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Research Article

Vertical Patterns in Lake Sturgeon (*Acipenser fulvescens*) Larval Drift within Two Rivers Directly Connected to Green Bay, Lake Michigan

Patrick S. Forsythe ,[1] Dave A. Lawrence,[1] Ashok Ragavendran,[2] Kari McClellan ,[3] Miguel A. Ortiz,[1] Tanna M. Dittmar,[1] Robert F. Elliott,[4] and Michael C. Donofrio[5]

[1]*Aquatic Ecology and Fisheries Laboratory, University of Wisconsin Green Bay, 2420 Nicolet Drive, Green Bay, WI 54311, USA*
[2]*Center for Computational Biology of Human Disease, Brown University, Box G-W101, 80 Waterman Street, Providence, RI 02912, USA*
[3]*U.S. Forest Service, Mount Hood National Forest, Clackamas River Ranger District, 16400 Champion Way, Sandy, OR 97055, USA*
[4]*U.S. Fish and Wildlife Service, Green Bay Fish and Wildlife Conservation Office, 2661 Scott Tower Drive, New Franken, Wisconsin 54229, USA*
[5]*Wisconsin Department of Natural Resources Satellite Center, 101 North Ogden Road Suite A, Peshtigo, Wisconsin 54157, USA*

Correspondence should be addressed to Patrick S. Forsythe; forsythp@uwgb.edu

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Fish larvae in riverine environments often disperse (e.g., drift) from areas of egg deposition at the time of hatch. Several components of drift can be important in terms of survival including timing, distribution in the water column, and body size. The longitudinal and cross-sectional aspects of larval lake sturgeon (*Acipenser fulvescens*) drift from upstream spawning sites have received considerable study. However, the vertical distribution of larval lake sturgeon in the water column has not been comprehensively evaluated with respect to river size, water depth, the size of larvae in drift over the entire drift period, and the effectiveness of traditional sampling gear (D-frame nets) designed to collect larvae along the river bottom. In 2013, we sampled larval lake sturgeon drifting from upstream spawning sites in the Menominee and Oconto Rivers (Wisconsin, USA) using traditional D-frame nets and custom fabricated sampling nets that vertically partitioned the water column. Drifting larval lake sturgeon were observed from the river bottom to the top of the water column in both systems. Vertical net section was a significant predictor of total larval catch with the highest catch occurring in nets towards the center of the water column but was dependent on net location within the rivers' cross section and downstream distance from spawning locations. 42% of larvae captured across both rivers were outside of the sampling capability of the traditional D-frame nets (i.e., fish would have drifted over the top). Studies seeking to describe larval production for lake sturgeon, as well as other fish species that exhibit drift in larval dispersal, need to consider a balance between net design and sampling the vertical/cross sectional profiles of rivers. Size-based vertical drift may also have consequences for studies seeking to estimate genetic parameters (e.g., diversity and parentage).

1. Introduction

Egg deposition in well-oxygenated waters and river substrates with deep interstitial spacing provides protection for the developing eggs of many benthic spawning migratory fishes [1]. The larval stage of migratory riverine spawning fishes is further characterized by a brief period of posthatch larval retention in the substrates, active downstream outmigration or "drift and dispersal" from spawning areas often induced by internal/external cues (e.g., depletion of the yolk sac; water temperature), and subsequent settlement in downstream nursery habitats [2]. Patterns in the outmigration behavior of larvae have been described for many migratory fish species [3–5], providing insights into adult spawning behavior and quantification of adult reproductive success, which can play an important role in species conservation and river management [6].

Lake sturgeon (*Acipenser fulvescens*) are a potamodromous species native to the Great Lakes that use freshwater tributaries for the purpose of reproduction [7, 8]. Larval lake sturgeon behavior at the time of dispersal downstream has been described extensively over the duration of a single outmigration pulse and as a function of the longitudinal and cross-sectional profiles of the riverscape [8–12]. Lake sturgeon outmigration at the point of first drift is largely nocturnal with catch numbers peaking over several consecutive days [8, 12, 13] as larvae drift continuously after leaving spawning habitats until suitable downstream habitat is reached. As lake sturgeon larvae drift downstream, individuals tend to become nonrandomly distributed in number and body size across the river channel suggesting a degree of active swimming [8] and a longitudinal pattern of decreasing abundance from where spawning activity took place. These drifting patterns are presumably driven in part by predator avoidance, benthic stream habitat that promotes settlement, and river flow at the onset of drift [1, 12].

Field methods used to collect larval lake sturgeon drifting in the water column include rectangular/D-frame nets of varying sizes placed on the stream bottom or, in rarer instances, nets that are deployed to sample specific water depths [1, 6, 14–16]. Early studies involving lake sturgeon suggested that larvae drift or move primarily along the river bottom [2]. Based on these studies, the predominant deployment strategy for capturing drifting lake sturgeon larvae was to place nets near or on the benthos. However, relatively recent research by Caroffino [14] and others [1, 15] supported a different conclusion in systems including the Peshtigo River (Northeast Wisconsin, USA), Rupert River (Quebec, Canada), and the Des Prairies River (Quebec, Canada); the vertical distribution of larval lake sturgeon during initial drift is relatively uneven in the river water column. Building upon this observation, Tucker et al. [16] showed a degree of vertically distributed drifting behavior for larval lake sturgeon in a relatively larger system (Lower Fox River, Wisconsin) and immediately downstream from areas of adult spawning and egg deposition.

A more specific view of the literature paints an increasingly complex and often conflicting picture with respect to vertical distribution of drift in larval lake sturgeon and sturgeon species as a group. For example, Kempinger [17] showed that the degree of larval vertical distribution varied interannually in the Wolf River (Wisconsin), and D'Amours et al. [1] found that the degree of vertical distribution of drift in lake sturgeon was dependent on the river section that was sampled. In contrast, Braaten et al. [18] reported that ~98% of free drifting larval pallid sturgeons were found dispersing along the river bottom. While this work has been insightful, the vertical distribution of lake sturgeon larvae remains underappreciated relative to our understanding of the longitudinal and cross-sectional profiles of drifting behavior. Few studies have reported vertical patterns in drift over an entire season, especially during peak drift, and there is a paucity of research comparing rivers that differ in size. Studies examining differences in the vertical distribution of drifting larvae according to body size and differences in catch between traditional D-frame bottom sampling nets versus nets specifically designed to sample the entire water column in discrete sections are rare [14]. Furthermore, to the best of our knowledge, no study to date has statistically accounted for variables impacting the vertical distribution of larval lake sturgeon catch during drift that are autocorrelated in space and time.

