels of genetic differentiation indicate limited successful admixture among populations, it does not preclude the possibility that non-natal adults are present but not reproductively active (a phenomenon that has been observed in anadromous salmonids [47]) or low fitness or phenological mismatch limit successful reproduction. Importantly, if assumptions about adult natal origin are incorrect, and spawning surveys are sampling an aggregate of natal and non-natal individuals, then there is the potential for bias in estimates of abundance, genetic diversity, and other population characteristics. Moreover, extensive upstream migration and occupancy of spawning habitats by non-natal individuals could suggest an incomplete understanding of the habitat requirements of Atlantic sturgeon across ontogeny and

an opportunity to refine critical habitat designations to improve conservation.

Here, we analyze over a decade of acoustic telemetry data to better understand spatiotemporal patterns in habitat use of natal and non-natal Atlantic sturgeon in the Delaware and Hudson rivers. As the only known spawning habitats for Atlantic sturgeon in the New York Bight DPS, these two rivers are managed concomitantly under the ESA [39]. Despite this, the two populations appear to be on different recovery trajectories. Overharvest of Atlantic sturgeon in the Hudson River caused a population collapse in the early twentieth century, eventually leading to a state-issued harvest moratorium in 1996 [26]. The population has since shown signs of recovery and is now believed to be one of the largest spawning populations throughout the species' range [30, 43]. Similarly, the Delaware River historically supported the largest Atlantic sturgeon fishery but started collapsing in the late 1800s due to overharvest and poor habitat quality [51]. Although the fishery was closed by 1998, spawning runs of Atlantic sturgeon in the Delaware River remain less than 1% of historical levels [57]. Today, recovery of Atlantic sturgeon in the Delaware River continues to be challenged by concerns centered around bycatch in marine and state fisheries, water quality, and vessel strike mortality, with the latter two appearing to be increasing in severity with climate change and an expanding commercial shipping industry [12, 13]. Accordingly, improved understanding of individual patterns of habitat use stands to not only increase our knowledge of Atlantic sturgeon life history but may also have important consequences for management and conservation of critical habitats within each river.

Methods

Fish collection and tagging

We monitored movements of Atlantic sturgeon that were acoustically tagged from 2005 to 2020 along the coast of Delaware or in Delaware Bay in spring and summer, respectively (Fig. 1). This location supports a mixed-stock aggregation, so we anticipated that the sample might include fish from multiple populations [9, 61]. All sampling was completed using 30 to 33 cm stretch mesh anchored gillnets deployed for 10–120 min, depending on environmental conditions and expected catch rates. All individuals were measured for total length (TL) and weight, tagged with a passive integrated transponder (PIT) tag, and a small clip of the upper caudal fin was excised and stored in 95% non-denatured alcohol for genetic analyses. An acoustic transmitter (Innovasea [VEMCO] V-16-6H, battery life 6–10 years) was also surgically implanted into individuals following protocols developed by Fox et al. [18]. When possible, a small

biopsy of the gonad was taken during acoustic tagging to determine sex and stage of sexual maturity using methods described by Van Eenennaam et al. [54].

Although we measured fish length at the time of capture, individuals could be acoustically detected for up to a decade later. Therefore, we estimated an individual's length at each date of acoustic detection using a von Bertalanffy growth model developed for Atlantic sturgeon in the New York Bight [16]. As we were only interested in adult movement and habitat use, individuals were excluded from the analysis in years where their estimated TL was < 1500 mm, which is the approximate minimum size of a sexually mature Atlantic sturgeon [54, 55].

Genetic sex and natal origin assignments

We isolated genomic DNA from fin clips using Genra Puregene Reagents (Qiagen) according to manufacturer's protocols. All samples were screened for 12 microsatellite disomic loci including *LS19*, *LS39*, *LS54*, *LS68*, *Aox12*, *Aox23*, *Aox45*, *AoxD44*, *AoxD165*, *AoxD170*, *AoxD188*, and *AoxD241* [24, 33, 36]. Using protocols modified from Kuhl et al. [34], we also used the *AllWSex2* primer to assign individual sex. Specifically, a fragment that amplified at > 26,000 relative fluorescence units (RFU) was considered a female and < 8,000 RFU a male. Samples with peaks that amplified between 8,000 and 26,000 RFU were classified as unknown sex.

A positive control sample with DNA from a female Atlantic sturgeon with a known multilocus genotype was included on each PCR plate for checking PCR amplification success and for checking correct binning success in the fragment analysis software. We also included a negative control sample with no DNA on each PCR plate to check for contamination. We reran all PCR amplifications for samples with missing data due to weak or unamplified alleles. All repeated amplifications were performed as single loci and not as a multiplexed PCR except for the sex marker which was done in multiplex as a control for PCR amplification.

We determined natal origin by performing individual-based assignment tests in the program GeneClass [46] using the Bayesian assignment criteria described by Rannala and Mountain [49]. With this analysis, allele frequency distributions are used to determine the likelihood that an individual originated from each of the 18 spawning populations in the genetic baseline described by White et al. [58]. This baseline includes populations from each of the five DPSs and two Canadian rivers and has been shown to have high sensitivity and specificity for natal origin assignments (see White et al. [58] for details).

For each individual, we calculated population-specific assignment scores by taking the likelihood of assigning to each population and dividing it by the cumulative



Fig. 1 Location of the Delaware and Hudson rivers in relation to the location Atlantic sturgeon was acoustically tagged (orange circle) along the coast of Delaware and in Delaware Bay

likelihood across all populations. Thus, assignment scores are a likelihood ratio ranging from 0 to 1, with higher values indicating a greater likelihood of having originated from a given population. Individuals were considered natal to a single population of origin when the population-specific assignment score was ≥ 0.80 . All individuals with an assignment score ≥ 0.80 to a population outside of the New York Bight DPS were considered non-natal

in our analyses. However, if an individual assigned with high likelihood to the Delaware population, then it would be considered non-natal when performing Hudson-specific analyses and vice versa for an individual classified as natal to the Hudson population when performing analyses on the Delaware River.

A few individuals were assigned with low likelihood to several populations and we were not confident about

a single population of origin. In these cases, we summed assignment scores across the five most likely populations, excluding scores to either the Delaware or Hudson population. If this cumulative score was ≥ 0.80 , an individual was classified as non-natal. If the cumulative score was still < 0.80 , an individual was classified as unknown and removed from the analysis.

Importantly, in the genetic baseline by White et al. [58], the Hudson River is represented by a mixture of presumptive spawning adults (i.e., individuals > 1500 mm TL) and river-resident juveniles (< 500 mm), whereas the Delaware River population is characterized by only river-resident juveniles. A major tenet of our analysis is based on the potential for natal and non-natal adults to co-occur at spawning habitats. If so, adults in the genetic baseline from the Hudson River could include both natal and non-natal individuals. Because the Hudson River population is represented by over 300 fish in the baseline, the presence of a small percentage of non-natal fish is not expected to change the outcome of individual-based assignment tests. However, given that we did not know the number of non-natal adults that could be present, we sought to increase confidence in assignment scores by repeating all individual-based assignment tests using a modified genetic baseline. In this modified baseline, adults in the Hudson River population were replaced by juvenile and young subadult Atlantic sturgeon (average TL 563 mm) that assigned to the Hudson River population with a score of ≥ 0.80 (see [59] for a description of this genotyping effort).

