Combining Fixed-Location Count Data and Movement Data to Estimate Abundance of a Lake Sturgeon Spawning Run: A Framework for Riverine Migratory Species

Lisa K. Izzo

Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont, USA

Gayle Barbin Zydlewski

School of Marine Sciences, University of Maine, Orono, Maine, USA

Donna L. Parrish

U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont, USA

Corresponding author: lisa.izzo@uvm.edu

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Abstract: Estimating abundance of migrating fishes is challenging. While sonars can be deployed continuously, improper assumptions about unidirectional migration and complete spatial coverage can lead to inaccurate estimates. To address these challenges, we present a framework for combining fixed-location count data from a dual-frequency identification sonar (DIDSON) with movement data from acoustic telemetry to estimate spawning run abundance of lake sturgeon (*Acipenser fulvescens*). Acoustic telemetry data were used to estimate the probability of observing a lake sturgeon on the DIDSON and to determine the probability that a lake sturgeon passing the DIDSON site had passed the site previously during the season. Combining probabilities with DIDSON counts, using a Bayesian integrated model, we estimated the following abundances: 99 (42–215 CI) in 2017, 131 (82–248 CI) in 2018, and 92 (47–184 CI) in 2019. Adding movement data generated better inferences on count data by incorporating fish behavior (e.g., multiple migrations in a single season) and its uncertainty into abundance estimates. This framework can be applied to count and movement data to estimate abundance of spawning runs of other migratory fishes in riverine systems.

Key Words: DIDSON, acoustic telemetry, lake sturgeon, Bayesian statistics, abundance

Introduction

Spawning migrations in rivers are a key part of the life history of diadromous as well some freshwater species. These migrations present an ideal time to monitor population trends due to the concentration of individuals in riverine habitats. While rivers serve as important migratory corridors, they have also been highly impacted by anthropogenic activity, which has led to major declines in abundance in both diadromous and potamodromous species (Limburg and Waldman 2009; Deinet et al. 2020). Because of these declines many riverine migratory species in North America have been listed as endangered, threatened, or vulnerable (McDowall 1999; Limburg and Waldman 2009; Haxton et al. 2016). The ability to monitor abundance of these populations is essential to management and tracking progress towards potential recovery.

Sonars (hydroacoustics) are used to observe fishes without capture and handling. Hydroacoustics use transmitted sound to provide metrics (counts) that can be used to estimate distribution and abundance of fish. Various hydroacoustic technologies include echo sounders, side-scan sonar, and high-resolution multi-beam sonars (Rudstam et al. 2012). High-resolution multi-beam sonar units such as the dual-frequency identification sonar (DIDSON), sometimes referred to as an “acoustic camera,” operate using a series of beams to create a video-like image of the observed area. This technology has been used in a variety of fisheries applications, such as assessments of multiple species of riverine migrating fishes (Hughes and Hightower 2015; Martignac et al. 2015), including salmon (Holmes et al. 2006) and sturgeons (Crossman et al. 2011; Mora et al. 2015, 2018). The use of a DIDSON also allows for continuous observation, even in turbid water or at night (Burwen et al. 2007), which can be advantageous to monitoring migrating fishes.

Despite the multiple advantages of using DIDSON to assess riverine migrating species, the technology presents several challenges, all related to ideal placement of the unit. First, flat sections of river help avoid blind spots and create the best images (Martignac et al. 2015). Second, ideally the beams should capture the entire width of the river channel; otherwise a weir or barrier should be used to direct fish through the beams (Petreman et al. 2014; Martignac et al. 2015). In some systems, installing a barrier might not be feasible due to recreational fishing and boat traffic, leaving the potential for gaps in spatial coverage. Lastly, selecting a location in the river with laminar flow can help minimize the back-and-forth milling behavior in fishes (Enzenhofer and Cronkite 2000) in order to not inflate counts (Martignac et al. 2015). Because unique individuals cannot be identified on DIDSON footage, ideally fish should migrate actively and uni-directionally past the DIDSON. However, multiple species of fishes that migrate in rivers display behaviors that involve multiple upstream and downstream movements over a single migratory season (Naughton et al. 2006; Frank et al. 2009; Holbrook et al. 2009; Larson et al. 2020; Izzo et al. 2021). These behaviors violate any assumption of unidirectional migration that might be used to estimate abundance and could lead to overestimates.

A potential method for working around the challenge of hydroacoustic methods is the use of telemetry. Telemetry can be used to collect an extensive amount of movement information from a small number of fish, making it especially useful when studying depleted populations. The inclusion of telemetry data in aquatic systems is useful in improving abundance estimates from mark-recapture models (Dudgeon et al. 2015; Withers et al. 2019), allowing for characterization of open populations (Shertzer et al. 2020), and accounting for individuals that may not be available for sampling in an overall abundance estimate (Sharples et al. 2009; Mora et al. 2018; Andrews et al. 2020; Kazyak et al. 2020). Since acoustic telemetry collects information on individual fish behavior, it has the potential to be used to estimate the degree of back-and-forth movement of fishes in a population or the proportion of individuals not observed due to gaps in spatial coverage from a fixed-location sonar device.

Both fixed-location count data and movement data are common in studies of riverine migrating fishes (Power and McCleave 1980; Gerlier and Roche 1998; Keefer et al. 2004; Holmes et al. 2006; Auer and Baker 2007; Hughes and Hightower 2015), and the application of Bayesian inference provides a way to combine these data sources to improve abundance monitoring of important species. Bayesian inference can be especially useful in situations where small sample sizes from depleted populations might limit the power of more traditional frequentist methods (Dorazio 2016). Bayesian models may also be used to estimate missing observations (Kery and Royle 2016). The estimation of missing values can be especially valuable if there are temporal gaps in monitoring, which can be an issue in highly dynamic riverine environments during the time of spawning runs (Auer and Baker 2007; Atkinson et al. 2016). Importantly, the use of Bayesian analysis allows for leveraging multiple data types to propagate uncertainties though a model to estimate parameters of interest, providing important information to managers on uncertainty around abundance estimates based on a variety of variables.

In this paper, we present a framework that combines fixed-location count data and movement data to estimate abundance of adult lake sturgeon (*Acipenser fulvescens*) during the spawning period in a tributary to Lake Champlain. Using an integrated Bayesian model, we corrected counts obtained from the DIDSON using data from tagged lake sturgeon to account for gaps in spatial coverage of the DIDSON and the potential for repeat migrations of lake sturgeon (Izzo et al. 2021) in the Winooski River, Vermont, USA. Through these methods, we were able to obtain the first estimate of abundance of spawning lake sturgeon in a Lake Champlain tributary while also minimizing handling of individuals from this endangered population and accounting for some of the challenges of sonar monitoring in rivers. While we demonstrate this framework using count data from a fixed-location DIDSON and movement data from acoustically tagged lake sturgeon, the approach could be used to estimate abundance of a variety of riverine migrating species. For example, it could be used in systems where other types of fixed-location count data (e.g., split-beam sonars, fish passage monitoring at dams) and/or movement data (e.g., radio telemetry, PIT arrays) are available. The addition of movement data in this model provides a way to create better inferences on count data collected in rivers by incorporating fish behavior, specifically multiple movements past a counting device, as well as the uncertainty around that behavior, into abundance estimates.

