ABSTRACT

Title of Document: INTEGRATING BIOTELEMETRY AND HYDROACOUSTIC DATA TO ESTIMATE THE ABUNDANCE OF THE FALL SPAWNING RUN OF ATLANTIC STURGEON IN THE MARSHYHOPE CREEK-NANTICOKE RIVER SYSTEM

Nicholas Christopher Coleman, Master of Science Degree, 2022

Directed By: Professor David H. Secor

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Once thought to be extirpated, fall spawning runs of Atlantic sturgeon (*Acipenser oxyrinchus*) have been rediscovered in the Nanticoke River-Marshyhope Creek system in Maryland and are currently listed as an endangered species within the Chesapeake Distinct Population Segment. Previously tagged adults predominate survey captures, suggesting a very small population size. A key challenge is to estimate abundance for such a small population distributed between presumed spawning reaches of the connected Nanticoke River and Marshyhope Creek. This study leverages data collected from a dense telemetry receiver array and multiple side-scan sonar surveys conducted from August to October to estimate reach

specific and superpopulation abundances in 2020 and 2021. I modified an approach that integrates mobile hydroacoustic data with biotelemetry, here applying for stationary telemetry receiver data. In 2020 and 2021, I estimated that 36 (95% confidence interval: 25-55) and 74 (95% confidence interval: 52-109) sturgeon used the Nanticoke River-Marshyhope Creek system, respectively. The higher estimate in 2021 coincided with higher sonar count data and low and stable river flows and temperature. Still, this large difference has no clear cause. Overall, run estimates support previous hypotheses that the Nanticoke system supports a very small population and that both the Marshyhope Creek and upper Nanticoke River serve as important areas for spawning activity. Going forward, enhanced sampling of the Upper Nanticoke River and targeted analysis assessing the relationship between phenology and environmental conditions would further develop our understanding of interannual changes in spawning run abundance.

INTEGRATING BIOTELEMETRY AND HYDROACOUSTIC DATA TO ESTIMATE THE ABUNDANCE OF THE FALL SPAWNING RUN OF ATLANTIC STURGEON IN THE MARSHYHOPE CREEK-NANTICOKE RIVER SYSTEM

By

Nicholas Christopher Coleman

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Professor David Secor, Chair
Professor Hongsheng Bi
Dr. Rose Jagus

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Introduction

Historically, the dynamic life history strategies of anadromous fishes were an evolutionary advantage that enhanced resiliency, but that resilience has been threatened by the growing effects of anthropogenic influences on environmental systems (Waldman et al. 2016). Anadromous fishes exhibit complex life cycles characterized by hatching from eggs in freshwater, moving into marine habitats as adults, and then returning to freshwater habitats to spawn. Damming and pollution have caused fragmentation of coastal and freshwater habitats and curtailed access of anadromous fishes to essential reproductive and nursery habitats. Overfishing, particularly during spawning runs, has severely depleted many populations of anadromous species. As a result of these anthropogenic pressures, Limburg and Waldman (2009) found that indices of abundance dropped more than 90% for 24 of 35 investigated populations of anadromous species in the North Atlantic. For depleted populations of anadromous fishes, a highly migratory life history and low abundance pose challenges in assessments of population demographics and abundance, spawning phenology, and habitat use, all of which is necessary information for successful management.

The history of Atlantic sturgeon (*Acipenser oxyrinchus*) on the eastern seaboard of the United States is an example of the complexities associated with anadromous species management, especially for those species that are depleted and exhibit strong selectivity for certain spawning and nursery habitats. Atlantic sturgeon range from the St. Lawrence River in Quebec, Canada to the St. Mary's River in Florida (Secor et al. 2022). Populations of Atlantic sturgeon once supported fisheries in every major coastal river along the Atlantic coast (Smith 1985; Secor and Waldman 1999; Secor 2002). At the peak of these fisheries around 1890, recorded landings totaled approximately 3.3 metric tons (Smith 1985). Today five NMFS-

designated Distinct Population Segments (DPS), spanning populations along the entire east coast of the US, are listed as endangered or threatened under the Endangered Species Act as a result of overfishing and habitat loss (NMFS 2012). Recent research and management have successfully aided in improving previous knowledge gaps regarding the abundance, timing and habitat-dependencies of spawning Atlantic sturgeon (Hilton et al 2016; Secor et al. 2022). Within the last 25 years, the number of recognized spawning tributaries has increased from eight to 19 (ASMFC 1998; NMFS 2017). Researchers have also discovered fall spawning runs of sturgeon in contrast to the prevailing view that spawning took place exclusively in the spring (Balazik and Musick 2015; Farrae et al. 2017; Markin and Secor 2020; Secor et al. 2022). Additionally, acoustic telemetry has revealed that sturgeon are spawning more frequently（Hager et al. 2020; Ingram and Peterson 2016) and traveling farther upstream than previously thought (Secor et al. 2022). Although these discoveries have significantly enhanced our understanding of Atlantic sturgeon spawning phenology and population dynamics, one of the main obstacles to the recovery of sturgeon populations remains the estimation of population abundance.

In the Chesapeake Bay, Atlantic sturgeon were once thought to be extirpated (Secor 1995; Grogan and Boreman 1998), but have been rediscovered in tributaries of Maryland and Virginia within the last 15 years (Balazik et al. 2012; Hager et al. 2014). As a result of their severely depleted status, the Chesapeake Bay DPS was designated as endangered in 2012 (NMFS 2012). In 2017, tidal regions in the Potomac, Rappahannock, York, Pamunkey, Mattaponi, James and Nanticoke rivers and in the Marshyhope Creek was designated as critical habitat for the Chesapeake Bay DPS (NMFS 2017). The Nanticoke River (NR)- Marshyhope Creek (MC) system is the smallest tributary of the designated critical habitats and supports a

genetically distinct, fall spawning run of Atlantic sturgeon (Secor et al. 2022). Small populations often preserve genetic and behavioral diversity within a species which facilitates perseverance against anthropogenic and environmental disturbances. Studying small populations can help identify varying evolutionary traits within a species range and predict flexibility to changing environmental conditions (Sinclair 1988; Ruzzante et al. 2006). Beginning in 2014, Maryland Department of Natural Resources (MD DNR) began capturing and implanting acoustic tags in sturgeon in the MC-NR system. High rates of recapture and genetic analysis indicated a small fall spawning run (<100) in this system (Secor et al. 2022). Small populations, such as the one hypothesized in this system, are difficult to census because individuals are less abundant and more difficult to capture with traditional gear types. This data insufficiency is a key constraint for scientists and managers to assess recovery goals for Atlantic sturgeon in the MC-NR system.

Spawning runs of Atlantic sturgeon provide the opportunity to observe aggregations of individuals in restricted estuarine environments and to develop estimates of abundance. Among methods to measure fish abundance in estuarine systems, hydro-acoustics has been employed in recent decades (Baumgartner et al. 2006; Martignac et al. 2014; McCartin et al. 2019; Kerschbaumer et al. 2020). Hydroacoustics are technologies that transmit sound through the water to create images and includes split-beam sonar, side-scan sonar, adaptive resolution imaging sonar (ARIS), and its predecessor dual-frequency identification sonar (DIDSON). These methods are non-invasive and allow for the observation of natural fish behavior, which is especially advantageous when monitoring rare, sensitive, endangered, or illusive fishes. Hydroacoustics rely on a transducer to emit a fan of acoustic beams through the water (Pollom and Rose 2016). When these beams come into contact with an object, they are reflected back to the transducer and create sonar images (Pollom and Rose 2016). Given this, target detection by

hydroacoustics is dependent on its relative density rather than on light, which can be obscured by turbidity, particularly in estuarine environments. Side scan-sonar is a well-established approach (Johnson and Helferty 1990; Foote 2009) commonly used in marine geology studies (Carmichael et al. 1996; Kaiser and Spencer 1994;). More recently with the improvement of software analysis, side scan sonar has been applied to fisheries research to identify and enumerate larger fishes such as sturgeon (Walker and Alford 2016; Fleming et al. 2018; Hughes et al. 2018; Andrews et al. 2020).

Within Atlantic sturgeon research and management, side-scan sonar has been used to generate count data that can be integrated with other methodologies to develop models to estimate abundance (Flowers and Hightower 2013, 2015; Vine et al. 2019). Inclusion of acoustic telemetry with hydroacoustic methods provides an opportunity to integrate information on individual movements and timing within the spawning reach with count data. Detailed movement records can be used for a variety of applications, including estimating rates of emigration and immigration, assessing habitat use, and estimating residency time (Lees et al. 2021). Many of the models created to estimate the abundance of sturgeons and other fishes from hydroacoustic data use a Bayesian approach, which is conducive to the inclusion of information from multiple data types (Dorazio 2015). Additionally, Bayesian inferences are optimal when working with limited data or small population sizes because the validity of analysis is not dependent on sample size (Dorazio 2015). This is especially advantageous when working with endangered species with low abundances, like Atlantic sturgeon. Kayzak et al. (2020) provided a novel approach to integrate mobile side-scan sonar surveys with mobile telemetry surveys using a Bayesian mark-recapture approach. Similarly, Izzo et al. (2021) integrated stationary ARIS observations with a telemetry array using a Bayesian approach. A method to integrate mixed

forms (i.e. mobile or stationary) of telemetry and hydroacoustic data has not yet been applied and could facilitate dynamic spatial and temporal abundance estimates.

This study aims to estimate spawning run size by integrating mobile side-scan sonar count estimates and telemetry array detections using a Bayesian approach for a very small spawning run of Atlantic sturgeon (*Acipenser oxyrinchus*) in the MC-NR system. Although tagged individuals have predominately been captured in the MC, it is hypothesized that the connected upper NR also serves as critical spawning habitat. Frequent and consistent rates of transition between the NR and MC during the spawning run would provide evidence of connected spawning reaches in these two systems. Spawning in this system occurs from mid-August to late September, but the precise phenology of the spawning run remains unknown. Previous telemetry data has suggested sturgeon continue to move into the system until mid-September and begin to exit shortly thereafter. Given this, data from August to October were used in this model. Objectives for this study include the following:

1. Estimate the abundance of the 2020 and 2021 fall spawning run of Atlantic sturgeon in the MC-NR system;
2. Assess reach occupancy and rates of transition in the system to determine the connectivity between the NR and MC;
3. Use modeled immigration and emigration to estimate residency and spawning run phenology. Examine the possible influences of temperature and flow on spawning run phenology.

To support these objectives a Bayesian model was adapted from Kazyak et al. (2021). Side-scan sonar surveys (2020: N=4; 2021: N=5) supported census counts of sturgeon within the MC throughout each season. An extensive telemetry array provided detailed movement behavior.

Methods

Study System

The MC-NR system is a small tidal estuary (about 75 km from its mouth to head of tide) located on the eastern shore of Maryland. The NR is a tributary of the Chesapeake Bay and receives the MC around river kilometer (rkm) 45 (Figure 1). Together, this system covers a watershed area of approximately 2934 km^2 (Secor et al. 2022). The relatively small size of the MC-NR is conducive for full telemetry and side-scan sonar coverage. Analysis of previously tagged adult Atlantic sturgeon (>1.4m total length) indicated that individuals enter the system as early as July, however the peak incidence occurs from mid-August through September. Although specific spawning areas within the MC are unknown, individual Atlantic sturgeon rove within the entire MC from its connection to the Nanticoke to areas above Federalsburg (river km 25) and several pulses of up-estuary movement are apparent (see animation at youtube/bFQhz7Pzlh0). Operationally, I defined the start of the study period as August 15 in 2020 and 2021. In order to account for interannual variation in acoustic receiver retrieval, the temporal window ended on October 26 in 2020 and October 31 in 2021.