The overall goal of this study was to examine the vertical distribution of larval lake sturgeon throughout a full season of larval drift in two separate river systems during a single field season. Our objective was to compare the vertical distribution patterns of larval drift between two Wisconsin rivers (Menominee and Oconto) that vary in morphology, size, water depth, and discharge using nets specifically designed to partition larval catch among discrete water depths. Our null hypothesis is that drifting lake sturgeon larvae collected during sampling were equally distributed within the water column from river bottom to surface. More specifically, drifting larval lake sturgeon would occupy all positions within the water column and that net type, location, and time of sampling would influence the size and number of larval lake sturgeons captured vertically in the water column within a short distance of upstream spawning site egg deposition and larval emergence. Additionally, we wanted to compare catch and the size of larvae at capture throughout the water column, specifically during peak larval drift events and between traditional (D-frame) and experimental vertical sampling nets. We further hypothesized that at least 50% of the larvae dispersing from upstream spawning sites, regardless of river depth, would drift over the D-frame net top and thus larval catch would be beyond the sampling capability of traditional, benthically oriented sampling gear.

2. Methods

2.1. Study Area and Experimental Design. This study was conducted in 2013 within the Lower Menominee and Oconto Rivers in Wisconsin (Figure 1). The Menominee River is 187 river kilometers long with a mean annual discharge of 89.9 m^3/sec (range 55.2–149.1 m^3/sec). Adult lake sturgeon that spawn in the Menominee River migrate upstream from Green Bay to a 3.7 km section of unrestricted river before encountering a hydroelectric dam. More than 200 adult lake sturgeon are known to spawn in this section of river on an annual basis [19]. The Oconto River, located 28 km south of where the Menominee River confluences with Green Bay (Figure 1), is smaller than the Menominee in length (91.6 km) and has a mean annual discharge of 16.8 m^3/sec (range 11.8–25.2 m^3/sec). Adult lake sturgeon have access to 24.1 km of river before migration is blocked by a hydroelectric facility. The number of annual spawning adults was last estimated to be around 25 individuals in 2005 [20].

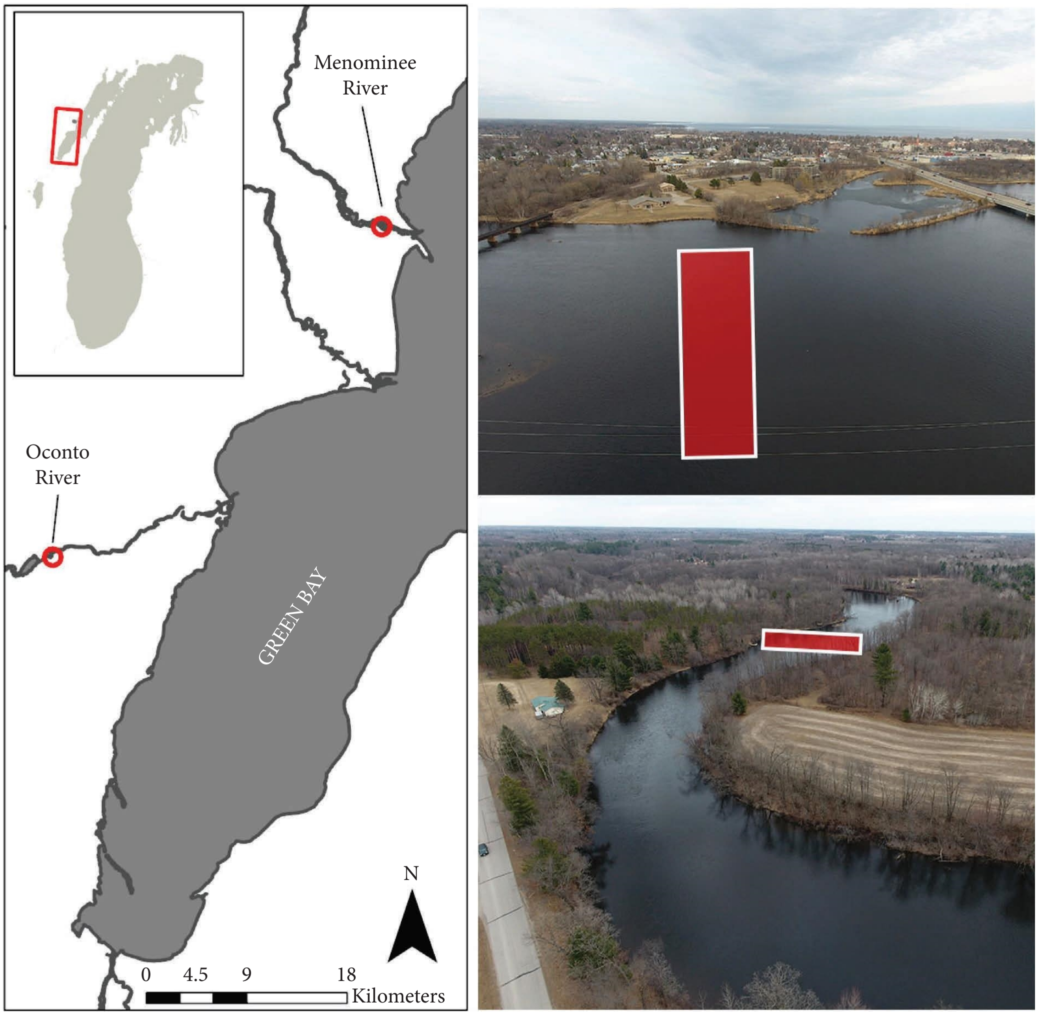

Figure 1: Map of the Menominee and Oconto Rivers (Wisconsin, USA) showing their proximity and confluence with Green Bay, Lake Michigan. Circles in the left panel show the approximate sampling locations for netting recently emerged and drifting larval lake sturgeon in the spring of 2013. The upper right panel shows the Menominee River sampling transect which is approximately 200 meters wide and where water depth required nets to be deployed by boat (left is upstream). The lower left panel is the Oconto River transect where the channel is approximately 25 meters wide with a wadable water depth (top of picture is downstream).

Sampling for drifting larvae consisted of bottom set, "half-moon shaped" D-frame drift nets that measured 77 cm across the base and 55 cm high at the opening, tapering to a 32 cm long detachable collection cup/bucket. The tapered net was made of knotless 1.6 mm nylon mesh and was 317.5 cm in length. D-frame nets have been used extensively for decades in the Great Lakes for collecting larval lake sturgeon [9, 10, 21, 22]. Four "vertical" nets were also designed and fabricated specially for this study. Vertical nets had a rectangular opening and measured 150 cm high × 76 cm wide and contained up to seven stackable rectangular sections with each section measuring 20 cm high × 76 cm wide that slid onto a main frame for a total of 140 cm of water sampling depth (Figure 2). Our vertical nets were similar in design to those used by Caroffino et al. [14] though our nets were longer and tapered more gradually. Each subsection of the vertical net was of 1.6 mm knotless nylon mesh sock that measured 240 cm in length with tapering to a detachable cup like the D-frame nets. Collection cups were "daisy-chained" together vertically to prevent entanglement when deployed in the water. The assembled net frame was reinforced by two backwards facing pieces of metal (or "skis") and a front mounted braided cable attached to two double-clawed, trap-net type anchors set in the river bottom. Vertical nets had a dry weight of 17.2 kg (~38 pounds).