Materials and methods

Study system

Lake Champlain is a long (193 km) and narrow (20 km at its widest point) lake on the eastern edge of the range of lake sturgeon that is bordered by the states of New York and Vermont in the US, and the province of Quebec in Canada. Historically, populations spawned in four Vermont rivers: the Missisquoi River, the Lamoille River, the Winooski River, and Otter Creek (Moreau and Parrish 1994). Following a sharp decline in harvest from a small commercial fishery in the late 1940s and 1950s (Halnon 1963), the fishery was closed in 1967 and the species was listed as endangered in Vermont in 1972. Following the listing, little information was collected on lake sturgeon until the late 1990s, when spawning was confirmed to still be occurring in the Missisquoi, Lamoille, and Winooski rivers (MacKenzie 2016).

No prior abundance estimate exists for lake sturgeon in any of the spawning tributaries to Lake Champlain, and traditional mark-recapture methods to estimate abundance have been deemed largely intractable due to difficulty capturing adult lake sturgeon and highly variable sampling conditions in the rivers (MacKenzie 2016). We focused sampling for this study on a single spawning tributary because prior sampling by Vermont Fish and Wildlife Department (VFWD) suggested that the Winooski River may represent the most productive spawning population in the Lake Champlain basin, as it has the largest number of adult spawners captured and tagged to date (MacKenzie 2019). The lake sturgeon spawning migration in the Winooski River is limited to the lower 17 km downstream of the Winooski One Dam, which was built on the site of a previous natural fall line (Fig. 1). The spawning run of lake sturgeon in the Winooski River takes place each year between late April and mid-June, and spawning has been confirmed in previous years by the presence of eggs and drifting larvae (MacKenzie 2016).

DIDSON deployment

A dual-frequency identification sonar (DIDSON, Sound Metrics Corporation, Bellevue, Washington) was deployed next to the shoreline using a modified, weighted H mount less than 1 km downstream of the spawning site (Fig. 1). The unit’s field-of-view faced across the river, perpendicular to the flow. The fixed-location site was chosen due to ease of access, a consistent and reliable power source from the nearby wastewater treatment plant, and a gently sloping sandy bottom that allowed the upper part of the sonar beam edge to track the surface of the water while the substrate is seen throughout most of the field-of-view (Martignac et al. 2015). Since lake sturgeon are bottom-oriented fish, this deployment allowed us to see the portion of the water column that we would expect lake sturgeon to migrate through, even under high water conditions. At the deployment site, the channel width was approximately 60 m, which is a comparatively narrow section of the Winooski River that lake sturgeon migrate through to reach the spawning site. Due to the high number of anglers and boats present in the area during June, constructing a diversion fence to direct fish through the beams was not possible.

The unit was operated 24 hours/day in low frequency mode (1.1 MHz, 48 beams) during the spawning period in 2017, 2018, and 2019 (Table 1). In 2017, we used a standard DIDSON unit, operating with a window length of 20 m. The window length of 20 m was chosen because preliminary tests with the DIDSON unit indicated that the resolution would be too low to accurately measure fish targets for identification as lake sturgeon (length > 1 m) if a 40 m window was used. The window starting distance was adjusted as part of testing throughout the season (between 5 and 10 m from the unit). We added a telephoto lens (Sound Metric Corporation, Bellevue, Washington) to the DIDSON in 2018 and 2019 to increase the resolution of the DIDSON in low frequency mode and increase cross-channel coverage by expanding the window length to 40 m. The telephoto lens increases return signals using narrower horizontal and vertical beam widths. Images are delivered in a concentrated 15° horizontal field-of-view (as opposed to the standard 29° horizontal field-of-view) with the same number of beams, allowing for observations of large fish targets at up to 40 m from the unit (S. da Costa, Sound Metrics, personal communication, February 2018). A spreader lens was added to the telephoto lens to bring the vertical field-of-view from the reduced 3° back to the standard 14°. The window length with the telephoto lens was set to 40 m, with the start of the window set to be 3 to 5 m from the unit. Footage was collected at 4–7 frames/second in 10-minute files and stored on a portable hard drive. We visited the site a minimum of two times a week during the season to change the portable hard drive, adjust settings, and service the unit if needed.

The DIDSON was operational for the entirety of the deployment period in 2017 and 2018. Three major storm events in 2019 caused abnormally high spikes in flow levels in the Winooski River that resulted in the capture of sediment in the lens that obscured the view of the DIDSON. Because of this, the DIDSON did not function during the 2019 season from 12 May to 15 May and 21 May to 2 June. Following the third storm event, we manually turned off the DIDSON on 7 June for the remainder of the season. We classified DIDSON footage in 2019 as “viewable” (able to see some potential lake sturgeon targets migrating upstream) and “not viewable” (no visibility to detect potential lake sturgeon targets moving upstream). While most hours of the season were classified as “not viewable” (n = 467), a total of 252 hours of footage were “viewable” (Table 1).

DIDSON data processing

DIDSON v5.25 software (Sound Metrics Corporation, Bellevue, Washington) was used to manually process all collected footage. We used the measurement tool to estimate the size of fish targets. For each potential lake sturgeon target, three length measurements were taken at different points in the footage to account for the tendency of length measurements from DIDSON footage to vary with swimming motion (Burwen et al. 2010). Targets consistently greater than 1 m in length were classified as lake sturgeon (Fig. 2). Other large fish present in the Winooski River during the deployment period included walleye (*Sander vitreous*), and redhorse (*Moxostoma spp.*), which are both much smaller than lake sturgeon (walleye < 700 mm TL, Bozek et al. 2011, redhorse < 800 mm TL, Pyron 1999), and longnose gar (*Lepisosteus osseus*). While longnose gar can sometimes reach sizes of more than 1 m, they typically migrate later in June in the Winooski River after lake sturgeon have left the spawning site (C. Mackenzie, VFWD, personal communication, June 2016). The difference in migration timing makes it highly unlikely that longnose gar were counted as lake sturgeon. All DIDSON files were viewed by one or two trained technicians, and then all lake sturgeon observations were checked by the first author before incorporation into the count model. Through this multi-step process, we greatly reduced any uncertainty in the DIDSON counts that would have influenced our results.

For each lake sturgeon target, the direction of movement (upstream vs. downstream) and the range from the unit was recorded. Since most lake sturgeon were noted to move through the footage at different ranges (e.g. entered at 10 m and exited at 15 m), we calculated an average range from the DIDSON for each lake sturgeon by taking the average of the closest and furthest distances from the unit that the fish was observed. The average range of lake sturgeon targets in the three years of the study was compared using a Kruskal-Wallis test, and differences between the years were determined by a Wilcoxon test with a Bonferroni adjustment for multiple comparisons ($\alpha = 0.05$).

Acoustic telemetry

Lake sturgeon used in the following analyses were captured and tagged as part of sampling conducted by VFWD from 2015 to 2018 to document the presence and movements of adults in Lake Champlain. Lake sturgeon were tagged with VEMCO (Halifax, Nova Scotia, Canada) V16-6L (69 KHz) acoustic transmitters that were 16 mm x 95 mm, weighed 34 g in air (14.9 g in water), were set to transmit their unique ID code every 60–180 seconds, and had an estimated battery life of 10 years (more information on tagging methods can be found in Izzo et al. 2021). To detect tagged lake sturgeon moving past the DIDSON, an array of 2–4 VEMCO VR2W stationary acoustic receivers was deployed in the Winooski River near the lake sturgeon spawning site (Fig. 1). Receivers were deployed each year in late April or early May and removed in late June or July (Table 1). Range testing of the array showed there was a small area of detection overlap between the lowermost receiver and the receiver next to the DIDSON, with the potential for tags to be detected on both receivers when downstream of the DIDSON site. Since the area of detection overlap was not of interest in terms of the abundance model, overlapping detections were ignored in further analyses.