When using the modified baseline, all individuals that originally assigned as non-natal still assigned as non-natal. However, for some fish, using the modified baseline did affect individual assignment scores and natal classification. Specifically, 12 individuals that originally assigned as unknown were assigned with high enough likelihood to be included in our analyses (either as non-natal, Delaware, or Hudson origin). Another 13 individuals that originally assigned to Hudson River population and one individual that assigned to the Delaware River population still had the highest assignment likelihood to that respective population, but with a score < 0.80 (average score = 0.70). Given that results of the two analyses were generally congruent, we used the baseline established by White et al. [58] for genetic assignment tests.

Acoustic arrays and monitoring

We monitored movement and habitat use of tagged Atlantic sturgeon using river-wide acoustic receiver arrays (Innovasea [VEMCO] VR2, VR2W, and VR2AR) that spanned the historic and presumed contemporary spawning sites in each river [11, 12]. Receivers in the Delaware River were maintained year-round in most years.

In the Hudson River, receivers were generally deployed several weeks before the beginning of spawning migrations and retrieved in late fall, as there was presumed minimal occupancy of adult Atlantic sturgeon in the winter and a high probability of ice over which could damage or displace equipment. In both rivers, there were changes to the number and spatial distribution of receivers across years. However, unless otherwise noted, receivers were approximately equally distributed throughout the study area each year.

The Delaware River had an extensive acoustic receiver network in Delaware Bay and up to 39 receivers in the river extending from river kilometer (rkm) 77 to approximately rkm 210 near Bordentown, New Jersey. In the Hudson River, the river-wide array was comprised of up to 54 receiver stations distributed from rkm 0 at the southern tip of Manhattan Island, New York to just below the Federal Dam at rkm 240 near Troy, New York. The Federal Dam is impassible to sturgeon and so rkm 240 represents the maximum extent of plausible upstream migration. From 2010 to 2014, there were also nine receiver stations downriver of rkm 0 in New York Harbor and five receivers in the East River; however, these receivers were not maintained after 2014.

Large, mixed-stock aggregations of Atlantic sturgeon occupy habitats in Delaware Bay and near the mouth of the Hudson River [10, 61, 62], but most of these individuals do not undertake significant upstream migrations. Because the purpose of this analysis was to understand riverine movement and habitat use, we excluded individuals from our analysis if they were never detected upriver of the typical salt front which occurs at approximately rkm 103 near Wilmington, Delaware in the Delaware River and rkm 55 near Bear Mountain, New York in the Hudson River.

Data analysis: developing space use sequences

Spatiotemporal patterns in habitat use within each river were explored using sequence analyses. Originally developed to understand patterns in DNA sequences in bioinformatics research, sequence analyses have since emerged as a powerful analytical framework for the analysis of sequential animal movement data [15]. In addition to being more temporally explicit than other common movement models, sequence analyses are an appealing option for understanding patterns in space use as they can more easily account for spatial autocorrelation in detections and missing data which may occur due to changes in receiver location or read range through time.

A sequence analysis is performed on a collection of individual sequences, each of which is a categorical time series representing an individual's discrete state through time. To build the sequences, we first subdivided each

river into ecologically relevant habitat segments with a particular emphasis on dividing spawning from non-spawning habitats. For the Delaware River, we used Atlantic sturgeon density estimates and river sediment composition reported by Breece et al. [12] to divide the river into five habitat segments (Fig. 2). This was necessary as the location of Atlantic sturgeon spawning in the Delaware River is not well-understood but is believed to occur between Claymont and Tinicum (approximate rkm 125–137; [21]) which is also the location of highest Atlantic sturgeon density reported by Breece et al. [12]. In addition, increased sturgeon densities have been reported near Burlington (rkm 187), but the ecological significance of that habitat segment is unclear. The Hudson River was subdivided into five habitat sections (Fig. 3), including the primary locations of Atlantic sturgeon spawning at Hyde Park (rkm 136) and a secondary spawning site at Catskill (rkm 177) that is believed to be less densely occupied [3, 11, 30, 54].

Receivers located within a habitat segment were grouped together and an individual’s daily location (state) was identified as the segment in which it was most frequently detected on that day. On days where an individual was not detected, we used the last-observation-carried-forward approach and assumed that the fish stayed in the same habitat segment until detected elsewhere. Observations were only allowed to carry forward

until the last detection date within a year. If a fish was not detected 1 year but was in a subsequent year, it was assumed to have remained in the lower estuary or ocean. A fish was considered missing before the year of first detection and if it failed to return to the river following the last year of observation. For the latter case, a fish may have gone missing either due to long return periodicity, movement to another river, tag failure or expiration, or mortality.

Because we were most interested in habitat use with respect to spawning season, individual sequences were trimmed to the putative spawning window in each river. Therefore, we developed sequences from detections that occurred between 1 March to 30 June in the Delaware River and 1 April to 31 July in the Hudson River [1, 11]. Due to pandemic-related restraints, receivers in the Hudson River were not deployed until June in 2020, so that year represents a reduced dataset.

Data analysis: identifying patterns in habitat use

Sequence analyses attempt to group individuals based on similar patterns of behavior. To do so, individual sequences are used to generate a dissimilarity matrix representing the optimal matching distance between all pairs of individuals. Distances are calculated by applying a pre-defined cost regime that assigns a penalty for each time step that two sequences are not observed in