2.2. Larval Lake Sturgeon Drift Sampling. Between May 20 and June 27 in 2013, sampling was conducted each night from 20:00 to 24:00 [8, 10] hours when the bulk of lake sturgeon larvae disperse (or "drift") downstream. Lawrence et al. [8] provide additional information on the seasonal chronology of drift netting, the selected sampling locations, and the cross-sectional profile of the sampling procedure used during the larval drift period in 2013. As a compliment to the Lawrence study, a minimum of two and maximum of four vertical distribution nets were set during the peak of

Figure 2: Description of the vertical nets used to sample drifting larval lake sturgeon. Panel (a) shows the 4 nets shortly after construction with backwards facing skis and bridles, (b) provides a side view of a single vertical net with each of the 7 collection bags consisting of knotless 1.6 mm·mesh nylon (317.5 cm in length), (c) is a front view of the a vertical net which is 150 cm tall × 76 cm wide and partitioned into 7 individual sections each 20 cm tall (net 1 is at the bottom and net 7 is at the top, and (d) provides a visual comparison vertical net against a traditional bottom sampling D-frame net.

larval drift, for 8 evenings within the entire drift period, either by boat or wading. Nets were deployed in a georeferenced and thus spatially consistent transect perpendicular to the water column approximately 800 m (Oconto) to 1250 m (Menominee) downstream from each river's hydroelectric facility. These upstream sampling locations were chosen for several important reasons. First, all lake sturgeon larvae emerging from spawning areas directly below the dam each night would likely pass the transect without settling and the position of larvae within the river cross section would be driven by the location of larval emergence upstream, and to a lesser extent, dominant river flows within this river reach. Second, transects minimized variation in cross sectional water depth, ranging from 0.45 to 0.74 m and 0.83–1.39 m in the Oconto and Menominee rivers, respectively, and thus reducing variation in the water depths sampled among the vertical and D-frame nets.

Vertical collection nets were equally spaced across both rivers but positioned towards the center of the river channel where larval drift was known to occur in high numbers based on the previous year of sampling [8]. Standard D-frame nets ($N = 6$ in the Oconto and $N = 10$ in the Menominee) were co-deployed within each transect to cover the entire river channel and were interspersed among the vertical nets. Net locations were georeferenced using GPS handheld units and deployed in approximately the same position each night along the river transect. Cod-end cups were emptied hourly during the 4-hour sampling window, and the number of larval lake sturgeon captured was recorded by net type, net location, and net height. Our collection permits dictated that larvae were to be released immediately after capture. Thus, the total length of each larval lake sturgeon captured was measured to the nearest 0.5 mm before being released downstream of the sampling transect. Most larvae (99%) were alive at the time of release. It is possible that eddy formation, clogging, back flow, or the physical presence of both net types at the sampled transect impacted the drift patterns of larval fish moving downstream. Any sort of modification to the current caused by our sampling was not evaluated other than observing that no differences in debris collection (or differences among other organisms in drift) were noticed, and based on visual observations, there was not a large or greatly significant eddy effect from either net type that would have invalidated their use for collecting lake sturgeon larvae.

Prior to drift sampling, an acoustic Doppler current profiler (ADCP) was used to produce a high-resolution, color-coded cross-sectional snapshot of instantaneous flow velocities, and the accompanying river channel benthic profile, as described by Lawrence et al. [8] for the Menominee and Oconto Rivers specifically, and further detailed in McElroy et al. [23], Lechner et al. [24], and Braaten et al. [18]. Briefly, transects of the river with the boat mounted ADCP (Menominee River) or hand towed ADCP (Oconto River) were conducted each evening immediately after nets were deployed and about 100 meters upstream from the sampling station. ADCP measurements were taken at 2000 hours before any larval fish were drifting out of the river (i.e., nightly emergence from upstream spawning sites happens later in the evening in both rivers around 2200 hours [8]). Net position was noted during each ADCP transect (plus the GPS location), and a measurement of water depth at the location of deployment was taken using a standard stadia rod. Instantaneous river velocities provided by the ADCP were used to estimate the average flow prior to larval sampling at every net position in the river channel each night to determine whether velocities varied among nets. This was accomplished by superimposing a scaled version of the D-frame and vertical distribution nets over the ADCP river flow profile. ADCP cell size depended on the river profile and depth (e.g., cell size was 0.86 m wide, 0.07 m deep on the Menominee River, and 0.47 m wide, 0.05 m deep for the Oconto River), but water velocities within all ADCP cells contained within superimposed net locations were averaged for an estimate of total water velocity per sample night observed at all net locations prior to larval sampling. Detailed cross-sectional profiles of each river with ADCP velocity estimates can be found in Lawrence et al. [8], but in general, water velocities ranged from 0.07 to 1.37 m/s across nets with velocity increasing towards the water surface as expected. For logistical reasons, repeated sampling with the ADCP was not performed at the end of larval sampling.

2.3. Data Preparation and Statistical Analysis. A generalized linear model was used to test whether drifting lake sturgeon larvae collected during sampling were equally distributed within the water column using the vertical net distribution data. Ideally, comparing larval densities (e.g., number of larvae sampled/volume of water) across vertical net sections each night would have been informative given the objectives of this study. However, flow meters were not available for every net, and ADCP measures of water velocity were only evaluated once per evening prior to larval sampling to measure velocity range across nets; therefore, extrapolating estimates of velocity to the entire sampling period to every net was not appropriate. The number of larvae captured (e.g., catch) and larval density estimates (see results) were also highly correlated ($P = 0.98$) suggesting that utilizing catch in the statistical models would not change our statistical results and interpretation. Thus, raw numbers of larval lake sturgeon captured (catch), and larval lake sturgeon size (mm), were modeled separately as dependent variables. Predictor variables included the day of sampling, vertical net section (#1–7), the interaction between these variables, and average water velocity for each vertical net section as estimated using the ADCP. All variables were treated as fixed effects.

The error structures of our response variables were modeled as both a negative binomial and Poisson distributions using log link functions for comparison, which is consistent with studies that model count data [8, 25, 26]. Parameters were estimated using Laplace likelihood approximation [27]. Models with different suites of variables were compared using model selection criteria (AIC, BIC) and assessed for overdispersion using the Pearson chi-square/degrees of freedom statistic for the conditional distribution. We present the models of best fit only. Given the differences in river depth and the fact that vertical net sections 5–7 were consistently above the water line in the Oconto River, except for 2 evenings of sampling, the vertical distribution data were analyzed separately for the Oconto and Menominee rivers.