To assess connectivity within the system and estimate rates of immigration, emigration, and residency, the MC-NR was partitioned into four reaches: the Lower NR, the Lower MC, and the Upper MC, and the Upper NR (Figure 1). The portion of the MC above rkm 22 to the most upstream receiver (rkm 28) was designated as the Upper MC. The NR from its mouth to its confluence with the MC (rkm 52) was designated as the Lower NR and the NR above this point was designated as the Upper NR. A telemetry positioning system (VPS; also described below) was deployed in the Lower MC near the confluence with NR to intercept spawners as they moved into this area of aggregation.

Average daily temperature was used as a factor to estimate rates of recruitment and persistence within the system. In 2020 and 2021, temperature data was recorded using an Honest Observer by Onset (HOBO) temperature data logger. The HOBO was deployed by Delaware Division of Fish and Wildlife in the NR at rkm 65 (Seaford, Delaware) in 2020 and at rkm 55 (near the mouth of Broad Creek) in 2021. Temperature data was recorded every 30 minutes for the duration of the deployment. Flow data was retrieved from the United States Geological Survey (USGS) hydrologic unit approximately 81 rkm upstream from the mouth of the NR (Bridgeville, DE). Average daily flow (ft^3/s) was calculated from data recorded every 15 minutes and used to explore the relationship between flow and persistence and recruitment.

Telemetry Array

Using gill nets, MD DNR and Delaware Department of Natural Resources and Environmental Control (DNREC) have captured and tagged Atlantic sturgeon in the MC-NR system since 2014 (N= 34 males; N= 9) females since 2014 (Table 1). Acoustic transmitters (VEMCO Model V16-6H) were surgically implanted according to procedures described in Secor et al. (2022). Adult spawning sturgeon have primarily been captured in the MC but individuals have also been captured in Broad Creek, a second smaller tributary of the NR (Figure 1). Tagged sturgeon, 147-252 cm total length, were frequently captured in spawning condition (flowing gametes and reddening around ventral scutes). Approximately 80% of tagged sturgeon were male (Table 1).

An array of VEMCO VR2W acoustic receivers was deployed when tagging began in 2014, increasing in number each year. In 2020 and 2021, 29 receivers were deployed in MC-NR system from March to November (Figure 1). Receivers were placed and maintained by MD DNR

every 1-2 km in the MC and upper NR. A detailed explanation on the deployment and maintenance of receivers can also be found in Secor et al. (2022). A dense array of receivers (VPS) was deployed at rkm 9 and rkm 4 respectively from August 27 to September 29 2020 and August 19 to October 28 2021 to evaluate ARIS detection efficiency in a separate study. In both years, the VPS consisted of 10 VR2AR 69 kHz units and two sync tags, which provided optimization of receiver positioning during post-deployment error analysis. Although not the focus of this study, the high density of receivers contributed to improved estimates of reach use and detection probability.

Using the previously defined reaches in the system, telemetry detections supported a daily encounter history matrix (or state matrix), which was created to describe the "state" of each tagged fish (*i*) for every day (*k*) of the period of interest. State refers to the reach a fish was detected where 2= Lower NR (LNR), 3=Lower MC (LMC), 4=Upper Marshyhope (UMC), and 5= Upper NR (UNR). If a fish was not detected on a given day, a state of 1 (Not Entered) was recorded (note this is different in the observation matrix where 1=Not Detected; see below). The modeling approach requires that each marked sturgeon was assigned to a single reach on a given day. When a fish was detected in multiple reaches in a single day, it's reach assignment was based on the individuals encounter history and my emphasis on the LMC. During such occasions, any sturgeon detected in the LMC on a given day was assigned the LMC. Due to enhanced receiver density in the LMC provided by the VPS, all individuals showed transit histories through the LMC, were they detected moving to UMC and UNR reaches. Operationally, individuals detected in the LNR and UNR in the same day were assigned to the UNR emphasizing the assumption that the UNR serves as a spawning reach, whereas the LNR does not. Daily encounter histories from the observation matrix provide data to estimate the

number and proportion estimates of tagged fish in each reach on a given day, and how fish transited among reaches (Table 6).

Side Scan Sonar

Side scan sonar surveys were led by Dr. J. Madsen (University of Delaware) and designed to canvas the entire LMC for adult Atlantic surgeon in weekly surveys. The surveys deployed an Edgetech 4125-P 600/1600kHz towfish dual-frequency system. The towfish was operated at 1600kHz, which provided high resolution. During surveys, the towfish had a range of about 70 m (35 m on either side), which provided consistent bank-to-bank coverage of the LMC. In 2020, surveys were conducted on four days: September 4, 11, 18, and 23. In 2021, surveys were conducted on five days: September 8, 15, 22, 27 and October 4. On average, surveys were approximately 22 rkm in length starting at the MC mouth and ending at the acoustic receiver location "Wright's Pier". September 8, 2021 was an exception and this survey covered a greater tidal extent of the MC, ending at rkm 27 (just south of Federalsburg). Two parallel (replicate) side-scan sonar transects were collected in opposing directions during each survey (i.e., upstream or downstream). A Garmin GPS76 unit was used to determine the location, course and speed of the vessel. The side-scan towfish was deployed off the vessel's bow approximately 1 m below the water's surface at approximate speeds of 7.4 km h^{-1} (4 knots). Each survey took approximately 2.5-3 hours. Analysis of side scan sonar survey data was conducted using SonarWiz software (Chesapeake Technology, Mountain View, CA). Post-processing of the side-scan sonar data included bottom tracking, applying equalized normal gain (EGN), and digitizing sonar targets. Based on the size range of adult sturgeon collected and tagged by MD DNR, a 140 cm threshold was used distinguish sturgeon from other targets. Acoustic shadows cast by side-

scan sonar targets were also used to identifying morphological features indicative of sturgeon (e.g. heterocercal tail). For each identified sturgeon-target the geospatial position, estimated total length, and time of observation were recorded.

Model Development

Marked individuals

Mark-recapture data from acoustic telemetry detections in 2020 and 2021 were analyzed using a Jolly-Seber (JS) open population model. In the context of single season open populations, the JS parameter $\boldsymbol{\beta}$ can be interpreted as "probability of arrival into the system" and ϕ; as the probability of remaining in the system (e.g., Lyons et al. 2016; Kazyak et al. 2020). Given my interest in understanding fall spawning run phenology, I sought to quantify (1) the number of marked sturgeon that used the MC-NR system (M^*), (2) when marked individuals entered the system ($\boldsymbol{\beta}$), and (3) how marked individuals moved among the three river reaches within the system (ϕ).

The Bayesian analysis of the JS superpopulation model includes multiple states (e.g., river reaches). More specifically, this approach uses state-space formulation by implementing data augmentation to estimate uncertainty regarding the superpopulation size (*N*). For this study, I defined the states as (1) not entered, (2) in the LNR, (3) in the LMC, (4) in the UMC, (5) in the UNR, and (6) exited system (see $\boldsymbol{\Omega}$ matrix). During data augmentation, a fixed number of non-detected individuals were added to individual-level encounter histories (y_{ik}) to inflate the total number of individuals to G. An inclusion parameter w_i, was given to each individual in the data set where $w_i = 1$ if the individual is part of the superpopulation and 0 otherwise. I assumed

(1) $$w_i \sim \text{Bernoulli}(\psi)$$

where ψ is the probability an individual in the augmented data set is part of the superpopulation (Royle and Dorazio 2008).

Recruitment of individuals into states 2-5 was cumulative throughout K occasions (72-day study period in 2020 and 77-day period in 2021) according to a multinomial distribution where b_k is the probability of entry on day k. I modeled b_k as a multinomial-logit function of time, $\text{mlogit}(b_k) = \beta_1 \times k$, as I hypothesized that sturgeon enter the Nanticoke system early in the season and the probability of entry declined thereafter (i.e., β_1<0.0). To accommodate the data augmentation process, the probability of entry at occasion k given an individual has not yet entered the population, η_k, was defined as:

(3) $$\eta_1 = b_1$$

(4) $$\eta_k = b_k/(1 - \sum_{t=1}^{k-1} b_t),\ k = 2, 3, \ldots K$$

(see Kéry and Schaub 2012 [Chapter 10]). On the first day of the season (15-August) marked sturgeon could be in states 1-5 with probabilities $1 - \eta_1$ (not yet entered), $\eta_1\theta_1^2$ (entered, state 2 [LNR reach]), $\eta_1\theta_1^3$ (entered, state 3 [LMC reach]), $\eta_1\theta_1^4$ (entered, state 4 [UMC reach]), or $\eta_1\theta_1^5$ (entered, state 5 [UNR reach]). Here, $\theta_1^{2:5}$ denotes the probability that a fish was in state 2, 3, 4, or 5 if it was in the system on day 1, and enforce $\sum \theta_1^{2:5} = 1.0$. For notation simplicity, I set $\boldsymbol{\xi}_{1:6}$ to be the set of probabilities on day 1, $\boldsymbol{\xi}_{1:6} = (1 - \eta_1, \eta_1\theta_1^2, \eta_1\theta_1^3, \eta_1\theta_1^4, \eta_1\theta_1^5, 0)$, which includes $\boldsymbol{\xi}_6 = 0$ since individuals cannot be in state "exited system" on day 1.

Transitions on days 2:K are defined by the matrix, **Ω** (Table 2) that describes entry, persistence, and transition probabilities (from row to column):

		k + 1						
		State	**1 (NE)**	**2 (NR)**	**3 (LMC)**	**4 (UMC)**	**5 (UNR)**	**6 (E)**
		1 (NE)	$1 - \eta_k$	$\eta_k\theta_2^2$	$\eta_k\theta_2^3$	$\eta_k\theta_2^4$	$\eta_k\theta_2^5$	0
	Ω =	**2 (LNR)**	0	$\phi_k\pi^{2,2}$	$\phi_k\pi^{2,3}$	$\phi_k\pi^{2,4}$	$\phi_k\pi^{2,5}$	$1 - \phi_k$
		3 (LMC)	0	$\phi_k\pi^{3,2}$	$\phi_k\pi^{3,3}$	$\phi_k\pi^{3,4}$	$\phi_k\pi^{3,5}$	$1 - \phi_k$

k		**4 (UMC)**	0	$\phi_k \pi^{4,2}$	$\phi_k \pi^{4,3}$	$\phi_k \pi^{4,4}$	$\phi_k \pi^{4,5}$	$1-\phi_k$
		5 (UNR)	0	$\phi_k \pi^{5,2}$	$\phi_k \pi^{5,3}$	$\phi_k \pi^{5,4}$	$\phi_k \pi^{5,5}$	$1-\phi_k$
		6 (E)	0	0	0	0	0	1

where:

η_k = probability a fish has enetered the system

ϕ_k = probability of staying in the system

π = probability of transitioning from reach j to l

θ = probability a fish is in reach j on day 1

1= Not Detected (Not Entered)
2= NR
3= Lower MC
4= Upper MC
5= Upper NR
6=Exited

I modeled the probability of staying in the system — i.e., persistence — as a function of average daily temperature, $\text{logit}(\phi_k) = \alpha_0 + \alpha_1 \times \text{temp}[k]$, reflecting my hypothesis of declining probabilities that a fish stays in the system as the season progresses and temperature declines (e.g., $\alpha_1 < 0$). Conditional on remaining in the system, $\pi^{j,l}$ describes the probability that a fish moved from reach j to l. Finally, θ_2^j is the probability that a fish that entered the system on day 2-K was in reach 2, 3, 4, or 5 on the day it entered. Specific to this study, I set $\pi^{2,4} = \pi^{4,2} = \theta_2^4 = \pi^{4,5} = \pi^{5,4} = \theta_4^5 = 0$ as my primary interest was sturgeon use of LMC. Given this, any fish transitioning through LMC was assigned to LMC on that day. Under these conditions, a fish could not transition between the LNR to the UMC [$\pi^{2,4}$ or $\pi^{4,2}$] in one day as it would have to pass through the LMC and would thus be assigned to LMC. Similarly, a fish could not transition from the UMC and the UNR [$\pi^{4,5}$ or $\pi^{5,4}$] without passing through the LMC and would thus be assigned to LMC.