All acoustic receiver files were corrected for clock drift using VEMCO VUE software and were filtered for false detections as recommended by Pincock (2012). If the time between the previous or next detection of a tag on a single receiver was more than 30 times the average tag delay (in this case, more than 3600 s or 1 h), the detection was deemed a suspected false detection and removed from further analysis. Following removal of false detections, detections of tagged lake sturgeon on receivers surrounding the DIDSON deployment site were manually examined and classified for use in the abundance model detailed below. A movement upstream past the DIDSON occurred when the series of detections of a tagged fish indicated that it moved from the lowermost receiver to the receiver next to the DIDSON, and then was either detected on one of the receivers upstream of the DIDSON (in 2018 and 2019) or disappeared from the receiver array for a period of > 30 mins (in 2017 when the upstream receivers were not deployed). A movement downstream occurred from a series of detections in the opposite direction. If no clear direction could be determined, the movement was recorded as unsure of direction. Unsure of direction movements were usually movements where the tagged fish was detected for a long period of time (> 1 hour) on the receiver next to the DIDSON, and it was unclear if the individual was holding in the range of the receiver or milling around in the area. Analysis of acoustic telemetry data revealed that tagged lake sturgeon were always detected in series on the acoustic receiver array from downstream to upstream, indicating that no tagged fish that were moving upstream were missed by the stationary receivers. Because of this, we did not estimate detection probability of the acoustic receivers for use in the abundance model.

Spawning run abundance estimates

To estimate abundance of adult lake sturgeon in the Winooski River during a given spawning season, we used an integrated Bayesian model to combine acoustic telemetry data and hourly counts from a fixed-location DIDSON (Fig. 3). Acoustic telemetry data were used to estimate the probability of observing a lake sturgeon on the DIDSON and further used to determine the probability that a lake sturgeon that was passing the DIDSON site had passed the site previously during the season. Estimated model parameters (Table 2) included the probability that passing lake sturgeon will be observed on the DIDSON, *po*, the true number of lake sturgeon targets, N_t, the repeat probability of a lake sturgeon passing the DIDSON site, *pr*, and the corrected abundance, N_C. The parameter N_C represents the estimated abundance of spawning lake sturgeon in the Winooski River in a given season. For all parameters (derived from acoustic telemetry or DIDSON counts), estimates are made only based on upstream movements. On the DIDSON footage, potential targets moving downstream were more difficult to distinguish from floating debris if no swimming motion was observed, so we have higher confidence in identification of lake sturgeon moving upstream. Additionally, we did not miss any detections on tagged adult lake sturgeon moving upstream (as described above), but some downstream detections were missed in 2019. For these reasons, we decided to ignore downstream movements in our model. The model parameters and their derivation are described below.

A zero-inflated Poisson regression was used to model the true number of lake sturgeon targets that moved upstream past the DIDSON, accounting for observation probability *po*. Use of a zero-inflation model allows for the separation of true zeroes (when lake sturgeon are not migrating past the site) from zeroes due to lake sturgeon that are preset, but not observed on the DIDSON. The model can be described by

$$z_t \sim Bernoulli(\psi) \tag{1}$$

$$N_t \sim Poisson\left(z_t \lambda_j\right) \tag{2}$$

$$y_t \sim Binomial(N_t, po_j) \tag{3}$$

where z_t estimated by equation (1) is the parameter that describes whether or not any lake sturgeon are moving past the DIDSON at hour t (the suitability at hour t for migrating lake sturgeon to be passing the DIDSON), N_t estimated by equation (2) is the true number of lake sturgeon targets moving upstream in hour t, y_t estimated by equation (3) is the hourly count of lake sturgeon targets observed on the DIDSON, and po_j is the probability that a tagged lake sturgeon moving upstream would be observed on the DIDSON in year j.

Data used to estimate observation probability of the DIDSON were obtained from the tagged lake sturgeon and modeled as a binomial process to estimate a yearly observation probability po_j that fed into equation (3) above. Only movements classified as upstream where the tag detection interval on the receiver next to the DIDSON was less than 30 minutes were used to estimate po_j. If a lake sturgeon target was seen moving upstream on the DIDSON footage at the same time that a tagged lake sturgeon was detected also moving upstream, we considered that tagged fish to be observed on the DIDSON (and assigned it a 1). If, on the other hand, no lake sturgeon target was seen moving upstream on the DIDSON footage or if the only lake sturgeon target seen was moving downstream, we considered that tagged fish to not be observed on the DIDSON (and assigned it a 0). The detection interval threshold of 30 minutes was chosen because when upstream movements took longer than 30 minutes, it was highly likely that multiple lake sturgeon targets would be observed moving through the area during the detection interval. This would decrease confidence that the lake sturgeon target observed on the DIDSON was actually the tagged lake sturgeon that was being detected, so we decided to ignore these movements in *po* calculations. Since some tagged lake sturgeon made upstream movements past the DIDSON multiple times during the season (see below), multiple upstream movements from the same individual fish were used in calculations of *po* as long as they met the 30-minute detection interval threshold.

To provide better estimates of the missing data from 2019, covariates were placed on the ψ parameter in the zero-inflated Poisson regression. The ψ parameter, which is the parameter responsible for predicting whether or not any lake sturgeon migrated past the DIDSON in a given time period, was modeled as a linear regression of diel period (*D*, day or night) and the number of days since the Winooski River reached 6 ºC (*S*). The diel period was included because analysis of adult lake sturgeon telemetry data (Izzo et al. 2021) revealed that the probability of lake sturgeon moving upstream is higher at night, including through the area where the DIDSON was deployed, so we would expect more true zeroes during daylight hours. The number of days since the Winooski River reached 6 ºC was chosen because spawning behavior in other systems begins after temperatures reach 6 ºC (Bruch and Binkowski 2002). The covariate *S* was used as a metric of a seasonal effect, as we would expect more true zeroes later in the spawning season. The linear predictors for the zero-inflated Poisson parameter ψ are outlined in equation (4) below (see Supplemental Fig. 1 for more information on the modeled relationships).

$$logit(\psi) = \beta_0 + \beta_1 \times D + \beta_2 \times S \tag{4}$$

The total number of lake sturgeon targets that moved upstream for year *j* was calculated as a sum of true number of lake sturgeon targets (N_t) moving past the DIDSON over the duration of the DIDSON deployment in each year. To correct for the possibility of a single lake sturgeon passing the DIDSON site multiple times, the total for the season was corrected using an estimated probability that a lake sturgeon passing the DIDSON site had previously passed the site during the season (repeat probability) pr in year j. Movements from acoustic telemetry data that were classified as upstream or unsure of direction were used to estimate pr_j, with the intention that unsure of direction movements would account for the potential milling of lake sturgeon in the area of the DIDSON. Each time a tagged lake sturgeon made an upstream or unsure of direction movement, that individual was either identified as a new fish (assigned a 0) or a fish that had been in the area before (assigned a 1). These data were also modeled as a binomial process to estimate a yearly repeat probability pr_j. The total corrected abundance (N_C) for each year was estimated as

$$N_{Cj} = \sum N_t \times (1 - pr_j) \tag{5}$$

Both observation probability and repeat probability were estimated on a yearly basis. Uninformative beta distributions were used as priors for the observation probability and repeat probability parameters. The prior used for the Poisson λ was an uninformative gamma distribution with a scale and shape of 0.001. An uninformative normal distribution with a mean of 0 and a variance of 1×10^3 was used for the priors on the βs in the zero-inflated Poisson model.