We also compared the total number of larval lake sturgeon captured and mean total length (mm) of captured larvae between the standard D-frame nets and vertical distribution nets. These analyses were conducted separately for each river. Our comparisons were partitioned in several ways to describe vertical drifting behavior with respect to (1) larval catch over the entire sampling season and (2) catch during the peak of larval drift which we defined as the two days of peak numbers caught for both net types. Since the catch data were highly skewed towards zero for both rivers and did not follow normal distributions, we compared the total number of lake sturgeon larvae captured, mean number of lake sturgeon captured per night, and mean body length between the D-frame and vertical nets using simple non-parametric Mann–Whitney U tests.

We provide a visual comparison of the open-faced surface area of vertical net sections 1–3 (bottom most three sections) and the half-moon surface area of bottom set D-frame nets in Figure 2 (Panel D). Nets 1–3 within the vertical structure are 44% larger by surface area relative to the D-frame net opening, and the top of the D-frame net overlaps with a small proportion (36%) of vertical net 3. For the two days of peak larval drift in each system, we first conservatively calculated the number of drifting larvae captured in vertical net sections 4–7 that represented individuals "missed" entirely by the D-frame nets. We chose to allow vertical nets 1–3 represent the area comparable to the D-frame net given that we did not know exactly where in vertical net 3 larvae were sampled from (the middle or wings of the net). However, given the abundance of drifting larvae captured in net section 3 in both rivers, we also calculated the percentage of overlap between net section 3 and the D-frame nets (~36%), multiplied nightly catch estimates in vertical net section 3 by this 36% overlap, and summed the partitioned catch from net section 3 with catches from net sections 1 and 2 to get a less-conservative "D-frame equivalent" estimate of catch for comparisons. Since larval catch could not be partitioned in the same way by size, we compared the mean body size of larvae caught in the "missed" sections (net sections 4–7) to the mean body size of larvae captured near the riverbed in net sections 1–3.

3. Results

3.1. Larval Drift in the Menominee River. Vertical and D-frame nets were set over eight days on the Menominee River in 2013 with the bulk of larval drift happening between 5/28 and 6/13. A total of 1,101 larval lake sturgeons were captured in the four vertical nets across seven vertical net sections (Figure 3). Catch per effort (lake sturgeon larvae/hour) across all vertical net sections ranged from 0.27 to 3.1, and larval density averaged 0.098 m^3/hour during the first net set. Approximately, 70% of the larvae were collected in nets 3 and 4 that were positioned along the center and southern portion of the Menominee River channel (Figure 3). Among the four vertical nets, 51.0% ($N = 561$) of the captured larval lake sturgeon were collected in vertical net sections 1–3 that sampled the lower half of the water column, and 49.0% ($N = 540$) of the captured larval sturgeon were in vertical sections 4–7 closer to the surface waters. Approximately, 9.4% of all larvae captured in the vertical nets were collected drifting along the river bottom in vertical net section 1. During the two days of peak larval drift in the Menominee River occurring on drift nights 4 (5/30) and 5 (5/31), a total of 686 total larvae were captured in the vertical nets. Of those larvae captured, a conservative total of 367 individuals ($N = 142$ night 4 and $N = 225$ night 5) were observed in vertical net sections 4–7, which was beyond the vertical sampling capability of the D-frame nets. An additional 100 larvae would have been missed by the D-frame nets if we consider those partitioned within net section 3 during these two peak nights (a total of 167 additional larvae if we partition out net 3 for the entire sampling season or 48.5% of the total).

The model of best fit based on AIC in the Menominee River assumed an error structure with a Poisson distribution. Net section was a significant predictor of total larval catch ($F_{6,131} = 6.18$, $P = 0.001$) while accounting for nightly or seasonal trends in lake sturgeon drift which was not a significant factor in this case ($F_{1,158} = 0.01$, $P = 0.90$). Water velocity among vertical net sections ranged from 0.07 to 0.75 m/s, and total larval catch was not associated with variation in water velocity in our best fitting model ($F_{1,131} = 3.19$, $P = 0.07$). Based on pairwise comparisons in the differences of least square means for each net section, significantly higher catch was observed in net sections 2, 3, 4, and 5 with the highest predicted catch in section 3 (Figure 3). When comparing the two net types, a total of 1181 larval lake sturgeon were collected in the 10 D-frame nets on the Menominee River spanning the river channel, which was 80 larvae more than the 4 vertical nets set during the same time over the drift season (CPUE ranged from 0.5 to 5.5 larvae/net hour). The total catch per area (assuming 8 days and 4 hours per day for each type) was 369 larvae per sq *m* of D-frame net and 259 larvae per sq *m* of vertical net. Mean larval catch between the net types was significantly different ($P < 0.05$) in 5 of the 8 sampling nights with the 10 D-frame nets slightly outperforming the 4 vertical nets with respect to catch, especially during the peak days of larval drift. For this reason, the observed seasonal "peak" in larval drift and seasonal profiles in drift activity were different depending on the net type used (Figure 4).

Larval lake sturgeon captured in the Menominee River vertical nets had a mean length of 19.4 mm (range 12–24 mm) with 21.7% of drifting larvae measuring greater than 20 mm. Mean larval length generally increased as the season progressed suggesting that drifting larvae originated from a single spawning event (i.e., larvae were not a mixture of sizes and developmental stages from multiple spawning episodes). We failed to reject the null hypothesis that larval length was different among vertical net sections ($F_{6,1061} = 0.13$, $P = 0.99$; Figure 5). Likewise, the proportion of larvae captured in net sections 4–7, or those likely "missed" by the D-Frame nets, was less than 1% larger in total length on average than those at the river bottom. Notably, lake sturgeon larvae captured in the D-frame nets, and those which came from a broader cross section of the river (i.e., D-frame nets were deployed equally across the entire river channel), measured 19.60 mm in total average length but were not statistically different in total length from larvae captured in the vertical nets when larvae among net sections were combined.

3.2. Larval Drift in the Oconto River. The Oconto River was sampled for a total of 8 days in 2013 from 5/20 through 5/27 using both net types. Only four of the seven vertical net sections were consistently under the waterline, so results are presented for vertical net sections 1–4. A total of 250 lake sturgeon larvae were captured over the season in the vertical nets, which encompassed one peak of downstream dispersal originating from upstream spawning locations and one spawning event. Approximately, half of the lake sturgeon larvae sampled were collected in the center of the stream channel in vertical net 3 (Figure 6). Catch per effort ranged from 0.19 to 1.60 lake sturgeon larvae per hour on average across all 4 net sections, and larval density during the first hour of collection ranged from 0.009 to 0.303 m^3/hour.