Together, the status of marked individual i on day k, (z_{ik}) is described as,

(5) $$z_{i1} \sim \text{Categorical}(\boldsymbol{\xi}_{1:5})$$

for day 1, where $z_{i1} = 1$ if individual i has not yet entered, 2 if it is in the LNR, 3 if in LMC, 4 if in UMC, and 5 if in UNR. For occasions 2-K, an individual may enter if not previously entered, persist and move among the reaches if previously entered, or permanently leave the MC-NR system,

(6) $$z_{ik} \sim \text{Categorical}(\mathbf{\Omega}_{z_{ik-1},k,1:6})$$

Combined with the latent inclusion variable, w_i, the product $z_{ik}w_i = 0$ if individual i never entered the system and $z_{ik}w_i > 0$ for any marked sturgeon that entered the MC-NR system on at least one day.

Individuals are detected by fixed acoustic receivers with probability p_j conditional on use of river reach *j* on occasion k and being part of the superpopulation ($w_i = 1$),

(7) $$y_{ik} \sim \text{Categorical}(\mathbf{P}_{z_{ik},i,k,1:5})$$

where $\boldsymbol{P}$ is the detection probability matrix (Table 3):

		Observation Matrix				
State Matrix		**1 (ND)**	**2 (NR)**	**3(LMC)**	**4(UMC)**	**5 (UNR)**
$\boldsymbol{P} =$	**1 (NE)**	1	0	0	0	0
	2 (NR)	$1 - p_{2,i,k}$	$p_{2,i,k}$	0	0	0
	3 (LMC)	$1 - p_{3,i,k}$	0	$p_{3,i,k}$	0	0
	4 (UMC)	$1 - p_{4,i,k}$	0	0	$p_{4,i,k}$	0
	5 (UNR)	$1 - p_{5,i,k}$	0	0	0	$p_{5,i,k}$
	6 (E)	1	0	0	0	0

where:

State Matrix Key
1= Not Entered (Not Detected)
2= NR
3= Lower MC
4= Upper MC
5= Upper NR
6= Exited

Observation Matrix Key
1= Not detected
2= NR
3= Lower MC
4= Upper MC
5= Upper NR

To account for differing spatial coverage of fixed receivers (Figure 1), I let detection probability vary by reach (*j*). During 2020 and 2021, five sturgeon received acoustics tags after

entering the system, and their detection probability was set to zero prior to tagging. Together, $p_{j,i,k} = \bar{p}_j \times I_{ik} \times w_i$, where $\bar{p}_j$ is the detection probability in reach j (zero if not yet entered or exited), I_{ik} is an indicator variable denoting if individual i had an active tag on day k, and w_i requires that detection probability is zero unless the individual is part of the superpopulation.

The number of marked individuals in reach j on day k is derived as

(8) $$M_{jk} = \sum_{i=1}^{G}(I(z_{ik}w_i) = j)$$

where G is the size of the augmented data set and $I(z_{ik}w_i) = j$ equals 1 if individual i was in reach j on day k. Similarly, the cumulative number of unique marked individuals that used reaches 2-5 on or before day k (i.e. 'marked superpopulation') is

(9) $$M_k^* = \sum_{i=1}^{G} I_{ik} .$$

Where I_{ik} is an indicator variable taking a value of 1 if individual i arrived in the study area on or before day k.

Importantly, these analyses of acoustically tagged individuals provide detailed information on when sturgeon entered the system, their probabilities of remaining in the system, and movements among reaches. Abundance estimates from analyses of only marked individuals (M_{jk}, M_k^*), however, only reference the marked population.

Count data and total abundance

Multi-pass side-scan sonar (SSS) counts in LMC on day k and pass v (n_{kv}) provided data to estimate the total number of individuals in the LMC on survey day k and how abundance changes across survey days (Kazyak et al. 2020). I assume that n_{kv} are binomial random variables from the total number of sturgeon in LMC on day k ($N_{k,3}$) and sss detection probability (p^{sss}). Specifically,

(10) $$n_{kv} \sim \text{Binomial}(p^{sss}, N_{k,3})$$

Multi-pass SSS data allows us to directly estimate the total number of sturgeon in LMC on day k. I then link these abundances to the population dynamics estimated in the Jolly-Seber model to describe how the population changes through time.

For example, at the population level I assume the distribution of individuals in the superpopulation on day 1, R_{1j}, are multinomial random variables,

(13) $$R_{1,1:J} \sim \text{Multinomial}(\boldsymbol{\xi}_{1:5}, N_K^*).$$

Where $\boldsymbol{\xi}_{1:5}$ was the previously defined set of probabilities for states 1-5 on day 1 (e.g., not yet entered, LNR, LMC, UMC, and UNR) and N_K^* is the cumulative number of individuals that used the MC-NR system in 2020 and 2021 (i.e. superpopulation; an estimated parameter), with $N_K^* \sim \text{Poisson}(\lambda)$. On day 1, $N_{1j} = R_{1j}$. For days >1, N_{kj} is the number of individuals on day $k-1$ that persisted ($S_{k-1,j}$), plus the number that moved to reach j on day k from another reach ($M_{j,k,s\neq j,}$), plus the number of individuals that first entered on day k to reach j (R_{kj}),

(14) $$N_{k,j} = S_{k-1,j} + M_{j,k,s\neq j} + R_{k,j}.$$

Where the persistence, movement, and recruitment probabilities are described in $\boldsymbol{\Omega}$ (however, see *Implementation* for parameterization considerations in JAGS). Similar to the marked populations, the cumulative number of individuals in the MC-NR system by day k (N_k^*; i.e. the superpopulation on day k) can also be derived as the sum of individuals that recruited by day k ($N_k^* = \sum_{t=1}^{k} R_t$).

Implementation

Our integration of the JS model with the N mixture model adheres to the conceptual framework outlined by Kayzak et al. (2020). I fit the model in JAGS (Plummer 2012) using the jagsUI package (Kellner 2015) accessed through R versions 4.2.0 (R Core Team 2022). I used vague priors for all parameters, specifically: $\text{Beta}(0.0001,1)$ ψ, Beta(1,1) for p and ϕ,

$\text{Gamma}(0.1, 0.1)$ for λ, and $\text{Norm}(0,0.1)$ for α_1 and β_1. For the JS model, I set the data augmentation value as G = 25, which adequately met the requirement that $G \gg M_K^*$. I ran five parallel Markov chain Monte Carlo simulations. Each chain contained 25,000 adaptation iterations, followed by 10,000 burn-in iterations, and 50,000 posterior iterations thinned by 10. Chain convergence was visually evaluated and verified using the Gelman–Rubin statistic (Gelman et al. 2013). I report results as posterior medians and 2.5th and 97.5th quantiles (95% CRI).

To achieve adequate mixing, I modeled daily reach-specific abundance ($N_{k,1:5}$) as multinomial random vairables with probablities reflecting the estimated proportion of the superpopulation in that reach on that day. Expected probabilities were derived from $\boldsymbol{\xi}$ and $\boldsymbol{\Omega}$ and reflect the full uncertainity in these parameters.

Results

Acoustic Detections and Observations

Since 2014, MD DNR and DNREC have captured and tagged 43 Atlantic sturgeon (34 males and 9 females) in the MC-NR system (Table 1). Of these, 82% of the males (n=27) and 22% (n=2) of the females have returned since initial tagging. Returning males averaged a relative return rate (number of years returned/year since tagging) of 0.7 (this excludes individuals tagged in 2021) and years between returns ranged from one to four years. Excluding males tagged in 2021, 26% of males that returned were not detected in the consecutive year after tagging. The two returning females had a relative return rate of 0.41 and years between returns ranged between two and three years. The acoustic array detected 17 tagged sturgeon in 2020 and 2021. Based on the data augmentation process described previously, I estimate that no tagged sturgeon went undetected. One female was detected in 2020 and two females were detected in 2021.

Overall, acoustic telemetry detection probability was high in both years. Median acoustic telemetry detection probability ranged from 0.89 to 1.00 in 2020 with the lowest detection probability observed in the LNR (Table 5). In 2021, median acoustic telemetry detection probability ranged from 0.76 to 1.00 and the lowest detection probability was observed in the UNR (Table 5). In both years, the highest detection probabilities were observed in the LMC and UNR. In both years, detection probability was at least 0.95 in three out of four reaches (Table 5).

Side-scan sonar detection probability was 0.95 (95% CRI: 0.74-0.99) in 2020. During side-scan sonar surveys, 90 sturgeon targets were identified, with an average of 23 targets per day (mean=11 per pass). In 2021, side-scan sonar detection probability was 0.85 (95% CRI: 0.65-0.94) and 202 sturgeon targets were observed with an average of 40 targets per day (mean= 20 per pass). The difference in the number of sturgeon targets observed (i.e. missed fish or fish that moved into the system during surveys) between the two replicate passes ranged 1-2 in 2020 and 1-5 in 2021.

Spawning Run Abundance

In 2020 and 2021, I estimated that 36 (95% credible interval: 25-55) and 74 (95% credible interval: 52-109) sturgeon used the MC-NR system, respectively (Figure 1). Given estimates of complete detection of tagged individuals in both years, it is estimated that tagged sturgeon accounted for 47% of the spawning run in 2020 and 23% of the spawning run in 2021. The cumulative number of unique individuals that entered the system peaked on September 17 in 2020 and much later, on October 25 in 2021 (Figure 2). Model estimations indicate that 50% of the spawning run entered by late August in both years: by August 19 in 2020 and by August 25 in 2021. Peak abundance in 2020 was estimated to have first occurred in the Nanticoke reaches

(n= 21) on August 30 and the in MC reaches (n=15) later on September 18 (Figure 2). In 2021, peak abundance was estimated to have first occurred in the Nanticoke reaches (n= 30) on September 1 and in the MC reaches (n=25) on September 8 (Figure 2). Peak abundance in the entire system (n=33) was estimated to have first occurred on September 6 in 2020 and September 8 in 2021 (n= 54). NR reaches supported more sturgeon in both years (Figure 3). Still, when comparing only presumed spawning reaches, the MC supported more sturgeon than the UNR (Figure 4).