Bayesian analysis was conducted using JAGS (Just Another Gibbs Sampler) run through package “rjags” (Plummer 2019) in Program R. The model was run using Markov chain-Monte Carlo (MCMC) methods, using three chains, each with 100,000 iterations and a 20,000-step burn-in period. Results were thinned by every 10th sample to reduce autocorrelation.

Convergence was assessed using the “coda” package and the Gelman-Rubin diagnostic (Plummer et al. 2006). Due to skewed posterior distributions for some parameters, the mode of the posterior is reported for the parameter estimate, and the 95% highest density intervals (HDI) are reported for the Bayesian credible intervals (CI). The posterior modes and HDIs were computed using the “bayestestR” package (Makowski et al. 2019).

Results

Data collected

Over three years of the study, the number of lake sturgeon targets counted moving upstream on the DIDSON ranged from 105 to 271 (Table 3, Fig. 4). The average range of lake sturgeon targets observed on the DIDSON was significantly less in 2019 (median = 18.5 m) and 2017 (median = 19.1 m) than in 2018 (median = 22.5 m, Wilcoxon test, $p < 0.05$). In 2018, 20% of lake sturgeon observations occurred at an average range of > 30 m from the DIDSON, the range at which they would not have been observed in 2017 using the standard lens.

Although VFWD had tagged 29 adult lake sturgeon (25 males, 2 females, 2 unknowns) between 2015 and 2018, 10 of those were assumed to be from spawning populations other than the Winooski River due to their capture locations (C. MacKenzie, VFWD, personal communication, November 2018). A total of 19 adults were tagged on the Winooski River spawning site between 2015 and 2016, including 18 males and one female. During the study period, a total of 20 individual tagged lake sturgeon were detected on acoustic receivers near the Winooski River spawning site. All these individuals were male, including the 18 males initially tagged on the Winooski River spawning site, one male that was tagged on the spawning site in another river in Lake Champlain (the Lamoille River) in 2016, and one male that was tagged in an area of Lake Champlain assumed to contain fish from the Lamoille River spawning population in the fall of 2018 (Izzo et al. 2021). In 2017, 10 tagged adult lake sturgeon made movements past the DIDSON (55% of tagged Winooski River males). In 2018, 18 tagged lake sturgeon made movements past the DIDSON (94% of tagged Winooski River males plus one Lamoille River male). In 2019, 17 tagged lake sturgeon made movements past the DIDSON (89% of tagged Winooski River males plus one Lamoille River male). The number of movements from acoustic telemetry data used to estimate the observation probability and repeat probability parameters also varied by year (Table 3), with 2018 having the lowest sample size as few tagged lake sturgeon made multiple movements past the DIDSON site. In 2019, most movements of tagged lake sturgeon past the DIDSON site (66%) were during hours when the view of the DIDSON was fully obscured, so these movements could only be used in the estimation of *pr* and not *po*.

Abundance model

The estimated observation and repeat probabilities varied over the three years of the study (Fig. 5). The observation probability was highest in 2018, with a posterior mode estimate of 0.74 (Fig. 5A), and the lowest in 2019, with a posterior mode estimate of 0.52 (Fig. 5C). Repeat probability was similar in 2017 and 2019 (posterior mode estimate of 0.79 and 0.80, Fig. 5D and 5F), but much lower in 2018 (posterior mode estimate of 0.27, Fig. 5E). We estimated 99 adult lake sturgeon (42–215 CI) in the 2017 spawning run (Fig. 5G), 131 adult lake sturgeon (82–248 CI) in the 2018 spawning run (Fig. 5H), and 92 adult lake sturgeon (47–184 CI) in the 2019 spawning run (Fig. 5I).

Discussion

The methodology we presented here offers a framework for estimating abundance of endangered lake sturgeon without excessive handling of a large number of individuals, particularly during the spawning period. While our study focused on lake sturgeon, the general model structure, implemented as an integrated Bayesian model that allows for propagation of uncertainty in a straightforward way, could be used on a variety of riverine migratory species. Counts using sonar in riverine systems are typically limited by the assumption that individuals migrate unidirectionally and are therefore not observed more than one time. This assumption is also relevant to fish monitoring at dams or weirs, where counts at a fixed location are often made based on video or by live observers. Counts from these locations need to be adjusted for fallback and reascension to avoid overestimating total escapement (Boggs et al. 2004; Naughton et al. 2006), though the adjustment factors used do not always incorporate uncertainty in the fallback estimates. Telemetry has become more widely used to monitor movement across aquatic systems (Hussey et al. 2015) and is useful in informing estimates of abundances using a variety of model types (Sharples et al. 2009; Mora et al. 2018; Withers et al. 2019; Andrews et al. 2020; Kazyak et al. 2020; Shertzer et al. 2020). The addition of telemetry data in our model generated better inferences on the DISDON count data by incorporating fish behavior (e.g., multiple migrations during a single season) and its uncertainty into the abundance estimates.

This study provides the first estimates of spawning lake sturgeon abundance in any of the spawning tributaries to Lake Champlain. No prior attempts were made to estimate lake sturgeon abundance in the Winooski River (17 km) or in Lake Champlain (surface area: 1269 km^2), before or after the listing in the 1970s, so we cannot compare these estimates to others. In the Upper Black River, Michigan (11 km to first upstream barrier), a small system (Black Lake surface area: 41 km^2) with a self-sustaining and robust lake sturgeon population, between 100 and 234 individuals were observed spawning each year between 2001 and 2008 (Forsythe et al. 2012). A study using split-beam sonar to count lake sturgeon in the Sturgeon River, Michigan (69 km to the first upstream barrier) estimated that the size of the spawning population was 350–400 fish (Auer and Baker 2007). Adult lake sturgeon that spawn in the Sturgeon River either migrate to Portage Lake (8.5 km^2) or Lake Superior (82,103 km^2) during non-spawning periods (Auer 1999). Our estimates suggest that the size of the Winooski River annual spawning run is less than the annual spawning run in the Sturgeon River but approaches the lower range of that observed in the Upper Black River in the early 2000s.

The estimated number of lake sturgeon migrating to the spawning site in each year of our study is relatively constant, but it is unknown how this value compares to the overall population size of adult lake sturgeon from the Winooski River. Lake sturgeon are intermittent spawners, with males typically spawning once every 1–5 years, and females spawning once every 4–9 years (Peterson et al. 2007). Spawning interval can vary by population (Auer 1999; Bruch et al. 2001; Smith and Baker 2005), and few studies report what proportion of the overall population participates in the spawning run each year. In the Upper Black River, estimates have suggested that between 20 and 35% of the total population spawns in each year (Larson et al. 2020). While we do not have data on the spawning periodicity of females in the Winooski River, it is important to note that tagged male lake sturgeon often migrated to spawn in back-to-back years (Izzo et al. 2021), and a large percent of tagged males that were initially tagged in the Winooski River participated in the spawning run in 2018 (94%) and 2019 (89%). To extrapolate our estimates to a total system population size, as done in other systems (Mora et al. 2018; Kazyak et al. 2020), more information on spawning periodicity and the proportion of tagged males and females that enter the spawning river in a given year is needed.