Despite the comparatively shallow water depths in the Oconto River, catch remained highest in net section 3 among the vertical net structures. Approximately, 76% of larvae were observed in net sections 2-3 (middle of the water column), and equal proportions of larvae were captured in section 1 (12% bottom) and section 4 (12% top). During the two days of peak larval drift in the Oconto River (Day 5 (5/24) and Day 6 (5/25)), vertical net section 4 captured 11 and 2 total larvae, respectively, which conservatively represent drift completely outside of the vertical sampling capability of the D-frame net. An additional 29 larvae would have been missed by the D-frame nets if we consider those partitioned within net section 3 during these two peak nights, and 106 additional larvae would have been missed during the entire sampling season is considered (i.e., 46% of the total catch would have drifted above the standard D-Frame drift nets if set in place of the vertical structures).

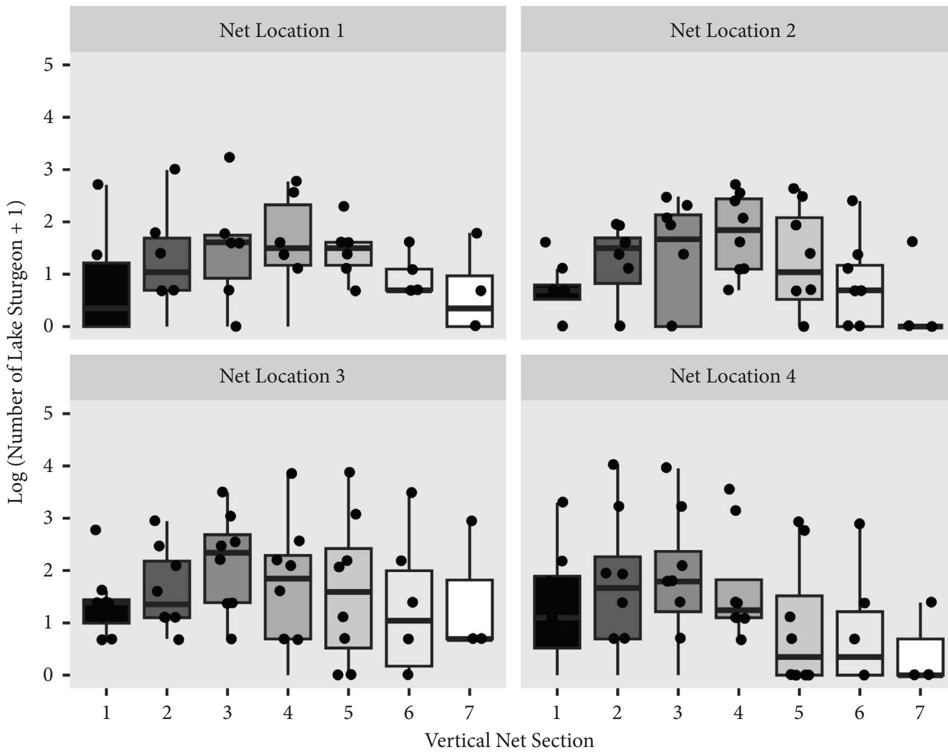

FIGURE 3: The number of larval lake sturgeon observed while drifting from upstream spawning sites in the Menominee River during the spring of 2013. Box plots illustrate the median and interquartile ranges of the data, while the jittered dots show the observed larval lake sturgeon catch within the 4 vertical nets set in 4 different locations. The y-axis is presented in the log scale adhering to the statistical analysis used and the non-normal (Poisson) distribution of catch. Larvae were collected using 4 nets specifically designed to sample the entire water column. Nets were deployed across the rivers' cross section, and nets 2 and 3 sampled the center of the river channel. Section 1 was the net bottom, and section 7 was at the water surface.

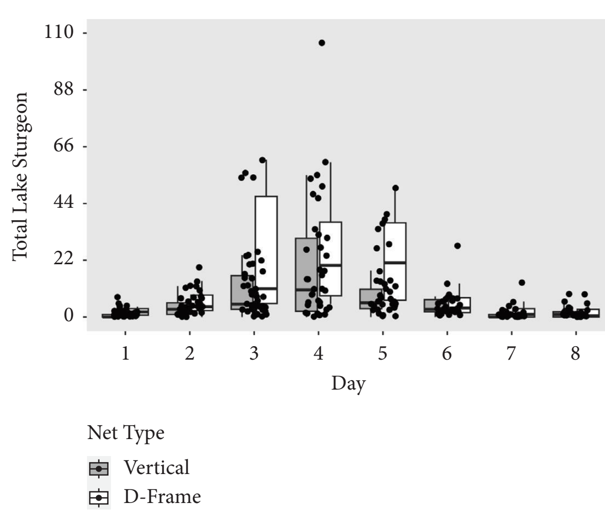

FIGURE 4: Number of drifting larval lake sturgeon collected in the Menominee River in 2013 by net type. Box plots illustrate the median and interquartile ranges of the data, while the jittered grey dots show the observed larval lake sturgeon catch within each net type. Vertical nets were designed to partition drift among 7 different net sections each sampled according to water depth. D-frame nets represented "traditional" sampling gear designed to sample near the river bottom. Both net types were interspersed across the rivers' cross section and were codeployed. Days 3, 4, and 5 were peak drift and occurred from May 30 to June 1.

The model of best fit for the Oconto River based on AIC assumed a negative binomial error distribution for catch but was not significantly different from the Poisson model. Net section was a significant predictor of total larval catch ($F_{3,35} = 9.19$, $P = 0.0001$) as similarly observed in the Menominee River. Significantly more larvae were collected