Reach Transition Probabilities

Reach occupancy of tagged fish was fairly consistent between years. Occupancy days, the number of days in which any of the tagged sturgeon were in a given reach, was the lowest in the UMC and highest in the LMC in both years of the study. Notably, only one tagged fish was detected in the UMC in 2021 for two days. Individuals that entered the system after August 15 had the highest probability of persisting in the LNR upon entry. Once individuals entered a given reach, the probability of persisting in that reach was higher than transitioning to another reach, with the exception of the UMC (Table 6). Individuals in the UMC had the highest probability of transitioning to the LMC.

Recruitment, Residency Duration, and Persistence

Temperature and flow conditions differed substantially between 2020 and 2021. Conditions in 2020 were characterized by relatively cooler water temperature and higher variations in flow with episodic high flow events (Figures 5 and 7). In contrast, conditions in 2021 were warmer, particularly during September, and there was a more gradual decrease in average daily temperature. Flow in 2021 was also much lower and more stable than in 2020.

During spawning run peak abundance in September, monthly temperature averaged 22.7 and 24.7 C, respectively in 2020 and 2021.

Daily recruitment probability declined with day and average daily temperature in both years of the study (Figure 5). The inverse relationship between daily recruitment probability and day was stronger in 2020 (-0.14; 95% CI: -0.21- - 0.08) than in 2021 (-0.06; 95% CI: -0.09- -0.04) (Table 5). Recruitment also appears to decline with average daily flow in 2021, but no such trend was observed in 2020 (Figure 7). In both years, the pattern of declining recruitment was influenced by the pre-existence of adults at the start of the estimation period. In 2020 and 2021, 35% (n=6) and 18% (n=3) of tagged sturgeon were in the system on or before August 15, respectively. Daily recruitment probability reached its asymptote around September 16 in 2020 and October 12 in 2021 (Figure 5).

As modeled, daily persistence estimates declined as a function of average daily temperature (Figure 6). The relationship between average daily temperature and persistence was similar between years: 2020; Alpha 1=0.32, 95% CI: 0.19- 0.50; 2021: Alpha 1=0.28, 95% CI: 0.16- 0.43. Daily persistence estimates decayed during the last two weeks of October in both years, particularly as temperature fell below 20 C (Figure 6). In both years, only one tagged fish remained in the system on the last day of the study period (Oct 26 in 2020 and Oct 31 in 2021) and was located in the LNR.

Estimated persistence periods were relatively the same between tagged male and female sturgeon. Based on estimates from the state-matrix, average residence in the system was consistent between years: 42 days in 2020 (range: 20-73) and 38 days (range: 2-73) in 2021. The only tagged female in 2020 was captured and tagged on September 1 and was estimated to have

spent 43 days in the system after capture. In 2021, the two tagged female sturgeon averaged an estimated 36 days in the system and males averaged 39 days.

Discussion

By adapting the Kazyak et al.'s (2020) Bayesian model, I generated initial estimates of spawning run abundance for Atlantic sturgeon in the MC-NR system. Spawning run estimates were 36 (95% CI: 25-55) and 74 (95% CI: 52-109) in 2020 and 2021, respectively. This two-fold difference in estimates mirrored higher side-scan survey counts in the LMC which totaled 90 in 2020 and 202 in 2021. Few studies have compared annual abundance estimates for the same system. In the York River system, another small tributary in the Chesapeake, mark-recapture estimates of spawning runs ranged from 75 (95% CI: 31-190) in 2013 to 157 (115-244) in 2014, displaying a similar twofold difference in abundance between consecutive years (Kahn et al. 2019). Despite the two-fold difference, modeled spawning run sizes for the MC-NR support the hypothesis that as the smallest free-flowing spawning run tributary for the species, the Marshyhope Creek-Nanticoke River system likely supports a very small population. Given both its small spatial scale and spawning run size, the MC-NR system is especially vulnerable to local anthropogenic influences.

Understanding observed twofold variations in spawning run abundance directs attention to sampling biases and model assumptions. Environmental conditions, hydroacoustic data collection methodologies (e.g., transducer pulse rate), and target fish characteristics all influence the detection probability of hydroacoustics (Steig et al. 2010, Izzo et al. 2021). Still, the low deviation of side-scan sonar counts between survey days each year would indicate against a systematic bias. This is further supported by high estimates of side-scan sonar detection probability in both years (Table 5; 2020: 0.95; 2021: 0.85). Similarly, the number of tagged fish

(N=17) detected did not vary between years. If differences in spawning run estimates were a result of tagged fish detection probability, we would expect to see a difference in the number of detected fish and reach detection probability, which was not supported by parameter estimates (Table 5). Consistency in data collection methodology and data formatting provided continuity in the model structure and no changes were made between years. Given this, I have no reason to believe that variations in spawning run abundance are a result of model bias. The 95% confidence intervals for spawning run estimates in each year did not overlap and support that estimated abundances are in fact different.

Aside from data inputs and modeling procedures, true interannual variation could have been driven by demographic changes or environmental factors. Skip spawning behavior is common in Atlantic sturgeon (Van Eenenaam et al. 1996; Stevenson and Secor 2000; Table 1) and could explain a large interannual change. However, males have a high annual return rate and comprise the majority of the run, which would indicate changes in female return rates owing to skipped spawning would have only a minor effect. Sudden changes in spawning run size owing to changes in year-class strength or sudden mortality events would seem unlikely based on the species life history (Gross et al. 2022). Further no apparent changes in size structure were apparent for tagged fish during the 2014-2021 period (Table 1). The effects of environmental conditions on sturgeon spawning run phenology is well documented in scientific literature and could influence how well the side scan sonar survey captured spawning runs (Erikson et al. 2002; Fernandes et al. 2010; Buchinger et al. 2022). I observed variations in the arrival of tagged fish and estimated daily recruitment that may be explained by differences in environmental conditions. As a result, the timing of side-scan sonar surveys may have inconsistently sampled spawning run abundances between years.

The Bayesian model supported daily persistence within most defined reaches of the MC and NR. Although roving behaviors have been noted between reaches (Secor et al. 2022), the degree of persistence could suggest that reaches were well defined in estimating daily reach abundance and the superpopulation abundance. The UMC reach was an exception: individuals in the UMC had a higher probability of transitioning to the LMC between consecutive days than staying in the UMC. This transition pattern could suggest that the UMC represents (1) a minority behavior, (2) an exploratory spawning run behavior, (3) that some individuals may overshoot spawning habitats and retreat, and/or (4) lower detections in the UMC are a result of reduced detection ranges in this shallow and sinuous UMC reach. Overshoot behaviors have been described in the spawning runs of other anadromous fishes and occur when individuals swim farther upstream and past intended habitat (Secor 2015). Keefer et al. (2008) analyzed the spawning run behavior of approximately 5,000 radio-tagged Chinook salmon in the Columbia River and found that 10% of these individuals overshoot their natal tributaries.

Comparison of daily abundance estimates between the Nanticoke River and Marshyhope Creek (Figure 1) indicate that Nanticoke River reaches supported more individuals in both years. When daily abundance estimates were compared in regions where spawning is assumed to occur (UNR and MC), the Marshyhope Creek reaches supported more individuals in both years (Figure 4). The discrepancy in ordering between these two comparisons is likely because the LNR is a staging area for spawning that takes place further upstream. Two forms of spawning run behavior have been identified for Atlantic sturgeon, directed and interrupted spawning migrations (Vine et al. 2019). Directed spawning runs occur when individuals transition directly from coastal marine habitats to estuarine spawning grounds. Interrupted spawning runs include a "staging" period in the lower portion of the tributary before upstream migration to spawning

grounds. Increased telemetry detections and longer periods of incidence indicate that staging occurs in the LNR around rkm 20 in late spring and summer (Secor et al. 2022).

My estimates of reach use support evidence for spawning in the MC and UNR. Previous sampling efforts have failed to collect sturgeon eggs in the MC-NR system, but strong indirect support for spawning came from gill net sampling that captured spawning-condition males and females in the MC, particularly in areas like rkm 18 where gravel substrate is present and telemetry records have detected aggregations of telemetered sturgeon in this area (Secor et al. 2022). Model estimates for reach-specific abundances are consistent with this evidence and highlight the importance of both the LMC and UNR, adding to the growing weight of evidence that spawning is taking place in both tributaries. Kahn et al. (2019) captured fall spawning run sturgeon in two tributaries of the York River, indicative of multiple spawning areas. Similar to my observations of a focus by the spawning run on the LMC, York River system individuals were more abundant in one tributary (the Pamunkey River) and individuals moved between the two tributaries. Large adults in spawning condition have been captured in the UNR, but sampling effort has primarily focused on the LMC. I suspect that the UNR may support a smaller number of spawners but it is important to consider that emphasis of side-scan sonar and tagging efforts in the LMC may underestimate UNR abundance (Figure 4). Furthermore, behaviors of tagged fish may only be representative of fish tagged in the LMC. Future studies should extend side-scan sonar surveys into the UNR and increase tagging effort in the UNR to account for the possibility of multiple spawning areas.

In 2020 compared to 2021, cooler water temperatures and associated rain events likely curtailed the duration of the recruitment period to the system. Recruitment approaches nil much earlier in 2020 than in 2021 (Figure 5). A similar pattern of a longer recruitment period in 2021

is observed in the telemetry data and daily abundance estimates. The number of unique individuals that entered the system reached its peak about a month earlier in 2020. Earlier arrival of tagged fish and a longer recruitment period support the previously proposed hypothesis that 2020 conditions influenced phenology and may have reduced overlap with side-scan sonar surveys. Water temperature cues have been investigated in the Savannah River, where the fall run initiated upstream movement into spawning tributaries when water temperature was between 24 C and 29 C (Vine et al. 2019). Average daily water temperature in 2020 began to decline consistently below 24 C around September 15, which is also around the time that the estimated cumulative number of sturgeon that entered the system peaked (September 17). In 2021, average daily water temperature did not begin to drop below 24 C until late September and subsequent declines in temperature were gradual.

Telemetry data indicates that sturgeon begin to depart from spawning tributaries in the Chesapeake Bay when water temperature consistently declines from 25 C to 20 C (Hager et al. 2020; Secor et al. 2022). After September 15 2020, daily average water temperature was at or below 20 C during 86% of days. In comparison, average water temperature was at or below 20 C for 34% of days in 2021. Estimated total abundance in the system begins to decline after September 15 in 2020, while it increases until about September 25 in 2021. More frequent rainfall in 2020 also resulted in higher flow and flashier conditions compared to 2021, which had generally low flow conditions that declined steadily. To my knowledge, Vine et al. (2019) provide the only analysis of environmental conditions on Atlantic sturgeon spawning cues and found no influence of flow on fall spawning run timing; however, the authors did find that high levels of flow were negatively associated with upriver movement of Shortnose sturgeon in the Savannah River. In summary, comparisons in environmental conditions between years indicate

that the spawning run recruitment period occurred over a shorted period in 2021, which likely reduced overlap with side-scan surveys. Whether this underestimated abundance in 2020 is unclear.