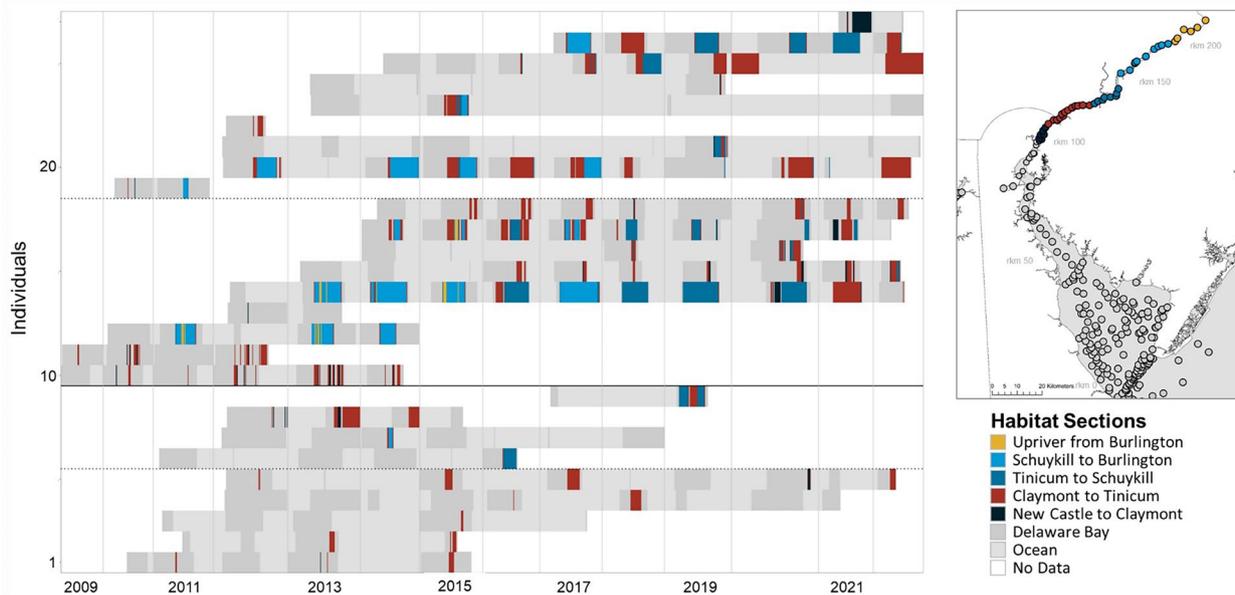


Fig. 2 Longitudinal sequence plot for 27 adult Atlantic sturgeon detected in the Delaware River from 2009 to 2022. Sequences display an individual’s daily location from 1 March to 30 June, with colors corresponding to habitat reaches displayed in the map. Females (bottom) and males (top) are separated by the solid black horizontal line. Within each sex, natal (bottom) and non-natal (top) individuals are separated by a dashed line. Individuals within each sex and natal origin group are sorted by tag year. Hence, fish tagged in later years have no data prior to first detection. Likewise, fish tagged early in the study may be missing data from tag expiration, straying, or mortality

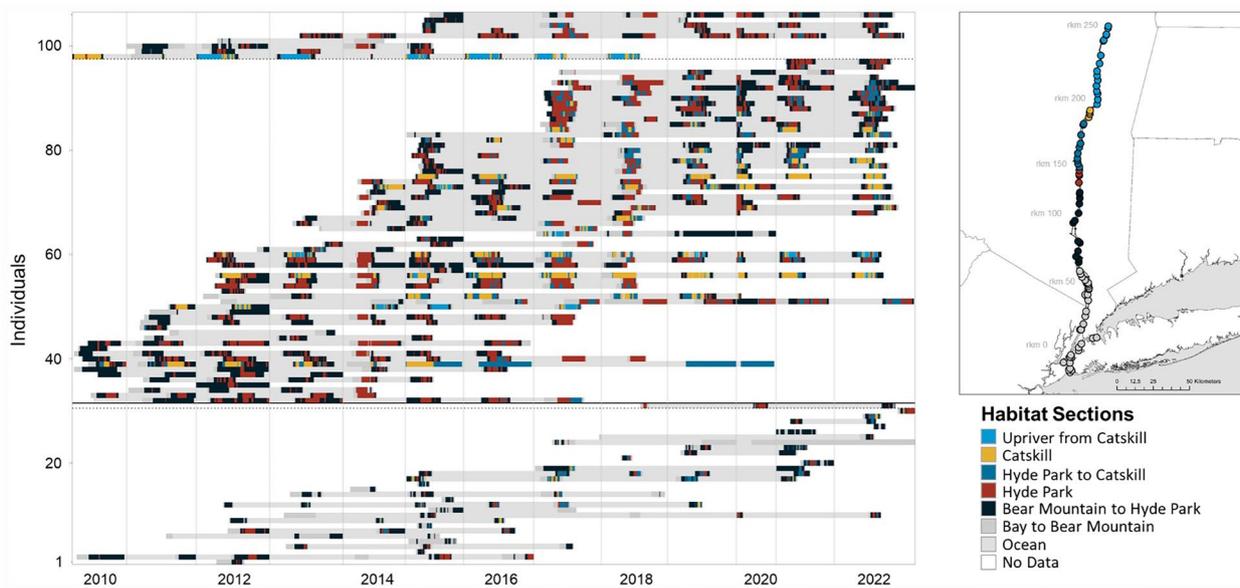


Fig. 3 Longitudinal sequence plot for 106 adult Atlantic sturgeon detected in the Hudson River from 2010 to 2022. Sequences display an individual's daily location from 1 April to 31 July, with colors corresponding to habitat reaches displayed on the map. Females (bottom) and males (top) are separated by the solid black horizontal line. Within each sex, natal (bottom) and non-natal (top) individuals are separated by a dashed line. Individuals within each sex and natal origin group are sorted by tag year. Hence, fish tagged in later years have no data prior to first detection. Likewise, fish tagged early in the study may be missing data from tag expiration, straying, or mortality

the same state [19]. For our analysis, we assumed a cost regime comparable to a generalized Hamming distance which preserves the original sequence length (and, therefore, time) by voiding insertions and deletions (i.e., deleting or adding dates in the longitudinal analysis) and applying a spatially explicit substitution cost. Pairwise substitution costs were quantified for each day, and we assigned a cost of 0 for two fish that occurred in the same habitat segment. Fish that were in different habitat segments were assigned a cost of 1 if segments were first-order neighbors and a cost of 2 if segments were second-order or higher neighbors. A transition from an observed habitat state to no data was assigned a cost of 3. Therefore, the highest pairwise dissimilarity is observed when two individuals are in a known and an unknown location. Increasing the cost of the no data state could increase spurious clustering if individuals from a single group are particularly data poor (i.e., assigning a high cost to missing data may result in significant differences between groups that reflect differences in data quality, rather than habitat use). However, our observed rates of missing data were generally similar between sexes and natal origins throughout time. In addition, sensitivity analyses suggested that, as long as the cost of the no data state was > 1 , our general conclusions were robust regardless of the penalty assigned to that state. Therefore, to emphasize the difference between an informative vs. uninformative state,

we elected to make inferences using a penalty matrix that assigned a cost of 3 when there were no data. Daily substitution costs were summed across the entire longitudinal sequence and used to populate the dissimilarity matrix.

To determine if natal origin or sex predicted patterns in habitat use, we used a regression tree to model the dissimilarity matrix as a function of the individual-level covariates. The starting node was comprised of sequences for all individuals. We then attempted to split the node using sex and natal origin (i.e., natal or non-natal) to produce branches that maximized the univariate pseudo- R^2 (see [53] for more details). Pseudo-F values were used to determine branch significance, and all branches estimated with $p < 0.1$ were retained for inferences.