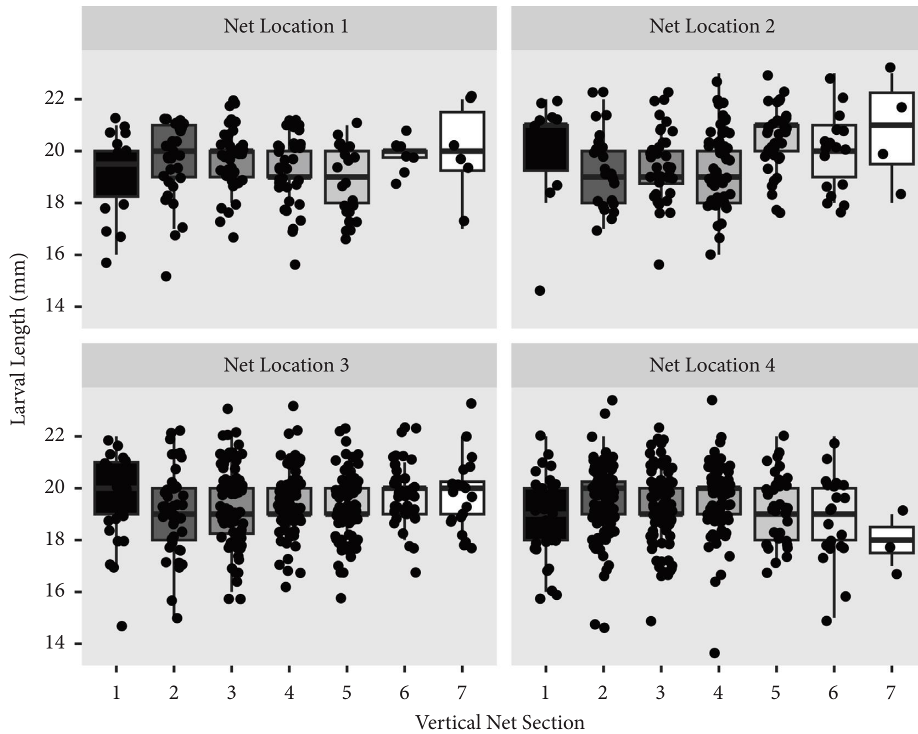

FIGURE 5: Total length of larval lake sturgeon captured while drifting from upstream spawning sites in the Menominee River during the spring of 2013. Box plots illustrate the median and interquartile ranges with all length data points within each net type presented as jittered grey dots. Larvae were measured to the nearest mm using a standard ruler in the field (catch and release) and as a function of the 4 vertical nets specifically designed to sample the entire water column (Figure 2). Nets were deployed across the rivers' cross section, and nets 2 and 3 sampled the center of the river channel. Section 1 was the net bottom, and section 7 was at the water surface.

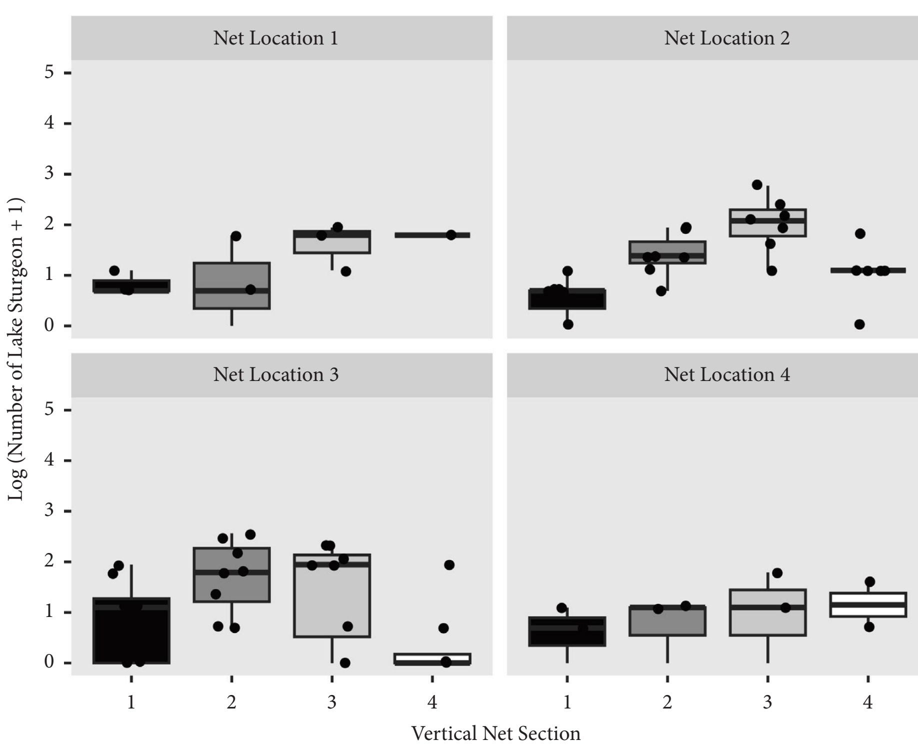

FIGURE 6: The number of larval lake sturgeon captured while drifting from upstream spawning sites in the Oconto River during the spring of 2013. Box plots illustrate the median and interquartile ranges with all catch data within the 4 vertical nets set in 4 different locations presented as jittered dots. The y-axis is presented in the log scale adhering to the statistical analysis used and the non-normal distribution of catch. Larvae were collected using 4 nets specifically designed to sample the entire water column (Figure 2). Nets were deployed equally across the rivers' cross section with nets 2 and 3 sampled the center of the river channel. Net section 1 was the net bottom, and net section 4 was at the water surface.

in net sections 2 and 3 based on pairwise least square mean comparison, supporting the descriptive statistics previously reported. Water velocity was not predictive of catch ($F_{1,35} = 0.06$, $P = 0.812$) as seen in the Menominee River, but there was a strong influence of sampling day on the Oconto River ($F_{7,35} = 3.85$, $P = 0.003$) with generally fewer larvae caught overtime after peak drift was observed.

In contrast to the Menominee River, total catch across the six adjacent and codeployed D-frame nets was 135 larvae, or 85% fewer larvae sampled relative to the vertical nets fishing at the same time. However, total catch as a function of the net area was 70.31 larvae per sq *m* of D-frame net and 58.82 larvae per sq *m* of vertical net. While the Oconto River vertical nets outperformed the D-frame nets nearly every night with respect to total catch for the entire season, no significant differences were found when summing all larvae captured by net type and comparing between individual sampling nights ($P > 0.05$). Plotting raw catch overtime, we see that the seasonal profile of larval drift activity was less defined using D-frame nets (i.e., peak drift was less apparent) and the indication of peak larval drift for the season lagged by several days (Figure 7).

Larvae sampled by the 4 vertical nets had an average total body length of 20.4 mm (±0.09 mm) with 58% measuring over 20 mm (Figure 8). Larval size increased from the river bottom to the surface, but the net section was not a significant predictor of larval size ($F_{3,214} = 0.05$, $P = 0.99$). However, significant differences in mean body length between net types were found when examining drift by night. For example, larvae captured in vertical nets were larger on sampling night 6 when compared to D-frame caught larvae. The 78 larvae captured in vertical net section 4, the uppermost section near the water surface outside the sampling range of the D-frame nets, had an average length of 21.0 mm and were 3.5% longer on average. Notably, three larvae captured in net section 6 on the Oconto River, when water levels had risen substantially a few times during the season so nets 5 and 6 were fishing (data not shown), were the largest recorded among all net types across both rivers in this study (mean body length = 22.3 mm). While the Oconto River larvae were larger on average at the time of drift (mean body length = 20.1 mm) than the Menominee River larvae (mean body length = 19.6) and larvae captured in the vertical nets (mean body length = 20.4 mm) were slightly larger in size than D-frame caught larvae (mean body length = 20.2 mm), these differences were not statistically significant in most of our comparisons ($P > 0.05$).