Acoustic telemetry data provided key information to estimate parameters in our model to compensate for challenges of the DIDSON on its own. This work adds to the growing body of literature where telemetry has allowed researchers to estimate abundance while accounting for fish behavior, particularly for sturgeon populations. Previously, telemetry data have been used to supplement mobile DIDSON surveys of green sturgeon (*A. medirostris*; Mora et al. 2018) as well as mobile side-scan sonar surveys of shortnose (*A. brevirostrum;* Andrews et al. 2020) and Atlantic sturgeon (*A. oxyrinchus*; Kazyak et al. 2020). Our model framework shows that telemetry data can also be useful in informing abundance estimates from fixed-location counting devices that are continuously monitoring a spawning run in a riverine environment.

Although the inclusion of acoustically tagged fish allowed us to estimate abundance in this river system, the limited number of tagged individuals led to uncertainty in the estimates. The uncertainty in our model is largely based on the uncertainty surrounding the estimates of the probability that a lake sturgeon was observed on the DIDSON and the probability that a lake sturgeon passing the DIDSON site had previously passed the DIDSON site during the season. These estimates were informed by the number of tagged lake sturgeon migrating in each year (n = 10 to 18 depending on the year). An increased number of tagged individuals would likely provide increased precision on these estimates, which would lead to increased precision on the overall abundance estimate. If applying this approach in other systems, it would be important to consider the number of tagged fish needed to obtain results with the necessary level of precision needed for the specific management question at hand.

Currently, the acoustic telemetry parameters estimated by the model are based on data from male lake sturgeon. Only two females were tagged by VFWD prior to this study due to difficulty in capturing females, and neither female entered the Winooski River for the spawning run during the three years studied. The multi-run behavior of lake sturgeon has only been documented in the Winooski River (Izzo et al. 2021) and the Upper Black River, Michigan (Larson et al. 2020), with both studies focusing on the behavior of male lake sturgeon. Females were also observed making multiple runs in the Upper Black River, though to a much lesser extent than males (D. Larson, Michigan State University, unpublished data). Based on this, we might assume that using only male lake sturgeon to inform our model could lead to a conservative estimate of abundance, as male lake sturgeon may be more likely to be observed multiple times on the DIDSON than females. Further information on female migratory behavior would help improve abundance estimates in the Winooski River. Additionally, future work with sturgeons or other species could expand the model to include sex specific differences in movement during the spawning period.

Based on trends in the DIDSON counts combined with the acoustic telemetry data, we believe that the data collected in this study captured the majority of the run in each year, including the primary peak in mid-May. While the goal of this study was to capture the entire spawning period of lake sturgeon in the Winooski River, high flows due to snow melt in mid- to late-April prevented safe deployment of the DIDSON until water levels dropped to between 85 and 140 m^3/s. In each of the three years of study, a few tagged lake sturgeon were detected in the upper river (just downstream of the DIDSON site) a few days prior to the DIDSON deployment. Based on these data, it is likely that some lake sturgeon were missed due to the truncated DIDSON monitoring period.

The probability that a lake sturgeon would be observed on the DIDSON (observation probability) varied over the course of the study depending on the setup of the lens. In 2017, a standard DIDSON lens was used, so only 20 m (~1/3) of the river channel could be seen. In 2018, the addition of the telephoto lens doubled the field-of-view of the DIDSON, allowing 40 m (~2/3) of the river channel to be seen. The change in lens corresponded to an increase in observation probability in 2018, as we were able to regularly observe lake sturgeon at a range of > 30 m from the unit. We expected the observation probability in 2019 to be similar to 2018; however, large storm events caused the lens to fill with sediment during the season. Even prior to total loss of visibility, lake sturgeon could only be seen in the near field-of-view (< 15 m) for multiple hours during the storm event, likely leading to missed observations during the period that the unit was still operating. We attribute the lower observation probability in 2019 to the impact of sediment on the DIDSON lens. While large storm events such as those in 2019 may not be common in the Winooski River, future work with the DIDSON in this system would benefit from including a sediment exclusion device to protect the lens (Atkinson et al. 2016).

The probability that a lake sturgeon passing the DIDSON site had passed the DIDSON site previously during the season (repeat probability) also varied in the three years of the study. Individuals were more likely to be observed multiple times in 2017 and 2019 than in 2018. Adult male lake sturgeon were also observed making more multi-run movements in 2017 and 2019, with more variability in discharge patterns leading to more fish moving back and forth through the Winooski River (Izzo et al. 2021). In contrast, the 2018 season included less variable discharge patterns, and fish typically making a single movement upstream and a single movement downstream during the spawning period (Izzo et al. 2021). The behaviors observed by the tagged male lake sturgeon throughout the entire Winooski River corresponded with the changes we saw in the estimated repeat probability. While it is possible that the probability of a lake sturgeon being observed on the DIDSON could be standardized with more years of study, our results show that the changes in lake sturgeon behavior year to year in the Winooski River could have a large influence on the probability that lake sturgeon passing the DIDSON site had passed the site previously in the season, and therefore, the ability to appropriately interpret DIDSON counts.

Environmental conditions such as temperature and discharge play a role in the migrations of many riverine migratory fishes (Alabaster 1990; Lucas and Baras 2001; Binder et al. 2010; Peterson et al. 2017). Because of the documented relationships between migration and environmental conditions, we would not only expect changes in the repeat probability from year to year, but also expect that it is possible for repeat probability and observation probability to vary within a single season. Unfortunately, due to low sample sizes of tagged fish, a limited window of time that these fish were moving past the DIDSON, and high variability in conditions (particularly discharge) over the three years of study, we were not able to incorporate within year variation into our model. Due to the flexibility of Bayesian analysis, extensions of the model in systems with higher sample sizes could include the effects of environmental conditions on fish movement and how that impacts observation or repeat probabilities. Additionally, a better understanding of environmental relationships with fish movement combined with more years of study could allow for the use of informative priors in these types of Bayesian models to better inform abundance estimates of riverine migrating fishes.

In this paper, we presented a framework for using movement data (in the form of telemetry) to account for the challenges of using a fixed-location DIDSON to obtain counts of a riverine migratory species. Despite the caveats discussed above, this method provides a minimally intrusive way to track changes in migratory fish abundance over time and monitor population recovery. Using this framework, we were able to produce the first estimate of abundance for lake sturgeon in the Winooski River, Vermont, USA while also minimizing handling of individuals from this endangered population and accounting for some of the challenges of sonar monitoring in rivers. Broadly, this approach is applicable to estimate abundance of a variety of riverine migrating species when fixed-location count data (e.g., DIDSON, split-beam sonars, fish passage monitoring at dams) and/or movement data (e.g., acoustic telemetry, radio telemetry, PIT arrays) are available. By adding movement data to this model and implementing the model using an integrated Bayesian approach, we provide a way to create better inferences on count data collected in rivers by incorporating fish behavior (e.g., multiple migrations during a single season) and its uncertainty into abundance estimates.

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Tables

Table 1. Summary of DIDSON deployment dates, the number of hours of DIDSON footage that was collected, and the deployment dates of the stationary acoustic receiver array that was used to detect tagged lake sturgeon moving past the DIDSON. *In 2019, high sediment loads due to multiple storm events obscured DIDSON footage, this table includes only the viewable hours that were collected.