Data analysis: quantifying diversity in habitat use

We calculated longitudinal Shannon entropy to examine heterogeneity in individual habitat use. When normalized by the maximum possible entropy given the number of sequence states, longitudinal Shannon entropy ranges from 0, representing an individual that spent all time in a single state, to 1, representing an individual that spent equal time in all states. Normalized individual sequence entropy (h) was calculated using the formula:

$$h = \frac{-\sum_{i=1}^s \pi_i \ln(\pi_i)}{\ln(s)}$$

where s is the number of habitat segments and π_i is the proportion of days in the i^{th} segment [see 19 for more in-depth discussion about entropy calculations]. To understand individual-level traits that influence diversity in individual habitat use, we modeled h as a function of sex and natal origin.

While sequence analyses provide insights into spatiotemporal patterns in habitat use, we also wanted to test for more general differences in the timing of in/outmigration, maximum upstream migration distance, and time spent in the river and primary spawning habitats. Therefore, we used linear mixed-effects models to estimate the effects of sex, natal origin, and von Bertalanffy-corrected length on the response variables. For all models, we included an interaction term between sex and natal origin as well as random effects for year and individual. We first explored a full model including all possible covariates and then removed all variables that were not significant at the level of $p=0.05$. All inferences were then made using this reduced model.

We conducted all analyses in the program R [48]. Sequences were generated and analyzed using the package TraMineR [19]. Linear regressions were fit using functions contained within the stats package and mixed effects models were performed with functions contained within the lmer4 package [5].

Results

Summary of all tagged fish

In total, 521 Atlantic sturgeon (TL range: 710–2,670 mm) were acoustically tagged between 2005 and 2020. Of these, 471 individuals were genotyped for our analyses. The sex ratio showed a slight bias towards females, with 238 females and 184 males. We did not obtain a field or genetic sex identification for 49 individuals. Of the 471 individuals genotyped, 383 had an assignment score ≥ 0.80 to a single population. Of these individuals, 164 (42.8%) assigned to the Hudson River population, which was the most numerically abundant population in the sample. There were also significant contributions from the James River Fall Run in Virginia ($n=76$; 19.8%) and Delaware River ($n=31$; 8.1%) populations. The remaining individuals assigned to 13 other populations, including fish from all five DPSs and both Canadian rivers (see Additional file 1: Table S1). The only baseline populations that were not represented in our survey were the fall run populations from the Edisto and Ogeechee rivers which originate in South Carolina and Georgia, respectively.

Atlantic sturgeon habitat use in the Delaware River

Between 2009 and 2022, 477 acoustically tagged Atlantic sturgeon were detected in Delaware Bay; however, only 27 individuals migrated upstream of the salt front at rkm 103. Of those 27 individuals, 14 were natal to the Delaware River. The 13 non-natal individuals assigned to the Hudson River ($n=8$), James River Spring Run (3), James River Fall Run (1), and the Canadian St. Lawrence (1) populations with an average assignment score of 0.94. Males comprised 67% of detected individuals (18 vs. 9 females).

Longitudinal entropy was similar between all males and females ($p=0.40$), as individuals from both sexes tended to spend multiple consecutive days within the same habitat segment. However, there were other significant differences in habitat use between sexes. Males migrated, on average, 48.6 km farther upstream ($p=0.003$) and females rarely occupied habitats upriver of rkm 150. On average, males spent 11 more days in the Delaware River ($p=0.05$) and returned to the river in consecutive years, whereas females more often skipped at least 1 year between repeat migrations ($p<0.001$). The timing of migration into the Delaware River and into the spawning reach from Claymont to Tinicum and number of days spent occupying habitat in the spawning reach was similar between sexes ($p>0.20$ for the effect of sex in all models). The effect of sex was marginally insignificant in regression tree analyses ($p=0.06$), likely because both sexes spent significant time in Delaware Bay and in the ocean (Table 1).

On average, non-natal individuals, particularly males, were more likely to return to the Delaware River in consecutive years ($p=0.001$), likely owing to the tendency for natal females to skip at least 1 year before returning. While natal individuals migrated 19.7 km farther upstream than non-natal individuals, the effect of natal origin was not statistically significant ($p=0.15$) and non-natal individuals, particularly males, were frequently detected upriver of rkm 150. Natal origin was also not a significant predictor in all other mixed-effects models and in the regression tree analysis ($p>0.40$ for the effect of natal origin in all models), highlighting similar patterns of in-migration, spawning area occupancy, and out-migration between natal and non-natal Atlantic sturgeon. Although natal origin was not a significant predictor in longitudinal entropy of regression tree analyses, natal males appeared to move among habitat reaches more frequently than did non-natal males (Table 2; Fig. 2).

Atlantic sturgeon habitat use in the Hudson River

From 2010 to 2022, we detected 106 tagged Atlantic sturgeon between rkms 55 and 240 in the Hudson River (31 females and 75 males). Approximately 91% of all fish detected in our study area in the Hudson River were natal

Table 1 Difference in movement and habitat use between male and female Atlantic sturgeon in two rivers

Response variable	Delaware river		Hudson river	
	Male	Female	Male	Female
Date of first detection in the river	<i>14 May</i>	<i>20 May</i>	17 May	26 May
Date of first detection in the primary spawning reach	<i>17 May</i>	<i>21 May</i>	31 May	10 June
Cumulative number of days spent in the primary spawning reach	6.4	6.1	9.4	3.8
Maximum upstream migration distance (km)	111.0	62.4	149.1	126.6
Date of outmigration	<i>5 June</i>	<i>30 May</i>	<i>29 June</i>	<i>27 June</i>
Total number of days in the river	21.4	10.4	42.2	31.9
Shannon longitudinal entropy	<i>0.47</i>	<i>0.41</i>	0.55	0.42
Number of years between consecutive detections	1.1	2.0	1.2	1.8

Within each river, the effect of sex on each parameter was explored using linear mixed effect models. Estimates appearing in italics were not significant at the level of $p=0.05$

Table 2 Difference in movement and habitat use between natal and non-natal Atlantic sturgeon in two rivers

Response variable	Delaware river		Hudson river	
	Natal	Non-natal	Natal	Non-natal
Date of first detection in the river	<i>15 May</i>	<i>17 May</i>	<i>19 May</i>	<i>16 May</i>
Date of first detection in the primary spawning reach	<i>19 May</i>	<i>17 May</i>	<i>1 June</i>	<i>1 June</i>
Cumulative number of days spent in the primary spawning reach	5.1	8.6	8.5	10.3
Maximum upstream migration distance (km)	103.7	84.0	145.2	146.8
Date of outmigration	<i>31 May</i>	<i>10 June</i>	<i>28 June</i>	<i>29 June</i>
Total number of days in the river	16.4	23.9	40.1	43.8
Shannon longitudinal entropy	<i>0.45</i>	<i>0.45</i>	0.52	0.49
Number of years between consecutive detections	1.3	1.1	1.3	1.4

Within each river, the effect of natal origin on each parameter was explored using linear mixed effect models. Estimates appearing in italics were not significant at the level of $p=0.05$

to the Hudson River population; however, one female and nine males were not. Of the non-natal individuals, three assigned with highest likelihood to the Delaware River population, three to the James River Fall Run population, two to the Kennebec River population (Maine), and one each to the Albemarle Complex (South Carolina) and the Pee Dee Spring Run (South Carolina) populations. Average assignment score for non-natal individuals was 0.88, providing strong support that they originated from outside the Hudson River. There were 34 additional individuals detected during the study but removed from analyses due to uncertain sex and/or natal origin. In total, 65% of all fish tagged in Delaware waters during this study that assigned to the Hudson River population were detected at least once in our study area in the Hudson River.