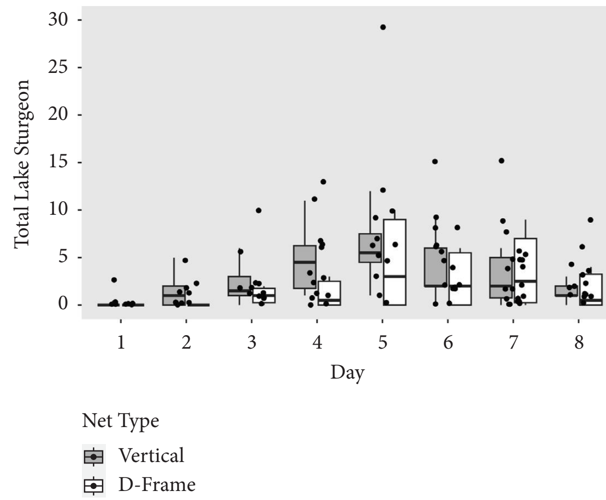

Figure 7: Number of drifting larval lake sturgeon collected during sampling by net type in the Oconto River in 2013. Box plots illustrate the median and interquartile ranges with jittered grey dots showing the observed larval lake sturgeon catch within each net type. Vertical nets were designed to sample different sections of the vertical water column (Figure 2). D-frame nets represent "traditional" sampling gear designed to sample at the river bottom. Both net types were interspersed across the cross section of the river. Days 3, 4, and 5 were peak drift and occurred from May 24 to May 26, 2013.

4. Discussion

Knowledge of the larval drifting behavior of riverine fishes is essential for understanding factors impacting recruitment and for accurately quantifying adult reproductive success. While some work has been aimed at assessing the vertical drifting patterns of larval fishes [28, 29] including sturgeon [14–16, 30], limited comparisons have been conducted across river systems and net types within the same sampling season. Results from this study add to a growing body of evidence that larval lake sturgeon drift is not uniform in space or time, as stated for other river systems where lake sturgeons spawn [9, 10, 14, 15]. Larval lake sturgeon in the Oconto and Menominee Rivers dispersed downstream while occupying all vertical portions of the water column that were sampled, regardless of the total water depth and the distance downstream of sampling, similar to findings reported for larval lake sturgeon by Caroffino et al. [14] in the nearby Peshtigo River, Wisconsin, and Verdon et al. [15] in Rupert River, Canada. Our results are also similar to those reported by Verdon et al. [15] for larval lake sturgeon in that the degree of surface vs. benthic drift orientation may change over space and time and that at least some larval drift at the water surface should be expected regardless of the conditions (i.e., 4.7% of all larvae captured in our study were sampled from the uppermost vertical net section closest to the water surface in both rivers).

Based on the results of this study, some lake sturgeon larvae will drift along the river bottom regardless of river depth. However, only 9.9% of all larvae captured in our vertical nets during the drift period were collected in vertical net section 1 along the riverbed, indicating that dispersing larvae in these Wisconsin systems are not primarily benthic as reported in other larval sturgeon studies [31]. Our results are generally concordant with Caroffino et al. [14] where the highest abundance of larval catch was in the net sections that sampled the water column approximately 0.20–1.00 m from the riverbed (~78.8% in our study). Notably, the abundance of larvae captured in section 3 of the vertical nets demonstrates that researchers do not necessarily need to sample the entire water column, but by increasing the vertical sampling area by even 0.15 m in the water column can substantially

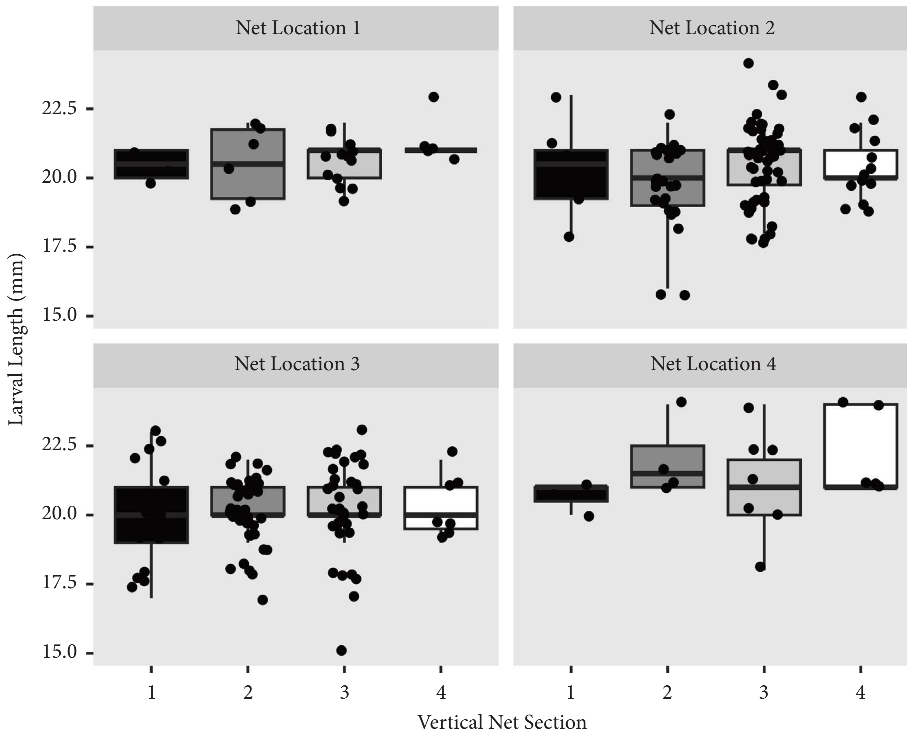

FIGURE 8: Total length of larval lake sturgeon captured in vertical net sections 1–4 for the four vertical nets deployed during the drift period in the Oconto River in 2013. Box plots illustrate the median and interquartile ranges with larval length data points within each net type presented as jittered grey dots. Larvae were measured to the nearest mm using a standard ruler in the field (catch and release). Nets were deployed in equal spacing across the cross section of the river with nets 2 and 3 sampling the center of the river channel. Net section 1 was the net bottom, and net section 4 was at the water surface.

increase catch. Given that velocity in rivers generally peaks midcolumn or increases from the riverbed to the water surface [32] and drift is assumed to be primarily passive for most sturgeon at this early life stage [29, 30], river velocity may be a dominant factor in propelling drifting larvae into vertical positions within the water column. One limitation of our study is that velocities were not measured across nets throughout the sampling period but just prior to larval sampling. Therefore, velocity ranges reported in this study represent those that larval lake sturgeon may occupy during drift in rivers sharing the general qualities of the Menominee and Oconto Rivers.