Year	DIDSON deployment	DIDSON hours collected	Receiver deployment
2017	10 May – 21 June	1005	24 April – 21 June
2018	9 May – 11 June	789	9 May – 18 July
2019	8 May – 7 June	252*	6 May – 16 July

Table 2. Parameters that were included in the model to estimate abundance of spawning lake sturgeon in the Winooski River, Vermont, USA. See Fig. 3 for schematic description of Bayesian integrated model used to estimate parameters.

Parameter	Parameter meaning	Data used for estimation
po	Probability of observing a lake sturgeon on the DIDSON	Acoustic telemetry
N_t	True number of lake sturgeon targets that moved past the DIDSON site	Acoustic telemetry + DIDSON counts
pr	Probability that a lake sturgeon passing the DIDSON site is a fish that has moved past the DIDSON site at least once before (is a repeat)	Acoustic telemetry
N_C	Lake sturgeon abundance, corrected for the occurrence of fish passing the site multiple times	Acoustic telemetry + DIDSON counts

Table 3. Summary of data collected by the DIDSON (sturgeon targets) and the stationary acoustic telemetry array (tagged sturgeon, movements of tagged lake sturgeon used for *po*, and movements of tagged lake sturgeon used for *pr*) that were used to estimate abundance of spawning lake sturgeon in the Winooski River, Vermont, USA. Only movements classified as upstream, where the tag detection interval on the receiver next to the DIDSON was less than 30 minutes, were used to estimate *po*, while the number of movements used to estimate the probability of a lake sturgeon target being a repeat (*pr*) was based on all upstream movements as well as unsure of direction movements.

Year	Lake sturgeon targets on DIDSON (n)	Tagged lake sturgeon in river (n)	Movements of tagged lake sturgeon used for *po* (n)	Movements of tagged lake sturgeon used for *pr* (n)
2017	271	10	15	38
2018	153	18	8	18
2019	105	17	17	86

Figure headings

Fig. 1. Map of the study area in the Winooski River, Vermont, USA. Acoustic receivers are indicated by black circles, and the approximate area of DIDSON coverage is denoted by the grey triangle. The acoustic receiver next to the DIDSON along with the acoustic receiver downstream of the DIDSON were deployed in all three years of the study; the acoustic receiver upstream of the DIDSON on the south side of the island was deployed in 2018 and 2019, and the acoustic receiver upstream of the DIDSON on the north side of the island was deployed only in 2019.

Fig. 2. A snapshot of DIDSON footage from (A) the view shown by the standard DIDSON unit used in 2017, including a 1.2 m lake sturgeon (indicated by white arrow) moving upstream, and (B) the view shown by the DIDSON with the telephoto lens used in 2018 and 2019, including a 1.4 m lake sturgeon (indicated by white arrow) moving upstream.

Fig. 3. Schematic describing the model used to estimate abundance of adult lake sturgeon migrating upstream during the spawning period in the Winooski River, Vermont, USA. Dashed boxes indicate submodels that were informed by acoustic telemetry data. Bold, square boxes indicate collected data, while grey circles indicate estimated parameters (po = observation probability of the DIDSON, pr = repeat probability, N_t = true number of lake sturgeon targets migrating upstream, and N_C = corrected abundance of lake sturgeon).

Fig. 4. Stacked barplot showing the number of lake sturgeon targets identified moving upstream on DIDSON footage (dark grey), the number of tagged lake sturgeon detected in the area of the DIDSON site (light grey), and the mean discharge on each day (m^3/s) in the Winooski River, Vermont, USA in (A) 2017, (B) 2018, and (C) 2019. Grey shaded dates in 2019 indicate days when sedimentation completely obscured the view of the DIDSON.

Fig. 5. Estimated posterior distributions for the observation probability (po, panels A – C), repeat probability (pr, panels D – F), and the corrected abundance estimate (N_C, panels G – H) for 2017 (top), 2018 (middle), and 2019 (bottom). The parameter estimates, reported as the posterior mode, are indicated by the dashed grey lines, and the shaded regions represent the Bayesian credible intervals, reported as the 95% highest density interval. For po and pr, the uninformative beta distributions ($\alpha = 1$, $\beta = 1$) that were used as priors are shown as dark grey lines.

Figures

Fig. 1.