Sequence analyses highlighted significant differences in habitat use between males and females (Fig. 3), a result that was corroborated by the first split of the regression tree ($p=0.01$). Sex-specific differences were largely driven by higher heterogeneity in habitat use by males ($p<0.001$, by longitudinal entropy analyses) including, on average, higher upstream migration

by 22.5 km ($p<0.001$). Males also migrated into the Hudson River an average of 10 days sooner ($p<0.001$), arrived at the primary spawning habitat at Hyde Park 10 days earlier ($p<0.001$), spent 5 more days ($p=0.005$) in Hyde Park, and spent 10 more days in the river ($p<0.001$) than did females. Males generally returned to the Hudson River in consecutive years, whereas females more frequently skipped at least 1 year before returning ($p<0.001$). Sex was not associated with outmigration timing and, in all models, the effect of individual length was either statistically and/or biologically insignificant (Table 1).

For the Hudson River, the effect of natal origin was not statistically significant ($p>0.9$) in any regression model, and natal and non-natal individuals had a similar average duration and timing of occupancy and habitat use heterogeneity (Table 2). Non-natal individuals also consistently migrated into upriver habitat patches, including one male that assigned with highest likelihood to the James River Fall Run and was detected every year from 2010 to 2018 with most time spent occupying habitats in the two most upriver sections. This fish's location after 2018

is unknown, but it is notable that the tag likely expired some time in 2019.

Movement of individuals between rivers

Three male Atlantic sturgeon that all assigned with highest likelihood to the Hudson River population were detected upstream of the salt front in both the Delaware and Hudson rivers. These three fish spent proportionally more time in the Hudson River, including significant time spent in the primary spawning reach at Hyde Park (Fig. 4A). Two of the three males also occupied habitats in the spawning reach between Claymont and Tinicum in the Delaware River and were detected as far upriver as rkm 150 (Fig. 4B). There were no instances of an individual making significant upstream migrations in both rivers within a single year, but it was not uncommon for fish to occupy habitats in Delaware Bay before migrating to the Hudson River.

Discussion

Conservation of highly mobile species can be challenging due to incomplete information about how individuals interact with habitats across space and time [42, 50]. Anthropogenic interactions with the environment are also fundamentally changing the distribution of ecologically important habitats, sometimes resulting in movement and space use observations that are incongruent with our understanding of species’ ecology [7]. Accordingly, improved understanding of cross-scale patterns of habitat use is important for the collection and interpretation of spatiotemporal demographic data and for adapting conservation strategies to meet contemporary challenges facing populations [35]. Using over a decade of acoustic telemetry data on two rivers, we demonstrate that natal and non-natal adult Atlantic sturgeon show similar patterns of riverine habitat use and frequently co-occur at the time and location of spawning. This

observation contradicts long-held assumptions that habitat use in upper tidal rivers was restricted to individuals from the natal population. Importantly, the significance of this finding may vary between rivers, as non-natal individuals were proportionally rare in the Hudson River but comprised nearly half of all detected individuals in the Delaware River. This result could simply reflect the relative size of the natal population in each river (i.e., non-natal fish were proportionally rare in the Hudson River because the natal population size is large relative to that of the Delaware), but additional study may be warranted to determine if the biogeophysical properties of each river leads to differential probability of non-natal occupancy. Taken together, this study demonstrates a greater use of non-natal freshwater habitats than was previously assumed, potentially highlighting opportunities for improved habitat conservation for the protection of Atlantic sturgeon populations across range-wide scales.

The eco-evolutionary significance of adult Atlantic sturgeon in non-natal rivers remains unclear, particularly for individuals that completed extensive upstream migrations in multiple consecutive years. Significant genetic differentiation between all spawning populations of Atlantic sturgeon, including the Delaware and Hudson, suggests that little gene flow occurs among populations [58]. It remains unclear whether non-natal straying is being driven by reproduction, habitat use, or potentially a combination of both as has been observed in Pacific salmonids [47]. Because individuals were captured outside of riverine environments, we do not know whether they were in spawning condition when they were detected in-river. Our analyses were restricted to individuals >1500 mm, and so all were plausibly sexually mature [4, 16]. In addition, one non-natal male in our analyses was recaptured during spawning surveys at Hyde Park in the Hudson River and expressing milt. Although milt expression can occur outside of spawning

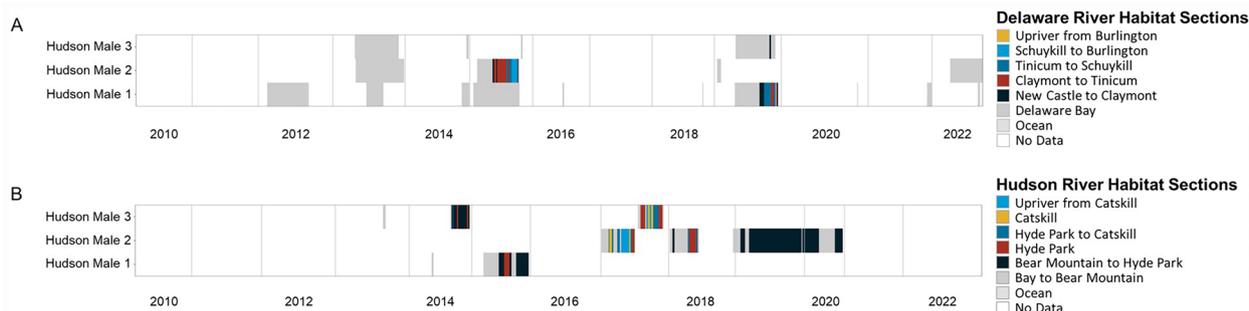


Fig. 4 Sequence plots for three Atlantic sturgeon that were detected in both the Delaware (A) and Hudson (B) rivers. All three individuals were male and assigned with highest likelihood to the Hudson River population. Note that, because the Delaware River was monitored from 1 March to 30 June and the Hudson River from 1 April to 31 July, dates on the y-axis are not consistent between plots

season, this result could suggest that at least a proportion of non-natal individuals may spawn outside of natal habitats. If so, it is possible that a pre- or post-zygotic mating barrier limits fitness and survival of offspring. Alternatively, intraspecific introgression in Atlantic sturgeon may occur, but is either rare or may have only recently increased in prevalence such that it was not detectable in recent genetic analyses of the Delaware and Hudson populations. While further investigation is warranted, hypotheses about factors limiting population admixture should be interpreted with caution given overall limited data.