As one of the smallest tributaries that supports the smallest documented spawning run for Atlantic sturgeon, the MC-NR system is exceptionally vulnerable to common factors threatening anadromous fish phenology such as anthropogenic disturbances and climate change. Multiyear estimates of abundance provided in this paper are important in evaluating vulnerability and developing recovery strategies that depend upon monitored population dynamics. Although some areas within the Marshyhope Creek and Nanticoke River are designated as Critical Habitat and are protected under the ESA, anthropogenic development still threatens to encroach on portions of this system. Improved estimates of spawning reach dependencies and spawning run phenology will delineate seasonal habitat use within Critical Habitat and can be used to support protection of specified areas within the MC-NR system. For example, plans to develop a commercial salmon aquaculture facility in the MC were recently averted because of the high density of sturgeon detected in this area (Wheeler and Cox 2022). Telemetry data and my preliminary spawning run estimates supported the theme that a very small spawning run depends on the MC and were used as key points by scientist, managers, and the public to advocate against the development of the aquaculture facility. This example highlights the importance of scientific communication and shows the potential that abundance and phenological information can have on influencing management of this protected species. Additionally, I present new evidence that spawning may also occur in the UNR. This area has not been surveyed as thoroughly as the MC and exclusion of this tributary in management decision-making would fail to protect the entire spawning run.

Fall spawning runs have only recently been described for Atlantic sturgeon (Balazik and Musick 2015; Farrae et al. 2017; Markin and Secor 2020). Understanding the timing of recruitment, residency, and persistence is necessary to fully understand the population dynamics of Atlantic sturgeon and prepare for management in an uncertain future. Among many other potential issues, climate change will alter historic patterns in temperature, flow, and dissolved oxygen (Najjar et al. 2010) which could impact spawning phenology and habitat for Atlantic sturgeon (Niklitschek and Secor 2005; Markin and Secor 2020. Mazzini and Pianca (2021) predict that marine heat waves in the Chesapeake Bay will increase in frequency and intensity throughout the rest of this century. Analysis of historic water temperature data from 1986-2020 collected from various locations throughout the bay indicate that marine heat waves have increased temperature by 3℃ on average (maximum temp ranging from 6-8℃) and were most prevalent during the summer (July-September; Mazzini and Pianca 2021). The increased prevalence of marine heat waves in summer months when sturgeon move into the Nanticoke system could shift spawning phenology later into the fall. Furthermore, model simulations assuming a bay wide 1℃ increase in average July water temperature in the Chesapeake Bay indicated increased mortality, decreased growth, and reduced suitable nursery habitat by 65% for juvenile Atlantic sturgeon (Niklitschek and Secor 2005). Given this, projected increases in average water temperature by 3℃ could seriously limit suitable spawning habitat and reduce the recruitment of juvenile sturgeon to adult populations in many Chesapeake Bay tributaries. Under current regional climate conditions, storms are also forecast to increase in frequency and intensity, which is expected to cause sporadic, high intensity discharge events (Najjar et al. 2010). In 2020, late-summer/fall storms and subsequent high discharge events in the MC-NR corresponded with rapid decreases in water temperature below 20℃. The combined effects of

increased summer temperature with increased storm frequency and intensity could result in a future scenario where sturgeon move into spawning tributaries later (i.e. water temperatures consistently exceed 28℃ later into the fall) and sturgeon exit earlier (i.e. storms and high discharge events cause rapid decreases in temperature below 20℃). Ultimately, this would result in a compression of historic fall conditions and limit the spawning period window. Small systems such as the Marshyhope Creek-Nanticoke River are less resilient to such changes in environmental conditions, therefore understanding how environmental conditions effect phenology is imperative to conservation of Atlantic sturgeon in this system.

Relevance to NOAA and the LMRCSC

NOAA is committed to the management and conservation of marine resources and the ecosystems that support them. The NMFS Office of Protected Resources is responsible for implementing the Endangered Species Act (ESA), which assesses the vulnerability of native species and the habitat they use, does so through a process that collaboratively engages fishery managers and stockholders to develop recovery plans and continued monitoring programs. The Chesapeake Bay distinct species segment (DPS) of Atlantic sturgeon is “Endangered” (NOAA 2017). Climate change, invasive species, and anthropogenic influences threaten Atlantic sturgeon in spawning reaches of the Nanticoke River and represent key assessment areas for quantifying population recovery. Results provided in this paper can be used to track the influences of encroaching threats on Atlantic sturgeon in this system, enhance the development recovery plans under the ESA, and further specify potential areas designated as Critical Habitat.

Table 1. Tagging history of all Atlantic surgeon available for detection in the MC-NR system. Shaded boxes indicate the year a fish was tagged, "X" symbolizes that the fish was tagged in the system in that year, and "D" represents occasions when fish were detected in a different system.

Date Captured	Transmitter Number	Total Length (mm)	Fork Length (mm)	Sex	Years Returned: 2014	2015	2016	2017	2018	2019	2020	2021
8/27/2014	A69-9001-27545	1575	1410	M		X		D				
8/27/2014	A69-9001-27544	2197	1923	F						D		
9/5/2014	A69-9001-27543	1918	1692	M		X	X	X	X	X	X	X
9/11/2014	A69-9001-26350	1524	1346	M		D	D	D	D			
9/11/2014	A69-9001-27546	1854	1676	F				X		X		X
9/11/2014	A69-9001-27547	1702	1346	M			D	D	D			
9/16/2014	A69-9001-26352	1816	1600	M		X	X	X	X	X	X	
9/16/2014	A69-9001-26351	1511	1346	M			X	X	X	X		
8/31/2015	A69-9001-26354	1499	1321	M			X	D	D			
8/31/2015	A69-9001-26353	1473	1422	M			X	X	X	X	X	X
9/15/2015	A69-9001-23900	1499	1327	M			D	D	D			
9/15/2015	A69-9001-23901	1683	1549	M			X	X	X	X	X	
9/17/2015	A69-9001-23902	1721	1549	M				X	X	X		X
9/29/2015	A69-9001-23904	1753	1549	M			X	X	X	X	X	X
9/29/2015	A69-9001-23903	1835	1626	M			X	X	X	X	X	X
10/7/2015	A69-9001-21062	1510	1340	M						X		
9/8/2016	A69-9001-21063	1575	1384	M					X	X		
9/14/2016	A69-9001-21064	1626	1499	M				X	X		X	
9/15/2016	A69-9001-21065	1626	1473	M				X	X	X	X	X
9/20/2016	A69-9001-21066	2337	2045	F						X		X
9/21/2016	A69-9001-21067	1854	1645	M					X	X		
8/15/2017	A69-9001-21068	2286	2070	F								
8/29/2017	A69-9001-21069	1750	1570	M					X	X	X	X
8/29/2017	A69-9001-21070	1566	1449	M					X	X		
9/13/2017	A69-9001-21072	1524	1463	M								
9/14/2017	A69-9001-21061	1670	1490	M								
9/21/2017	A69-9001-21060	1800	1670	M					X			
9/20/2018	A69-9001-10157	1950	1770	M							X	X
9/26/2018	A69-9001-18009	1685	1495	M						X	X	X

9/27/2018	A69-9001-18010	1861	1630	M						X	X	X
9/5/2019	A69-9001-18978	2120	1779	F								
9/9/2019	A69-9001-10159	2520	2250	F								
9/12/2019	A69-9001-10158	2180	1930	F								
9/18/2019	A69-9001-18977	1950	1761	F								
9/19/2019	A69-9001-18979	1758	1522	M								X
8/25/2020	A69-9001-18980	1844	1720	M								X
9/1/2020	A69-9001-18981	2155	1900	F								
9/10/2020	A69-9001-6276	1650	1460	M								
9/14/2020	A69-9001-18983	1750	1585	M								X
9/21/2020	A69-9001-6274	1750	1570	M								
9/7/2021	A69-9001-18982	1803	1612	M								
9/15/2021	A69-9001-18984	2019	1803	M								
9/27/2021	A69-9001-18985	1734	1511	M								

Table 2. Transition probability matrix for sturgeon in the MC-NR system. Matrix is read from left to right where "k" is the reach location on a given day and "k+1" is the probability that a fish stays in that reach or transitions to another reach on the next day.

		k + 1						
k	**Ω =**	**State**	**1 (NE)**	**2 (NR)**	**3 (LMC)**	**4 (UMC)**	**5 (UNR)**	**6 (E)**
		1 (NE)	$1-\eta_k$	$\eta_k\theta_2^2$	$\eta_k\theta_2^3$	$\eta_k\theta_2^4$	$\eta_k\theta_2^5$	0
		2 (LNR)	0	$\phi_k\pi^{2,2}$	$\phi_k\pi^{2,3}$	$\phi_k\pi^{2,4}$	$\phi_k\pi^{2,5}$	$1-\phi_k$
		3 (LMC)	0	$\phi_k\pi^{3,2}$	$\phi_k\pi^{3,3}$	$\phi_k\pi^{3,4}$	$\phi_k\pi^{3,5}$	$1-\phi_k$
		4 (UMC)	0	$\phi_k\pi^{4,2}$	$\phi_k\pi^{4,3}$	$\phi_k\pi^{4,4}$	$\phi_k\pi^{4,5}$	$1-\phi_k$
		5 (UNR)	0	$\phi_k\pi^{5,2}$	$\phi_k\pi^{5,3}$	$\phi_k\pi^{5,4}$	$\phi_k\pi^{5,5}$	$1-\phi_k$
		6 (E)	0	0	0	0	0	1

where:

η_k = probability a fish has enetered the system

ϕ_k = probability of staying in the system

π = probability of transitioning from reach j to l

θ = probability a fish is in reach j on day 1

1= Not Detected (Not Entered)
2= NR
3= Lower MC
4= Upper MC
5= Upper NR
6=Exited

Table 3. Detection probability matrix describing the probability of detection for tagged sturgeon in the NR-MC system.

		Observation Matrix					
State Matrix	***P* =**		**1 (ND)**	**2 (NR)**	**3(LMC)**	**4(UMC)**	**5 (UNR)**
		1 (NE)	1	0	0	0	0
		2 (NR)	$1-p_{2,i,k}$	$p_{2,i,k}$	0	0	0
		3 (LMC)	$1-p_{3,i,k}$	0	$p_{3,i,k}$	0	0
		4 (UMC)	$1-p_{4,i,k}$	0	0	$p_{4,i,k}$	0
		5 (UNR)	$1-p_{5,i,k}$	0	0	0	$p_{5,i,k}$
		6 (E)	1	0	0	0	0

State Matrix Key
1= Not Entered (Not Detected)
2= NR
3= Lower MC
4= Upper MC
5= Upper NR
6= Exited

Observation Matrix Key
1= Not detected
2= NR
3= Lower MC
4= Upper MC
5= Upper NR

Table 4. Example of state matrix for six detected Atlantic sturgeon in MC-NR system where 1= Not detected, 2= LNR, 3= LMC, 4= UMC, and 5= UNR.

	t	t+1	t+2	t+3	t+4	t+5	t+6	t+7
Sturgeon 1	1	1	1	2	2	2	3	3
Sturgeon 2	2	2	3	4	4	5	5	4
Sturgeon 3	1	1	1	1	2	2	3	2
Sturgeon 4	1	1	2	3	4	4	3	4
Sturgeon 5	2	2	2	5	5	2	2	1
Sturgeon 6	1	2	3	4	3	2	1	1

Table 5. Estimated median detection probabilities for acoustic telemetry in each river reach ($\bar{p}_{jl}$), side-scan sonar detection probability (p^{sss}) and the relationship between probability of recruitment and day (beta1), and the relationship between temperature and persistence (Alpha1). 95% credible limits are presented for each parameter.