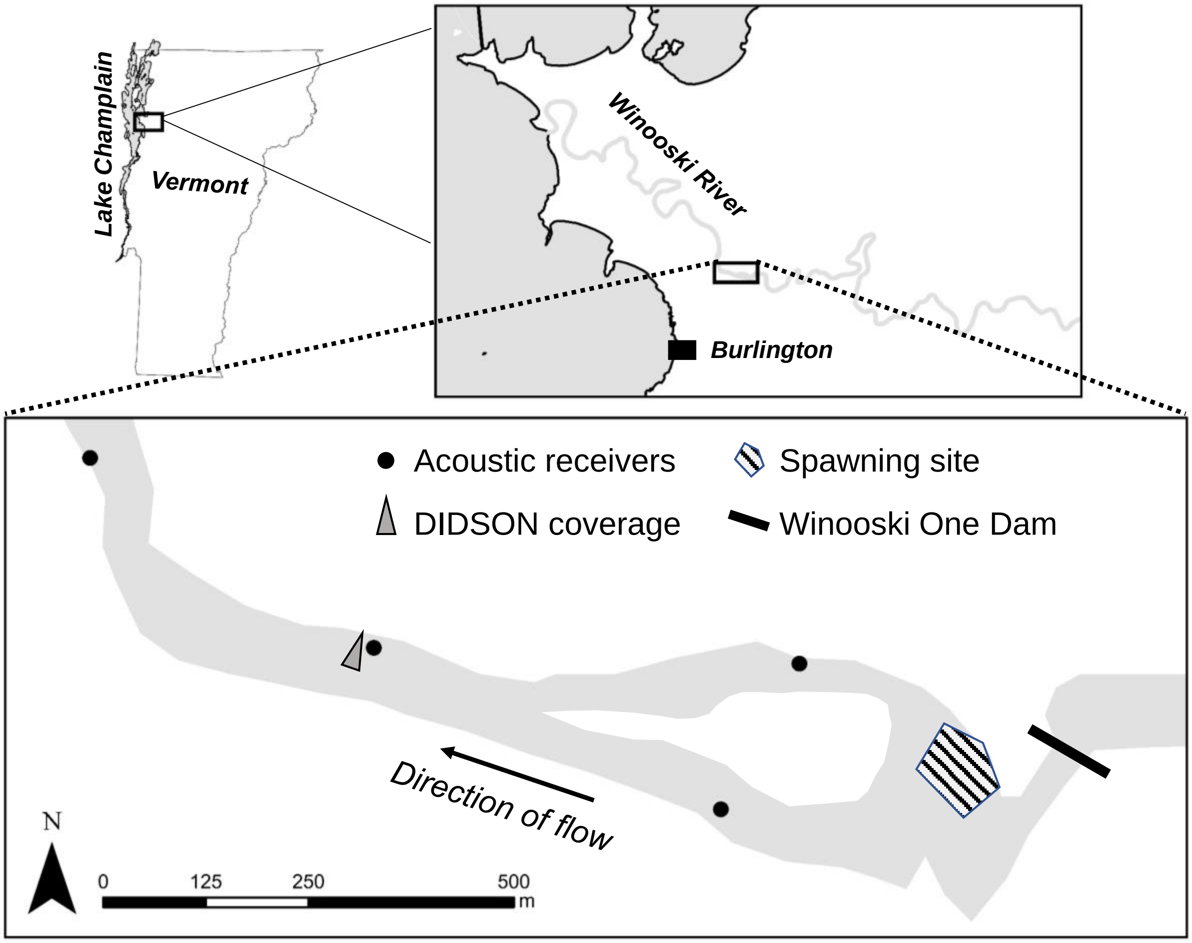
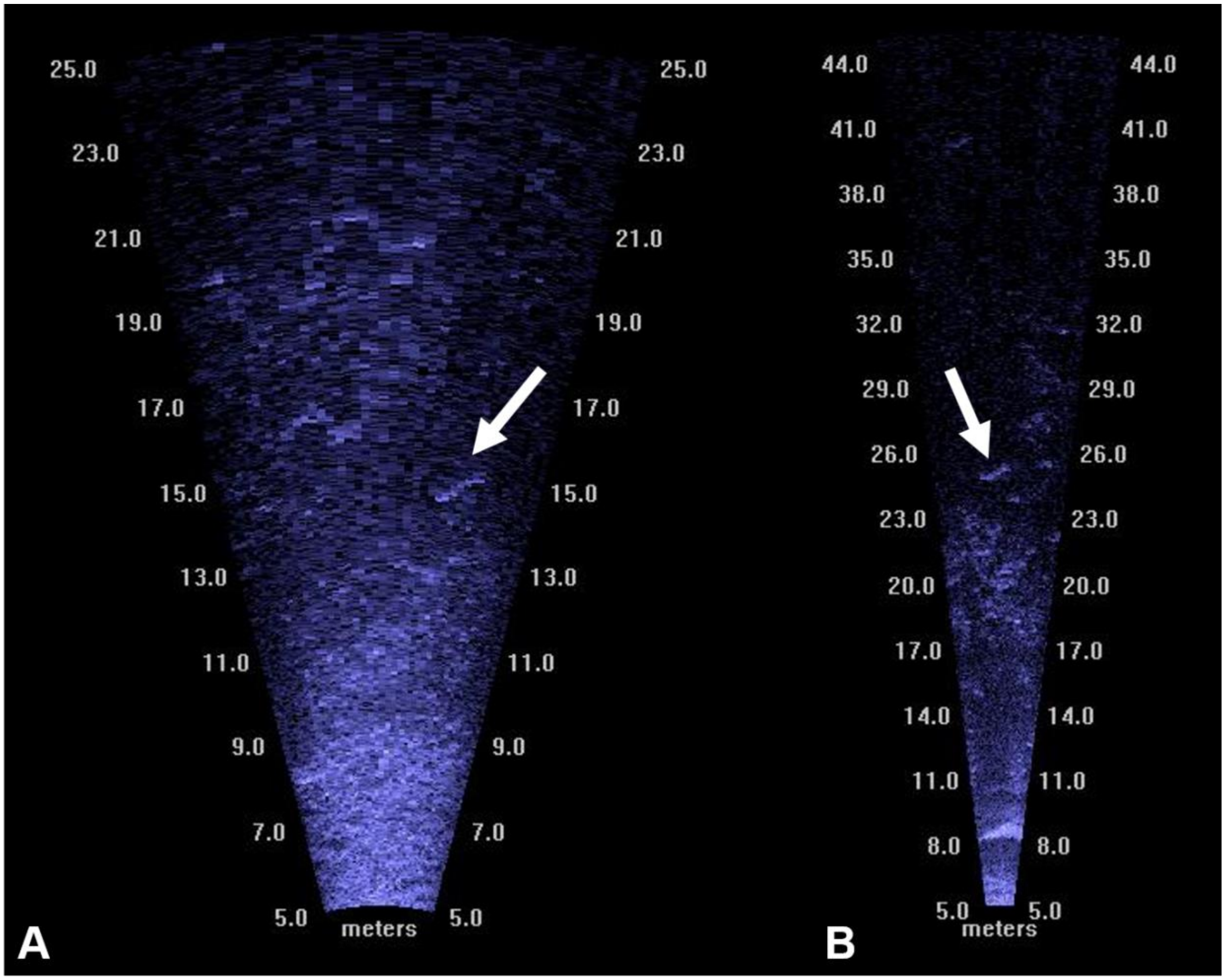


Fig. 2.



A
25.0 25.0
23.0 23.0
21.0 21.0
19.0 19.0
17.0 17.0
15.0 15.0
13.0 13.0
11.0 11.0
9.0 9.0
7.0 7.0
5.0 5.0
meters
B
44.0 44.0
41.0 41.0
38.0 38.0
35.0 35.0
32.0 32.0
29.0 29.0
26.0 26.0
23.0 23.0
20.0 20.0
17.0 17.0
14.0 14.0
11.0 11.0
8.0 8.0
5.0 5.0
meters

Fig. 3.