Observed patterns of non-natal straying could also be explained through social learning, including the potential for adopted migration [52]. Adopted migration posits that, rather than inheritance of natal homing, juveniles adopt movement and migration strategies that are consistent with the behaviors observed in the co-occurring adult population. Highly mobile juveniles may enter a stage of behavioral lability while outside of natal habitats and adopt the migration pattern of co-occurring individuals from a non-natal population. While most juvenile Atlantic sturgeon remain in freshwater or estuarine habitats, there have been rare reports of young individuals engaging in long-distance marine migrations and co-occurring as part of mixed-stock aggregations in bays and estuaries [59]. If Atlantic sturgeon uses social cues to learn migration strategies, then these highly mobile juveniles may adopt a migration pattern that is inconsistent with adults from their natal population and more like individuals that were encountered in the mixed-stock aggregation. To date, adopted migration theory has been difficult to validate with empirical evidence, but studies suggest it may occur in herring in the Gulf of St. Lawrence, where spring-spawned juveniles adopted migrations consistent with numerically dominant fall-spawn adults [37]. However, adopted migration theory may not fully explain our observation of Atlantic sturgeon migrating into multiple rivers. Therefore, additional studies linking juvenile to adult movement vagility and quantifying patterns of interannual habitat use may be warranted to investigate the potential role of adopted migration or other social learning mechanisms for understanding non-natal straying.

Extensive use of non-natal habitats by adult Atlantic sturgeon adds to our understanding of species' life history and spatiotemporal habitat requirements. In accordance with ESA listing, critical habitat designations have been defined in each spawning river with the goal of protecting all habitats occupied by Atlantic sturgeon [41].

As natal and non-natal individuals had similar patterns of space use, it is unlikely that additional habitat protections are likely to benefit non-natal sturgeon populations. However, river-specific critical habitat designations are largely subject to the distribution of the natal population. If a population were to become extirpated, as is a concern in the Delaware River given low population size estimates and on-going demographic threats [12, 60], then habitat conservation and use restrictions might be relaxed. As our study highlights, this could have negative consequences for Atlantic sturgeon populations throughout the entire species' range. For example, over half of Atlantic sturgeon detected in the Delaware River were non-natal and assigned to seven different spawning populations and four DPSs. Loss of Atlantic sturgeon critical habitat designations in the Delaware River could turn this important habitat into an ecological trap that endangers populations at range-wide scales [6].

Our findings may also provide insights into demographic trajectories recently observed in both river systems. Because natal individuals comprised most fish detected in the Hudson River, it is likely that recent signs of population recovery [44] are indicative of increased recruitment of the Hudson River population. Conversely, the presence of a significant proportion of non-natal individuals in the Delaware River may explain why increases in reported ship strike mortalities [13] have not been met with a concomitant demographic decline in the Delaware River population of Atlantic sturgeon. The presence of non-natal individuals in the Delaware River also suggests that demographic estimates based on adult enumeration may need to be interpreted with caution, as the presence of non-natal individuals could bias estimates of population size.

Consistent with previous studies in the Hudson River [11], females tended to migrate into the river later and spend less time there than did males. Our study adds to this knowledge by also highlighting sex-specific differences in the heterogeneity of habitat use. In both rivers, males moved further upstream than females and moved among habitat reaches more frequently. Because males spent fewer consecutive days occupying any one habitat reach, they infrequently co-occurred with tagged females over spawning habitats, particularly within the Hudson River. Limited overlap in spawning reaches was further exacerbated by proportionally few females that were detected in the Hudson River. As one extreme example, 14 tagged natal females were detected in the Hudson River in 2015, of which six were never detected in Hyde Park. Of the eight tagged females that were

detected in Hyde Park, there were only 4 days where two tagged females overlapped with at least one tagged male. Although the number of tagged individuals likely represents less than 20% of all adults in the spawning run [30], this result highlights the vulnerability of even the most robust spawning populations to disturbances that may occur at small temporal or spatial scales. Small changes in habitat quality at Hyde Park or migration interference could particularly limit access of females to spawning habitats and significantly influence recruitment dynamics.

Importantly, we acknowledge the limitations of probabilistic individual-based assignment methods and recognize the potential for mis-assignment to bias results of our analyses. While populations in the Delaware and Hudson rivers are genetically distinct, the differentiation between them is lower than levels of differentiation observed with populations outside of the New York Bight DPS [58]. Therefore, it is not unexpected that individuals from the Hudson River population may occasionally mis-assign to the Delaware River population, and vice versa. However, simulation analyses have shown that we should expect the misassignment rates between these populations to be less than 7% [57]. Moreover, in both the Delaware and Hudson rivers, non-natal individuals assigned to populations outside the New York Bight DPS, where misassignment rates are much lower. We also used conservative criteria to classify individuals as non-natal, removing individuals from the analysis if likelihood of assignment was < 0.80 . Taken together, this suggests that our overall conclusions are robust to potential misassignments.

Conclusions

Using over a decade of acoustic telemetry data, we show significant evidence of straying in adult Atlantic sturgeon in two mid-Atlantic rivers. This finding contrasts our traditional understanding of Atlantic sturgeon ecology, including the long-held assumption that adult populations only occupy freshwater habitats in their natal rivers. While the proportion of non-natal individuals present varied by year and river system, these findings may help explain demographic trends recently observed in each population. Moreover, our results suggest that considerations for intraspecific variation in movement and habitat use may allow for more efficacious management and conservation of demographic and phenotypic diversity in federally endangered populations of Atlantic sturgeon.

Abbreviations

ESA Endangered Species Act
TL Total length

rkm River kilometer
DPS Distinct population segment

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-024-00366-1>.

Additional file 1: Table S1. Number of acoustically tagged Atlantic sturgeon that assigned to each spawning population, separated by sex and tag year.

Acknowledgements

We thank Bill Post for comments on an earlier draft and Wilhelmina Fox for support during data analyses. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions

SW performed data analyses and was the primary writer of the publication. MB, DF, AH, and IP collected fish, organized telemetry records, and refined data analyses. CB, BL, and RJ performed all genotyping. DK and AW oversaw project management and funding. All authors contributed to manuscript review and approved the final draft.

Funding

This study was funded in part by the Bureau of Ocean Energy Management through Interagency Agreement M20PG00003 with the U.S. Geological Survey.

Availability of data and materials

All datasets used in this publication are available upon request.