Estimated Parameters	**2020 (median)**	**95% CI**	**2021 (median)**	**95% CI**
$\bar{p}_{j2}$	0.89	0.85-0.92	0.95	0.91-0.98
$\bar{p}_{j3}$	1.00	0.99-1.00	0.99	0.98-1.00
$\bar{p}_{j4}$	0.95	0.77-1.00	0.76	0.25-0.99
$\bar{p}_{j5}$	1.00	0.97-1.00	1.00	0.98-1.00
p^{sss}	0.95	0.74-0.99	0.85	0.65-0.94
Beta1	-0.14	-0.21 - -0.08	-0.06	-0.09- -0.04
Alpha 1	0.32	0.19-0.50	0.28	0.16-0.43

Table 6. Estimated reach transition probabilities by Atlantic sturgeon in the MC-NR system. NE represents the occasion when individuals transitioned from not entered into the system where NE_1 is the probability that an individual transitioned on or before August 15, NE_2 is the probability that an individual transitioned after August 15, and k is the day of observation. See thesis text for reach abbreviations.

		2020				**2021**			
		k +1				**k + 1**			
	State	**2 (LNR)**	**3 (LMC)**	**4 (UMC)**	**5 (UNR)**	**2 (LNR)**	**3 (LMC)**	**4 (UMC)**	**5 (UNR)**
k	**1 (NE_1)**	0.50	0.30	0.10	0.10	0.14	0.57	0.14	0.14
	1 (NE_2)	0.57	0.13	0	0.30	0.84	0.09	0	0.07
	2 (LNR)	0.92	0.04	0	0.03	0.88	0.06	0	0.06
	3 (LMC)	0.05	0.89	0.03	0.02	0.03	0.93	0.01	0.03
	4 (UMC)	0	0.61	0.39	0	0	0.54	0.46	0
	5 (UNR)	0.06	0.07	0	0.88	0.05	0.06	0	0.89

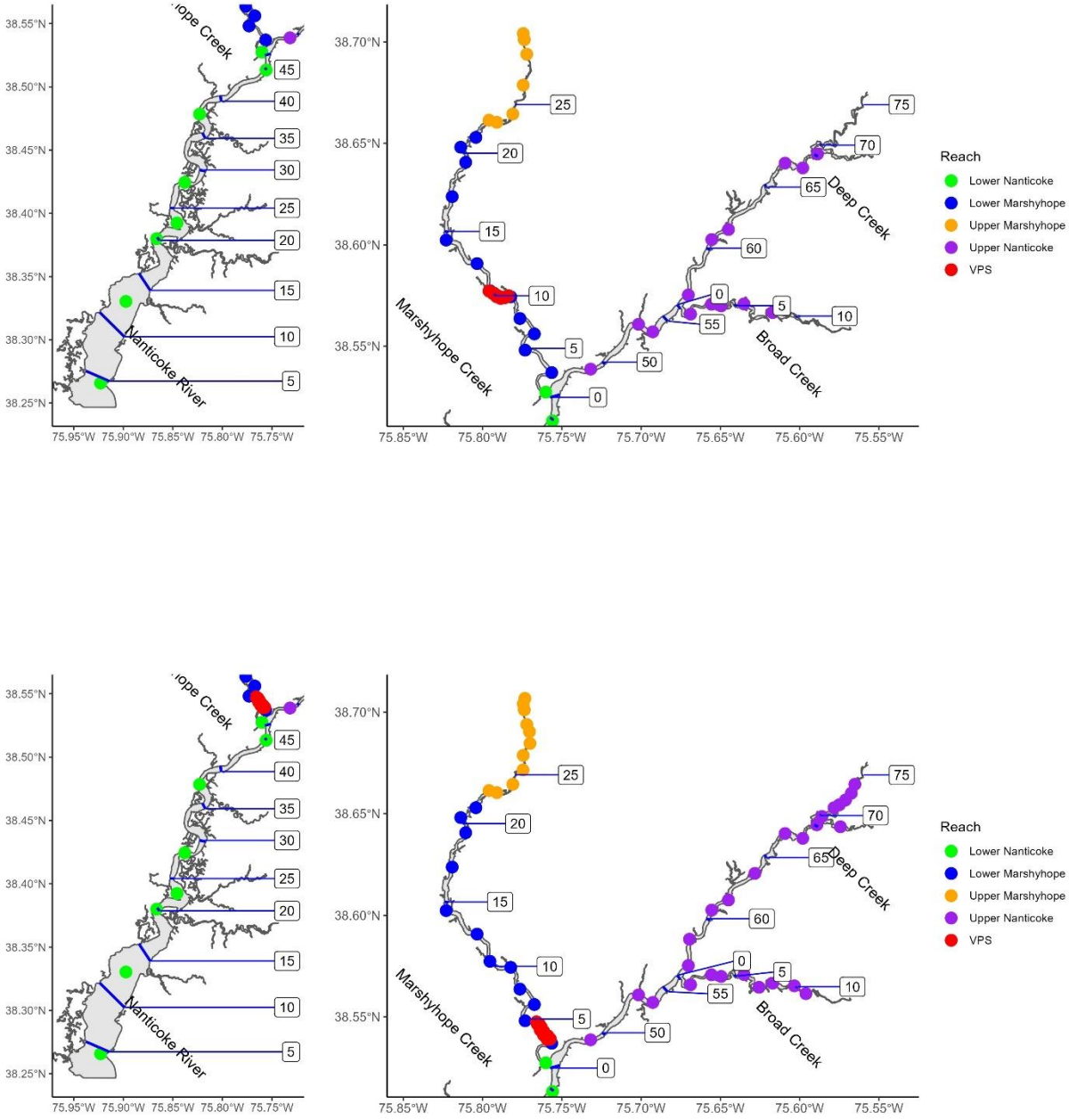


Figure 1. The Marshyhope-Nanticoke River system, showing spawning reaches (differing colors) and the location of VEMCO receivers (circles) deployed in 2020 (upper panel) and 2021 (lower panel).

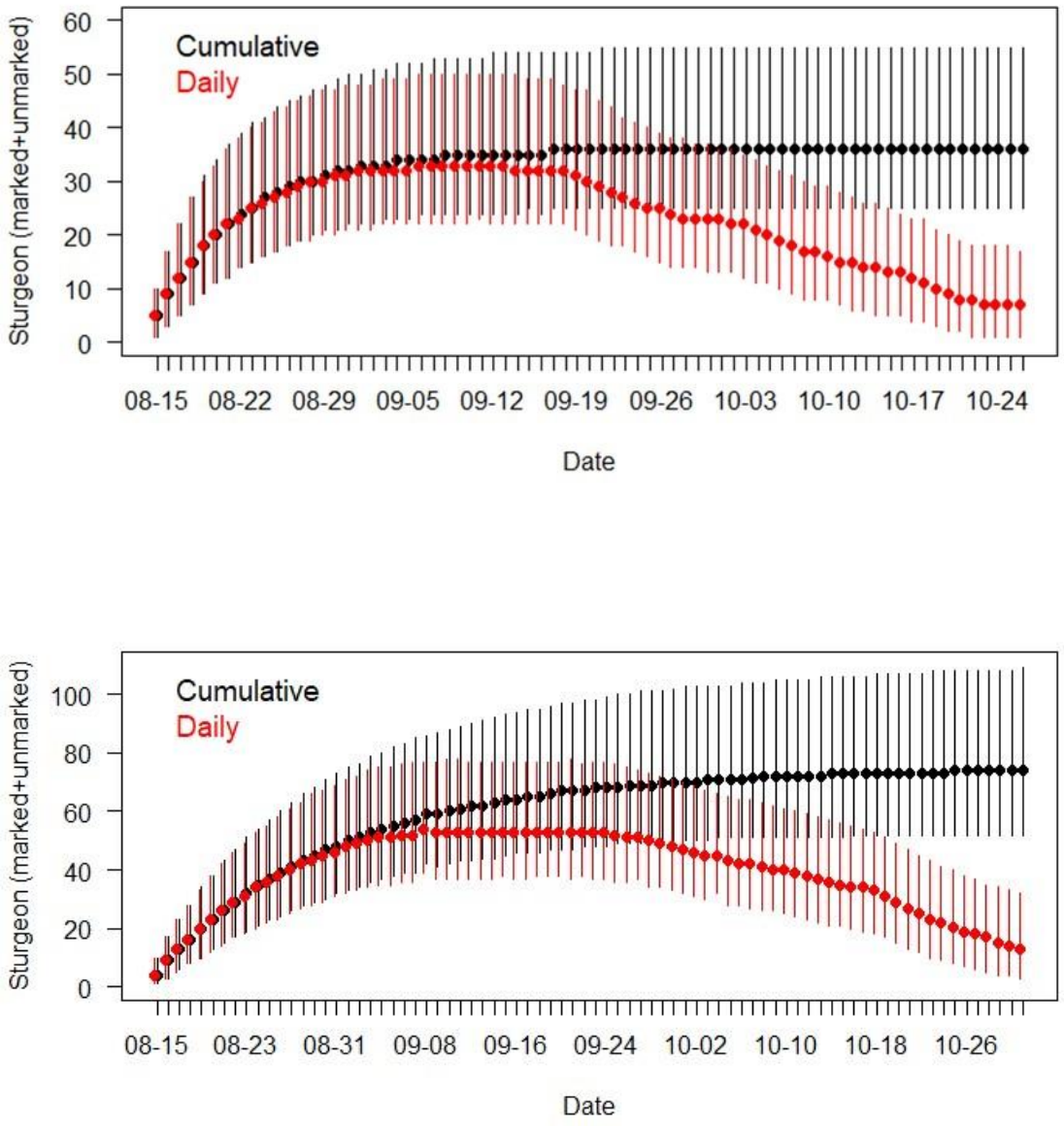


Figure 2. Cumulative (black) and daily (red) abundance estimates of Atlantic sturgeon in the MC-NR system in 2020 (top) and 2021 (bottom).