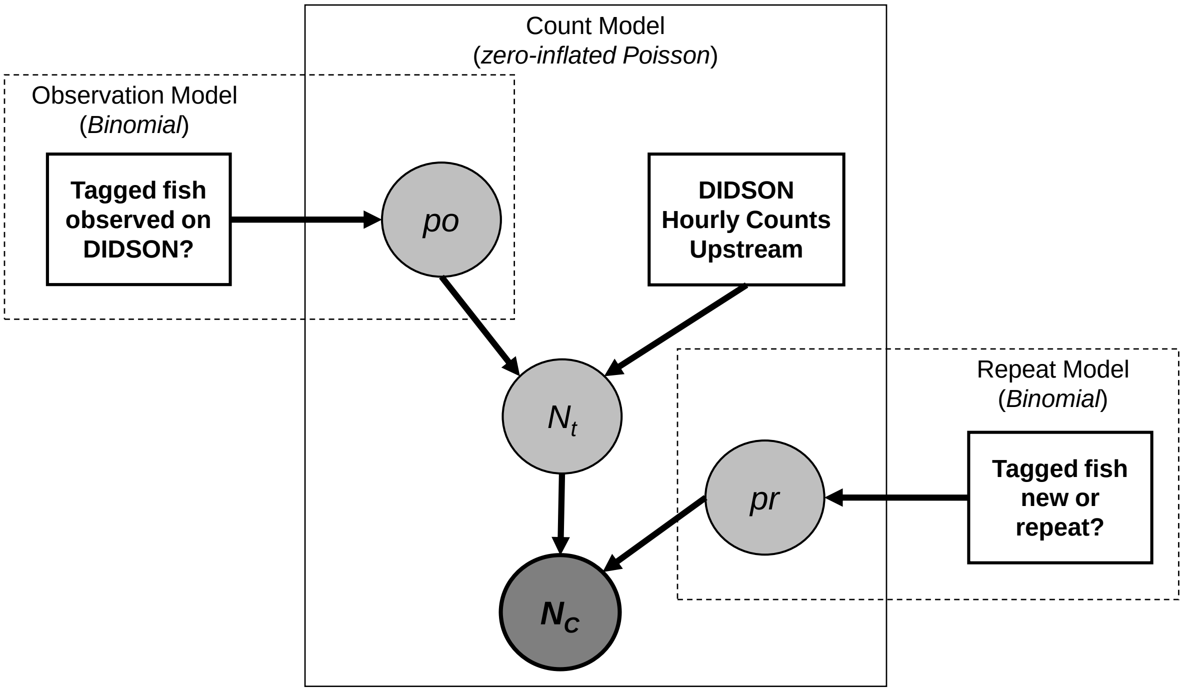
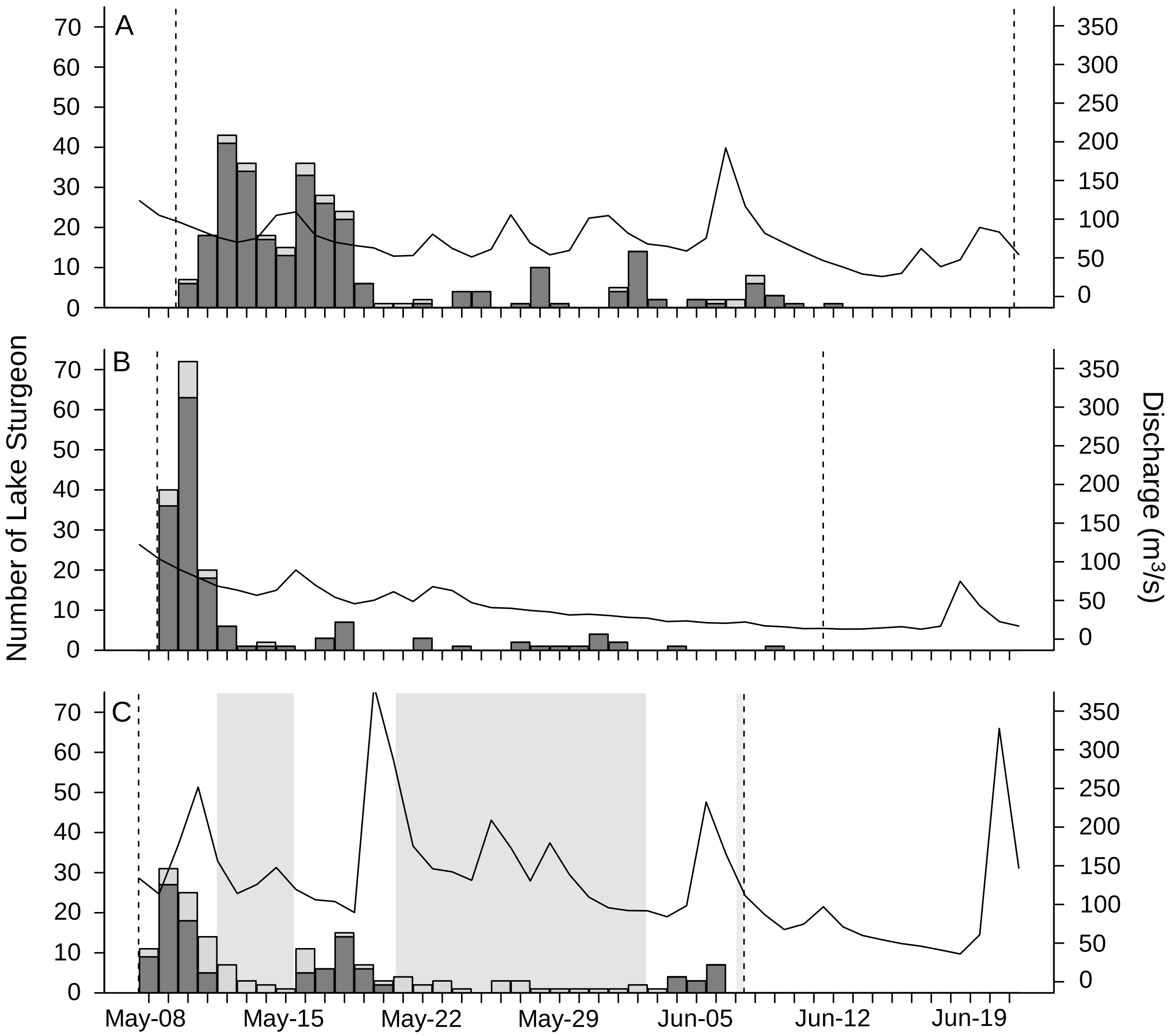
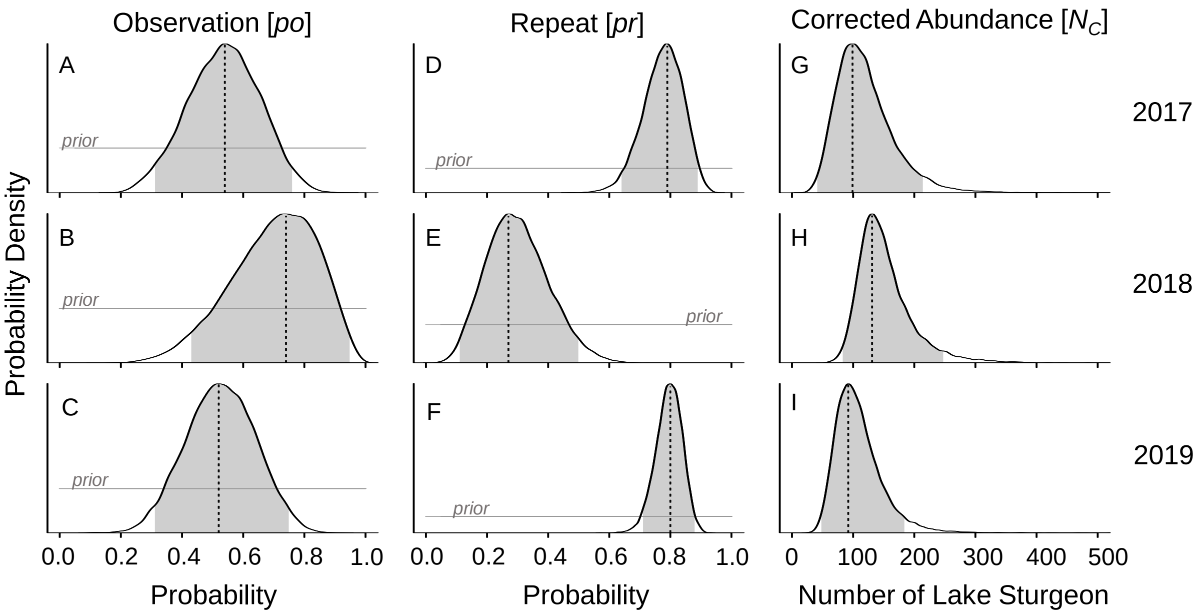

Count Model
(*zero-inflated Poisson*)
Observation Model
(*Binomial*)
Tagged fish observed on DIDSON?
po
DIDSON Hourly Counts Upstream
N_t
Repeat Model
(*Binomial*)
pr
Tagged fish new or repeat?
N_c

Fig. 4.


A
B
C
Number of Lake Sturgeon
Discharge (m³/s)
0
10
20
30
40
50
60
70
0
50
100
150
200
250
300
350
May-08
May-15
May-22
May-29
Jun-05
Jun-12
Jun-19

753 Fig. 5.


Observation [po]
Repeat [pr]
Corrected Abundance [N_C]
A
D
G
2017
B
E
H
2018
C
F
I
2019
prior
prior
prior
prior
prior
prior
Probability Density
0.0 0.2 0.4 0.6 0.8 1.0
0.0 0.2 0.4 0.6 0.8 1.0
0 100 200 300 400 500
Probability
Probability
Number of Lake Sturgeon

754