Declarations

Ethics approval and consent to participate

All sampling and tagging procedures were approved by the Delaware State University Institutional Animal Care and Use Committee under protocol 2015-DF-4-01 and were conducted under the authority of National Marine Fisheries Service Protected Resources permit #16507.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

Author details

¹U.S. Geological Survey Eastern Ecological Science Center, Kearneysville, WV, USA. ²College of Earth Ocean and Environment, University of Delaware, Lewes, DE, USA. ³Department of Agriculture and Natural Resources, Delaware State University, Dover, DE, USA. ⁴Cornell University in Cooperation With New York State Department of Environmental Conservation, New Paltz, NY, USA. ⁵Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife, Dover, DE, USA. ⁶School of Natural Resources, West Virginia University, Morgantown, WV, USA.

Received: 21 January 2024 Accepted: 11 April 2024

Published online: 24 April 2024

References

1. Atlantic States Marine Fisheries Commission (ASMFC). Atlantic sturgeon benchmark stock assessment and peer review report. Washington, DC, USA. 2017.

2. Atlantic Sturgeon Status Review Team (ASSRT). Status review of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*). Report to National Marine Fisheries Service. Northeast Regional Office. Gloucester, MA, USA. 2007.
3. Bain MB. Atlantic and shortnose sturgeon of the Hudson River: common and divergent life history attributes. *Environ Biol Fishes*. 1997;48:347–58.
4. Balazik MT, McIninch SP, Garman GC, Latour RJ. Age and growth of Atlantic sturgeon in the James River, Virginia, 1997–2011. *Trans Am Fish Soc*. 2012;141:1074–80.
5. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. *J Stat Softw*. 2015;67:1–48.
6. Battin J. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv Biol*. 2004;18:1482–91.
7. Beever EA, Hall LE, Varner J, Loosen AE, Dunham JB, Gahl MK, Smith FA, Lawler JJ. Behavioral flexibility as a mechanism for coping with climate change. *Front Ecol Environ*. 2017;15:299–308.
8. Bonte D, Dahirel M. Dispersal: a central and independent trait in life history. *Oikos*. 2017;126:472–9.
9. Breece MW, Fox DA, Haulsee DE, Wirgin II, Oliver MJ. Satellite driven distribution models of endangered Atlantic sturgeon occurrence in the mid-Atlantic Bight. *ICES J Mar Sci*. 2018;75:562–71.
10. Breece MW, Fox DA, Oliver MJ. Environmental drivers of adult Atlantic sturgeon movement and residency in the Delaware Bay. *Mar Coast Fish*. 2018;10:269–80.
11. Breece MW, Higgs AL, Fox DA. Spawning intervals, timing, and riverine habitat use of adult Atlantic Sturgeon in the Hudson River. *Trans Am Fish Soc*. 2021;150:528–37.
12. Breece MW, Oliver MJ, Cimino MA, Fox DA. Shifting distributions of adult Atlantic sturgeon amidst post-industrialization and future impacts in the Delaware River: a maximum entropy approach. *PLoS ONE*. 2013;8:e81321.
13. Brown JJ, Murphy GW. Atlantic sturgeon vessel-strike mortalities in the Delaware Estuary. *Fisheries*. 2010;35:72–83.
14. Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Assessment and status report on the Atlantic sturgeon *Acipenser oxyrinchus* in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada; 2011.
15. De Groeve J, Van de Weghe N, Ranc N, Neutens T, Ometto L, Rota-Stabelli O, Cagnacci F. Extracting spatio-temporal patterns in animal trajectories: an ecological application of sequence analysis methods. *Methods Ecol Evol*. 2016;7:369–79.
16. Dunton KJ, Jordaan A, Secor DH, Martinez CM, Kehler T, Hattala KA, Van Eenennaam JP, Fisher T, McKown KA, Conover DO, Frisk MG. Age and growth of Atlantic sturgeon in the New York bight. *N Am J Fish Manage*. 2016;36:62–73.
17. Erickson DL, Kahnle A, Millard MJ, Mora EA, Bryja M, Higgs A, Mohler J, DuFour M, Kenney G, Sweka J, Pikitch EK. Use of pop-up satellite archival tags to identify oceanic-migratory patterns for adult Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* Mitchell, 1815. *J Appl Ichthyol*. 2011;27:356–65.
18. Fox DA, Hightower JE, Parauka FM. Gulf sturgeon spawning migration and habitat in the Choctawhatchee River system Alabama-Florida. *Trans Am Fish Soc*. 2000;129:811–26.
19. Gabadinho A, Ritschard G, Müller NS, Studer M. Analyzing and visualizing state sequences in R with TraMineR. *J Stat Softw*. 2011;40:1–37.
20. Grunwald C, Maceda L, Waldman J, Stabile J, Wirgin I. Conservation of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*: delineation of stock structure and distinct population segments. *Conserv Genet*. 2008;9:1111–24.
21. Hale EA, Park IA, Fisher MT, Wong RA, Stangl MJ, Clark JH. Abundance estimate for and habitat use by early juvenile Atlantic sturgeon within the Delaware River Estuary. *Trans Am Fish Soc*. 2016;145:1193–201.
22. Hawkes C. Linking movement behaviour, dispersal and population processes: is individual variation a key? *J Anim Ecol*. 2009;78:894–906.
23. Haxton T, Gessner J, Friedrich T. A review of the assessment techniques used for population monitoring at different life stages of sturgeons. *Environ Rev*. 2024;32:91–113.
24. Henderson-Arzapalo A, King TL. Novel microsatellite markers for Atlantic sturgeon (*Acipenser oxyrinchus*) population delineation and broodstock management. *Mol Ecol Notes*. 2002;2:437–9.
25. Hendry AP. A critique for eco-evolutionary dynamics. *Funct Ecol*. 2019;33:84–94.
26. Hilton EJ, Kynard B, Balazik MT, Horodysky AZ, Dillman CB. Review of the biology, fisheries, and conservation status of the Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus* Mitchell, 1815). *J Appl Ichthyol*. 2016;32:30–66.
27. Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE. Aquatic animal telemetry: a panoramic window into the underwater world. *Science*. 2015;348:1255642.
28. Jeltsch F, Bonte D, Pe'er G, Reineking B, Leimgruber P, Balkenhol N, Schröder B, Buchmann CM, Mueller T, Blaum N, Zurell D. Integrating movement ecology with biodiversity research-exploring new avenues to address spatiotemporal biodiversity dynamics. *Move Ecol*. 2013;1:1–3.
29. Kahn JE, Hager C, Watterson JC, Russo J, Moore K, Hartman K. Atlantic Sturgeon annual spawning run estimate in the Pamunkey River Virginia. *Trans Am Fish Soc*. 2014;143:1508–14.
30. Kazyak DC, Flowers AM, Hostetter NJ, Madsen JA, Breece M, Higgs A, Brown LM, Royle JA, Fox DA. Integrating side-scan sonar and acoustic telemetry to estimate the annual spawning run size of Atlantic sturgeon in the Hudson River. *Can J Fish Aquat Sci*. 2020;77:1038–48.
31. Kazyak DC, White SL, Lubinski BA, Johnson R, Eackles M. Stock composition of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) encountered in marine and estuarine environments on the US Atlantic Coast. *Conserv Genet*. 2021;22:767–81.
32. Kieffer MC, Kynard B. Annual movements of shortnose and Atlantic sturgeons in the Merrimack River. *Massachusetts Trans Am Fish Soc*. 1993;122:1088–103.
33. King TL, Lubinski BA, Spidle AP. Microsatellite DNA variation in Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) and cross-species amplification in the Acipenseridae. *Conserv Genet*. 2001;2:103–19.
34. Kuhl H, Guiguen Y, Höhne C, Kreuz E, Du K, Klopp C, Lopez-Roques C, Yebra-Pimentel ES, Ciorpac M, Gessner J, Holostenco D. A 180 Myr-old female-specific genome region in sturgeon reveals the oldest known vertebrate sex determining system with undifferentiated sex chromosomes. *Philos T Roy Soc B*. 2021;376:20200089.
35. Liedvogel M, Chapman BB, Muheim R, Åkesson S. The behavioural ecology of animal movement: reflections upon potential synergies. *Anim Migr*. 2013;1:39–46.
36. May B, Krueger CC, Kincaid HL. Genetic variation at microsatellite loci in sturgeon: primer sequence homology in *Acipenser* and *Scaphirhynchus*. *Can J Fish Aquat Sci*. 1997;54:1542–7.
37. McQuinn IH. Year-class twinning in sympatric seasonal spawning populations of Atlantic herring. *Clupea harengus* *Oceanogr Lit Rev*. 1997;11:1358.
38. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, Baktoft H, Beardsworth CE, Bertram MG, Bijleveld AJ, Brodin T. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*. 2022;375:eabg1780.
39. National Marine Fisheries Service (NMFS). Endangered and threatened wildlife and plants; threatened and endangered status for distinct population segments of Atlantic sturgeon in the northeast region. *Fed Reg*. 2012;77:5880–912.
40. National Marine Fisheries Service (NMFS). Endangered and threatened wildlife and plants; final listing for two distinct population segments of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) in the southeast. *Fed Reg*. 2012;77:5914–82.
41. National Marine Fisheries Service (NMFS). Endangered and threatened species; designation of critical habitat for the endangered New York Bight, Chesapeake Bay, Carolina and South Atlantic distinct population segments of Atlantic sturgeon and the threatened Gulf of Maine population segment of Atlantic sturgeon. *Fed Regist*. 2017;82:39160–274.
42. Ogburn MB, Harrison AL, Whoriskey FG, Cooke SJ, Mills Flemming JE, Torres LG. Addressing challenges in the application of animal movement ecology to aquatic conservation and management. *Front Mar Sci*. 2017;4:70.
43. Pendleton RM, Adams RD. Long-term trends in juvenile Atlantic sturgeon abundance may signal recovery in the Hudson River, New York, USA. *N Am J Fish Manage*. 2021;41:1170–81.
44. Peterson DL, Schueller P, DeVries R, Fleming J, Grunwald C, Wirgin I. Annual run size and genetic characteristics of Atlantic sturgeon in the Altamaha River. *Georgia Trans Am Fish Soc*. 2008;137:393–401.