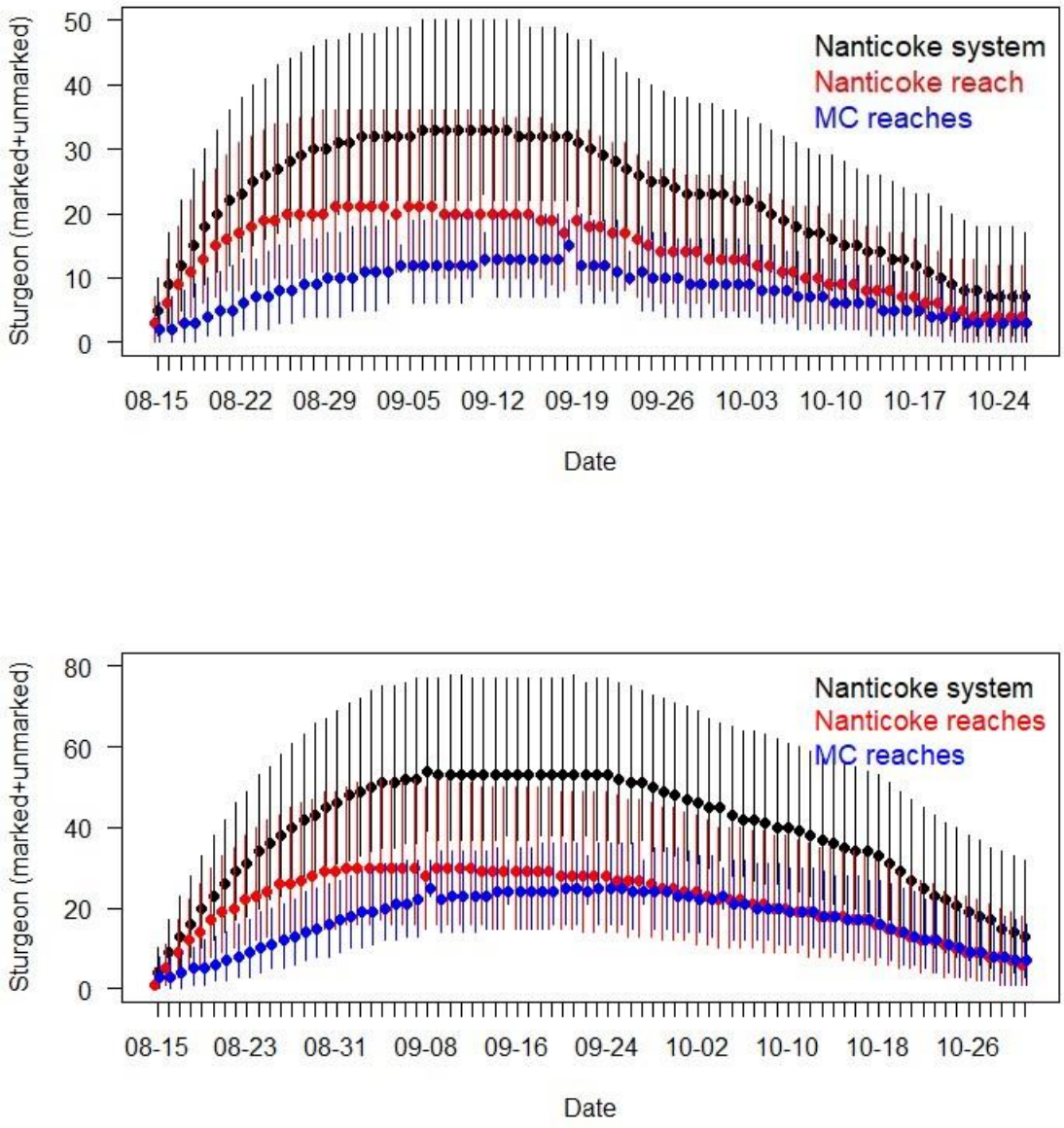
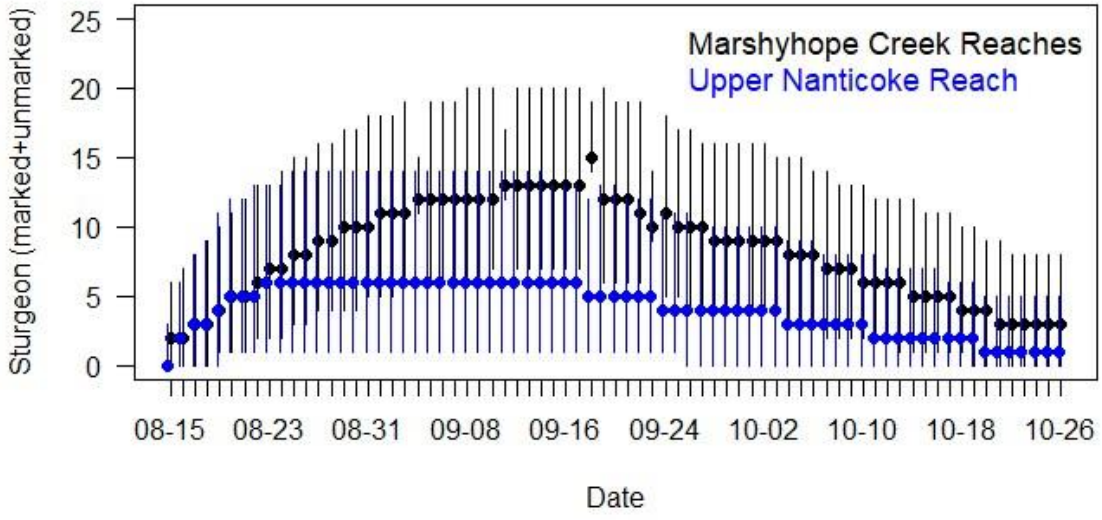


Figure 3. Daily abundance estimates of Atlantic sturgeon in the MC-NR system in 2020 (top) and 2021 (bottom). Points in the black represent estimates for both the Nanticoke and MC, points in the red represent estimates for the NR reaches (2 and 5), and points in the blue represent estimates for the MC reaches (3 and 4).



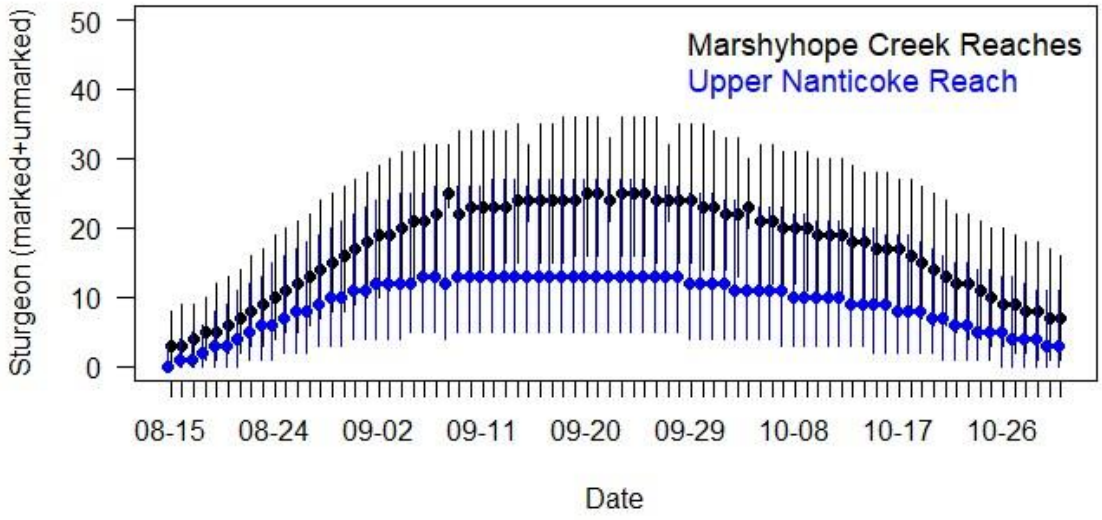


Figure 4. Estimated daily abundance of tagged and untagged sturgeon in the MC reaches and Upper NR reach.

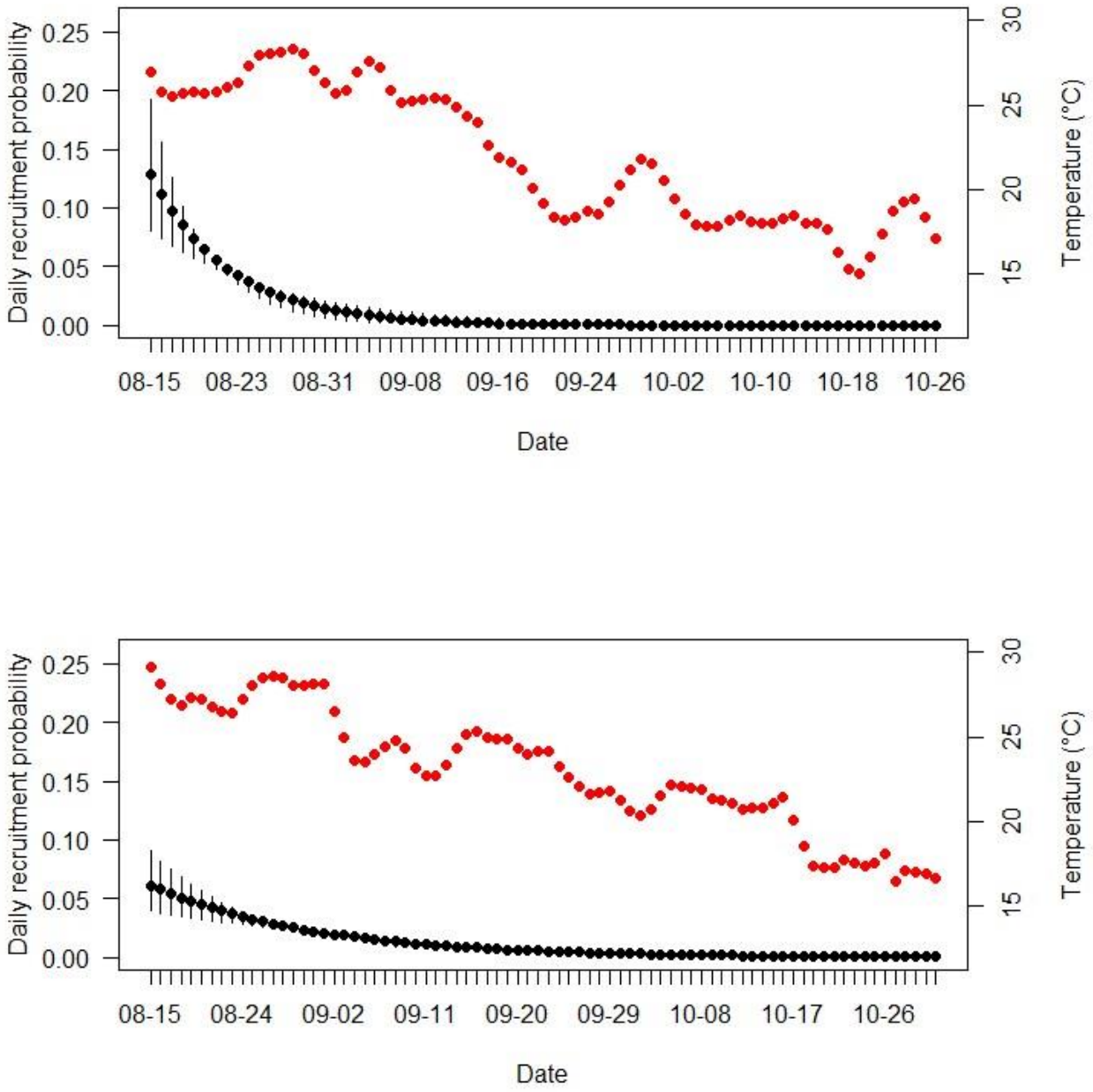


Figure 5. Estimated daily recruitment probability of Atlantic sturgeon (black) in the MC-NR system in 2020 (top) and 2021 (bottom) with average daily temperature data (red).