In both the Menominee and Oconto Rivers, drifting larvae were distributed horizontally as larvae were consistently captured across the river channel in our study and in previous work by Lawrence et al. [8], using D-Frame drift nets. Although net position across the river was statistically negligible in terms of explaining overall catch, higher abundances of drifting larvae were captured in the center of the river channels in both rivers, which could be driven by increasing water velocity in the thalweg. These results are consistent with trends reported by Pollock et al. [13] but contrast with results from Tucker et al. [16] in the nearby Lower Fox River, Wisconsin, where drifting lake sturgeons were never captured in the centermost portion of the river channel. Discrepancies between results in our study and other systems such as the Lower Fox River could be due to a variety of factors including the location of upstream spawning activity (Fox River adult lake sturgeon spawn predominately on the east shore) or differences in the cross-sectional velocity profiles among river systems. Marotz and Lorang [33] discuss how upstream vertical and lateral river velocity gradients can distribute passively drifting larval sturgeon widely across channels downstream of spawning areas (e.g., drift dispersion hypothesis), thus allowing drifting larvae to be sampled across the whole river channel. Although the Oconto and Menominee Rivers differ considerably in size and overall discharge, similar patterns of larval distributions across the river channels were observed and velocities recorded at each net prior to larval sampling were generally not a significant predictor of catch abundances providing potential support that larvae have been distributed widely across the channel by upstream velocities within a relatively short distance from areas of egg deposition. Not taking an additional ADCP measurement after larval sampling when back-pressure may have been detectible and the inability to record velocity at each net during the larval sampling period limits our ability to determine if any modification was made to the current by the vertical nets. Future work would benefit from evaluating the influence vertical nets have on current patterns and potentially eddy formations and determining what effect this may have on larval lake sturgeon behavior and catch numbers.

Body size plays an important role for larval fish as larger individuals are believed to be more reactive, have better swimming abilities, and are less susceptible to starvation

[34–36]. In our study, larval body sizes were comparable to larval lake sturgeon sizes reported in other systems at the time of drift [9, 10, 16, 37]. However, results from our study remain inconclusive given the lack of statistical differences in body size among net sections and between the vertical and D-frame nets that were sampling different portions of the water column. It is possible that a size-based vertical drift pattern among larvae exists, but there were no statistical differences in mean body size among sections for larvae captured in this study. Empirical work assessing how factors such as body size may be driving horizontal [9] and vertical movement patterns [14] during larval drift and what role this has for survival have been limited for wild sturgeon, aside from controlled laboratory studies. While the lack of knowledge during this critical time-period is most likely due to the difficulties in monitoring and tracking larval sturgeon given the high mortality rates observed from predation [11], and the inability to utilize biotelemetry and hydroacoustic technology on fish of that small of body size [30], our research suggests that field-based studies seeking to quantify size-based behaviors and survival should be encouraged.

Traditional D-frame nets placed on or near the riverbed have been utilized in other studies for capturing larval lake sturgeon as they drift downstream as these nets are assumed to yield the highest capture rate and capture a representative sample of the overall larval production during the drift period [10, 14, 38]. During our study, total catch in the D-frame nets was higher than catch in the vertical nets in the Menominee River; however, there were 10 D-frame nets deployed and therefore greater sampling area as opposed to only 4 vertical nets in most situations indicating higher effort needed when using D-frame nets. Notably, the conservative estimates of catch for vertical net sections 4–7 (representing the area outside the sampling capability of the D-frame nets) captured nearly the same number of larvae on the Menominee River as vertical net sections 1–3, indicating that larval catch abundances could be nearly double by doubling the vertical sampling area. These differences are further exacerbated when comparing the "D-frame equivalent" estimate of catch (partitioning out vertical net section 3 by overlapping area with the D-frame net) to larvae that would have been missed by the D-frame nets. However, this strategy may not be applicable to other sampling years or to other rivers as shown by our results on the Oconto River where vertical net section 4 only caught 30 larvae total (~7.8% of the total river catch). Similarly, Tucker et al. [16] found no increases in catch when utilizing vertical nets indicating that results can vary across rivers.

Factors that may cause variation across rivers and should be considered in sampling designs include water depth and sampling proximity to spawning areas. Based on their own assessments, Verdon et al. [15] propose that larval drift sampling cover the complete vertical water column and river width or researchers should utilize a sampling strategy covering at least 1% of the total river flow in larger rivers. Unless specific limitations exist, we further suggest that nets which vertically partition catch should be used in rivers where water depth is less than 1.5 meters so that most of the water column can be sampled rather than utilizing traditional D-frame nets where only a portion of the water column is sampled. Additionally, sampling proximity to spawning locations should be considered given that downstream dispersal can vary based on body size [9], and capture number can vary based on net location [1, 9]. Focusing efforts on capturing a greater number of larvae using techniques such as sampling closer or further away from spawning areas (within 150 m as done by Kempinger [17]; within 800–900 m as performed in this study and by LaHaye et al. [37]; or several km downstream) may allow for vertical drift patterns to be more discernible within the cohort and avoid the assumption that all larvae captured at one site are genetically and behaviorally representative of the entire annual drifting cohort.

Regardless of sampling gear utilized during the drift period, accurate assessments of drifting larval sturgeon abundance within a sampling season can be obtained when gear limitations are considered [9, 16, 22]. Net types and deployment strategies should be tailored to the dominant research question. One concern from the results of our study is whether the vertical distributions of larvae have the potential to bias genetic-based adult spawner estimates. Current genetic techniques use multilocus genotype data from captured larval lake sturgeon for estimating the effective number of breeders and adult reproductive success during the spawning season [22, 38–40]. These techniques assume that family groups have equal catch probabilities and are equally represented in the larval samples that are genotyped. However, the proportional contributions of drifting larvae from different female parents have been shown to substantially vary between sampling nights based on drifting larval lake sturgeon captured in traditional D-frame nets [41]. Additionally, Hunter et al. [22] found that estimated adult reproductive success varied with sample size and that genotyping more larvae increased the effective number of breeders indicating that samples from the traditional D-frame nets may not be capturing all family groups that are contributing offspring. Results such as these are important when considering lake sturgeon conservation programs where a cohort of benthic drifters (often more genetically diverse than larvae produced from direct gamete takes and artificially crossed), [42] are captured and stocked to supplement adult populations; these programs are common practice in the Great Lakes region and may be unintentionally selecting certain family groups based on drift behavior.

Future work would benefit from not only assessing the vertical distribution of drifting lake sturgeon but also assessing whether larvae from different family groups utilize differential portions of the water column during the drift period. Empirical work such as this will help determine whether the "missed" larvae observed in our study with the D-frame nets are indicative of a potential bias in adult reproductive success estimates. Additionally, this work is needed across river systems as the proportions of "missed" larvae could increase as rivers get larger and deeper as shown in our study with the larvae missed on the Oconto River being smaller in comparison to the larvae missed on the much larger, deeper Menominee River. Accurately assessing coarse relative larval drift abundances and estimating adult reproductive success are critical for the recovery and restoration of lake sturgeon populations within the Great Lakes region.

Data Availability

The raw capture data and R code used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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