45. Phillips BL, Brown GP, Shine R. Life-history evolution in range-shifting populations. *Ecology*. 2010;91:1617–27.
46. Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A. GENECLASS2: a software for genetic assignment and first-generation migrant detection. *J Hered*. 2004;95:536–9.
47. Quinn TP. The behavior and ecology of Pacific salmon and trout. 2nd ed. Seattle: University of Washington Press; 2018.
48. R Core Team. R: a language and environment for statistical computing. Vienna: R Found Stat Comput; 2022.
49. Rannala B, Mountain JL. Detecting immigration by using multilocus genotypes. *Proc Natl Acad Sci USA*. 1997;94:9197–201.
50. Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA. Conserving mobile species. *Front Ecol Environ*. 2014;12:395–402.
51. Secor DH, Waldman JR. Historical abundance of Delaware Bay Atlantic sturgeon and potential rate of recovery: life in the slow lane: ecology and conservation of long-lived Marine Animals. *Am Fish Soc Symp*. 1999;23:203–16.
52. Secor DH. Migration ecology of marine fishes. Baltimore: JHU Press; 2015.
53. Studer M, Ritschard G, Gabadinho A, Müller NS. Discrepancy analysis of state sequences. *Sociol Methods Res*. 2011;40:471–510.
54. Van Eenennaam JP, Doroshov SI, Moberg GP, Watson JG, Moore DS, Linares J. Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. *Estuaries*. 1996;19:769–77.
55. Van Eenennaam JP, Doroshov SI. Effects of age and body size on gonadal development of Atlantic sturgeon. *J Fish Biol*. 1998;53:624–37.
56. Waldman JR, Grunwald C, Stabile J, Wirgin I. Impacts of life history and biogeography on the genetic stock structure of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*, Gulf sturgeon *A. oxyrinchus desotoi*, and shortnose sturgeon *A. brevirostrum*. *J Appl Ichthyol*. 2002;18:509–18.
57. White SL, Johnson R, Lubinski BA, Eackles MS, Secor DH, Kazyak DC. Stock composition of the historical New York Bight Atlantic sturgeon fishery revealed through microsatellite analysis of archived spines. *Mar Coast Fish*. 2021;13:720–7.
58. White SL, Kazyak DC, Darden TL, Farrae DJ, Lubinski BA, Johnson RL, Eackles MS, Balazik MT, Brundage HM, Fox AG, Fox DA. Establishment of a microsatellite genetic baseline for North American Atlantic sturgeon (*Acipenser o. oxyrinchus*) and range-wide analysis of population genetics. *Conserv Genet*. 2021;22:977–92.
59. White SL, Pendleton RM, Higgs AL, Lubinski BA, Johnson RL, Kazyak DC. Integrating genetic and demographic data to refine indices of abundance for Atlantic sturgeon in the Hudson River New York. *Endanger Species Res*. 2024;53:115–26.
60. White SL, Sard NM, Brundage HM III, Johnson RL, Lubinski BA, Eackles MS, Park IA, Fox DA, Kazyak DC. Evaluating sources of bias in pedigree-based estimates of breeding population size. *Ecol Appl*. 2022;32: e2602.
61. Wirgin I, Breece MW, Fox DA, Maceda L, Wark KW, King T. Origin of Atlantic Sturgeon collected off the Delaware coast during spring months. *N Am J Fish Manage*. 2015;35:20–30.
62. Wirgin I, Roy NK, Maceda L, Mattson MT. DPS and population origin of subadult Atlantic sturgeon in the Hudson River. *Fish Res*. 2018;207:165–70.
63. Wirgin I, Waldman JR, Rosko J, Gross R, Collins MR, Rogers SG, Stabile J. Genetic structure of Atlantic sturgeon populations based on mitochondrial DNA control region sequences. *Trans Am Fish Soc*. 2000;129:476–86.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.