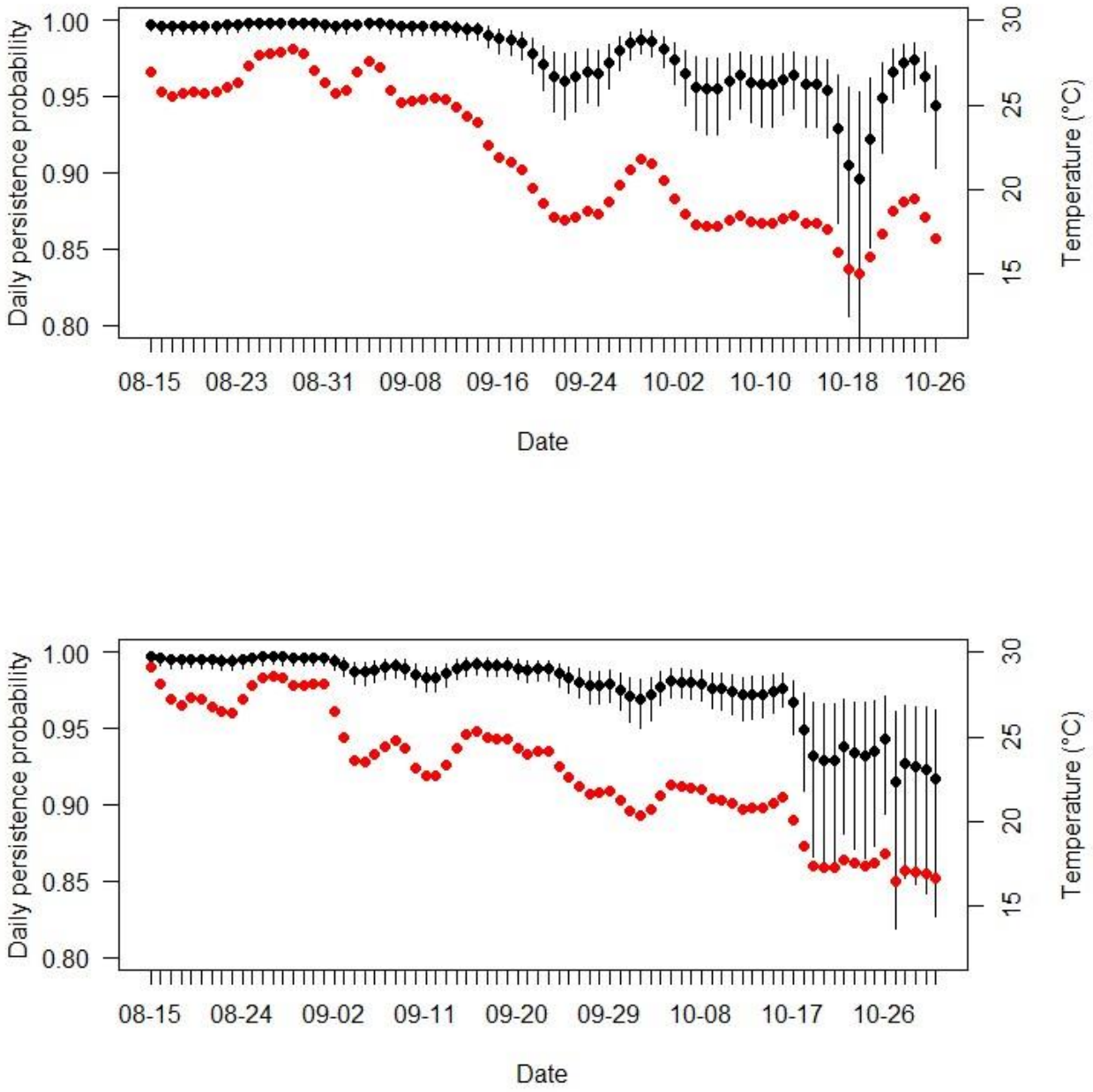


Figure 6. Estimated daily persistence probability of Atlantic sturgeon (black) in the MC-NR systemin 2020 (top) and 2021 (bottom) with average daily temperature data (red). Note that persistence was modeled as function of temperature.

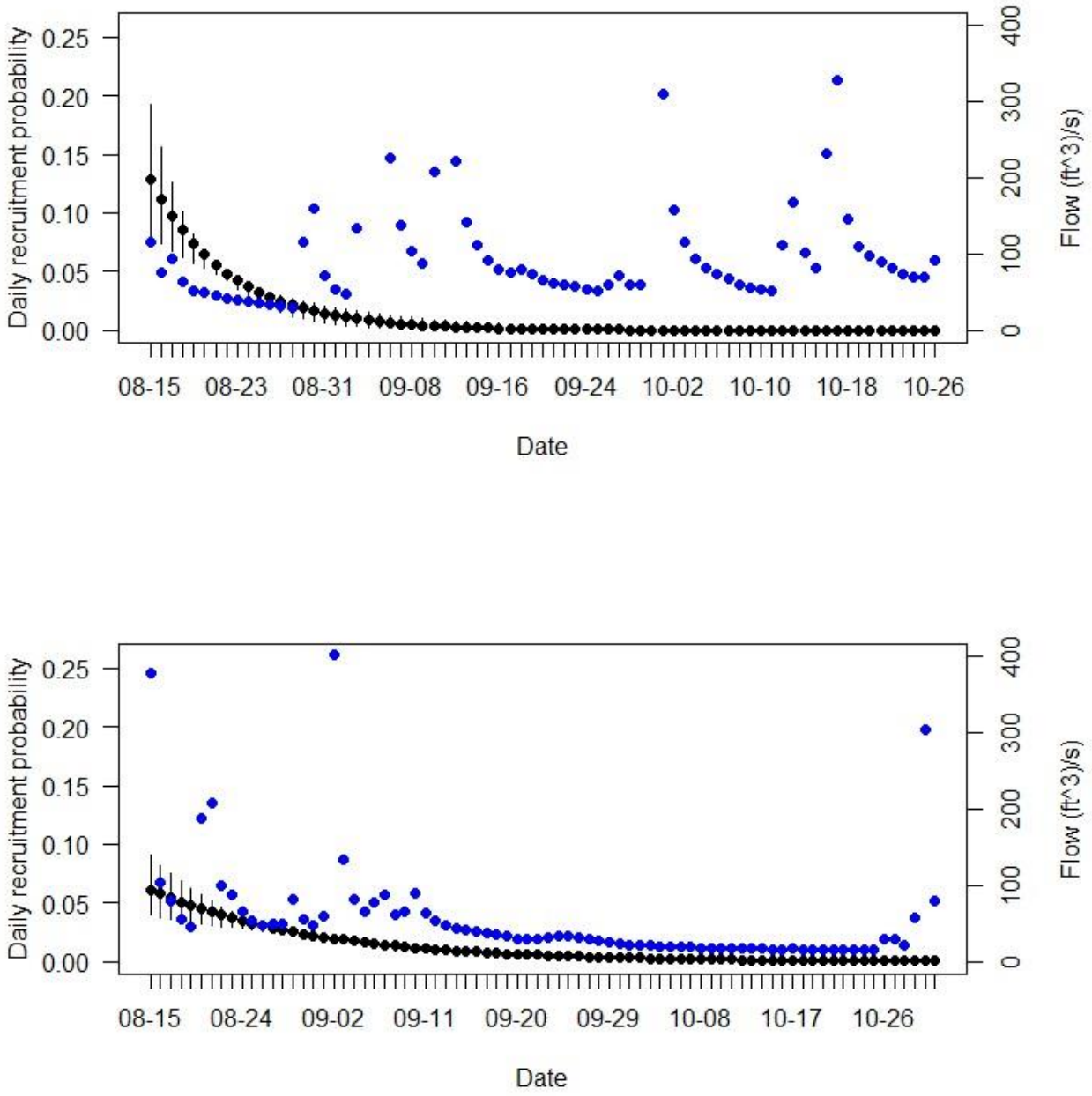


Figure 7. Estimated daily recruitment probability of Atlantic sturgeon (black) in the MC-NR system in 2020 (top) and 2021 (bottom) with average daily flow data (blue).

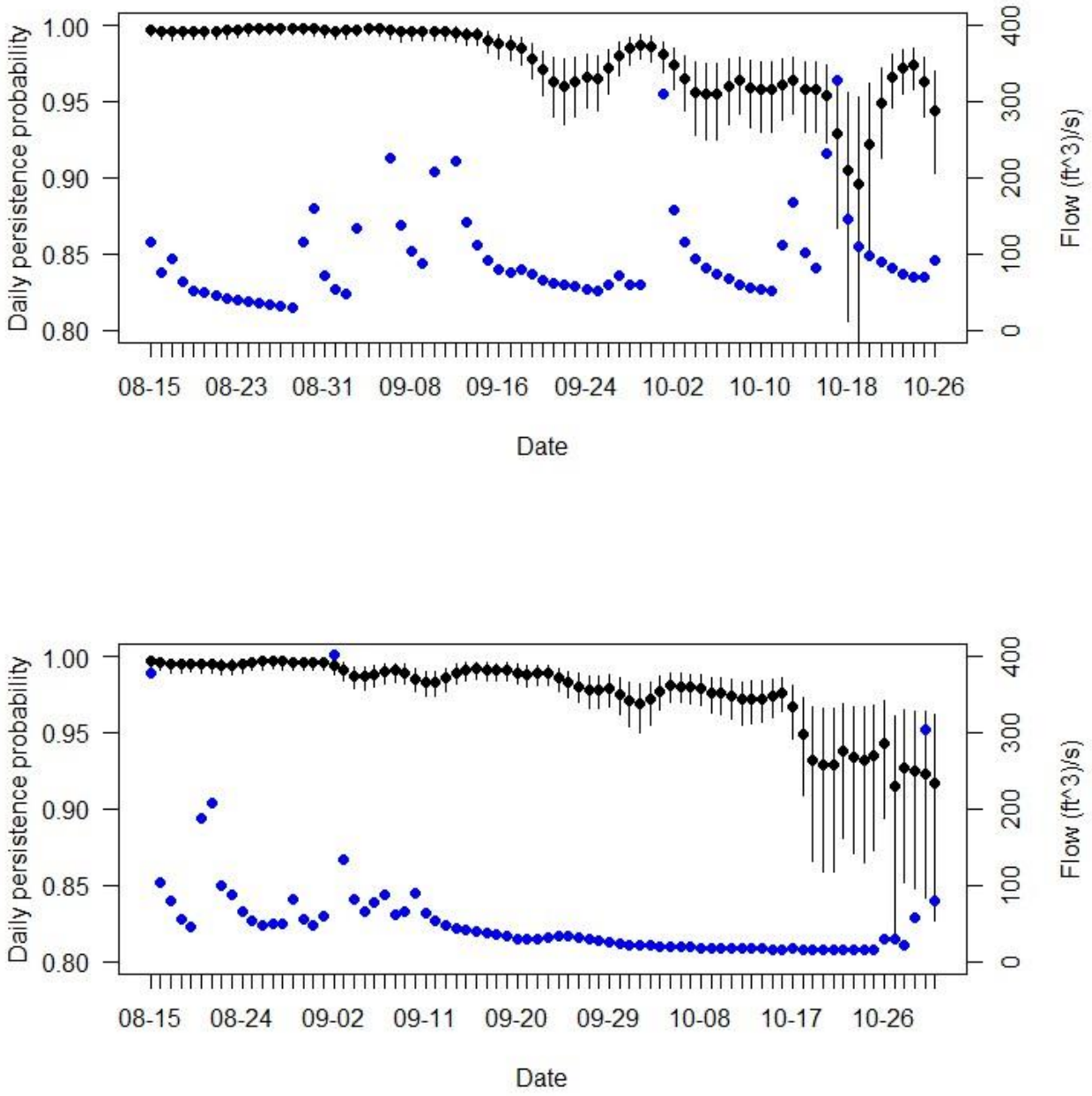


Figure 8. Estimated daily persistence probability of Atlantic sturgeon (black) in the MC-NR system in 2020 (top) and 2021 (bottom) with average daily flow data (blue)

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