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ARTICLE

Movements, habitat use, and entrainment of stocked juvenile lake sturgeon in a hydroelectric reservoir system

Jonathan Hegna, Kim Scribner, and Edward Baker

Abstract: Identifying movement and habitat use patterns is essential for fish passage efforts and the conservation of threatened species. We used acoustic telemetry to track the movements of 44 juvenile lake sturgeon (*Acipenser fulvescens*) throughout Kleber Reservoir in northern Michigan. On average, lake sturgeon moved 502 m between telemetry positions, with age-2 lake sturgeon moving longer distances than age-1 lake sturgeon. Areas with high numbers of lake sturgeon detections were clustered near the forebay, while zones with low numbers of detections were clustered toward the head of the reservoir. Analyses showed that 66.4% of the variance in habitat use could be explained by physical habitat features. Reservoir areas with ample deepwater habitat, fine soft substrates, and limited macrophyte vegetation were the most frequently occupied and, thus, may provide suitable habitat conditions to support juvenile lake sturgeon. We observed that 54.4% of the age-1 and 52.8% of the age-2 lake sturgeon stocked into Kleber Reservoir were entrained. Reservoir size, morphology, and the location of suitable habitat in relation to hydroelectric infrastructure may be key factors that affect entrainment rates.

Résumé : La détermination des motifs de déplacement et d'utilisation de l'habitat est un aspect essentiel des efforts visant le passage de poissons et la conservation d'espèces menacées. Nous avons utilisé la télémétrie acoustique pour suivre les déplacements de 44 esturgeons jaunes (*Acipenser fulvescens*) juvéniles à la grandeur du réservoir Kleber, dans le nord du Michigan. Les esturgeons jaunes parcouraient en moyenne 502 m entre les points de détection télémétrique, les poissons de deux ans se déplaçant sur de plus longues distances que les poissons d'un an. Les secteurs où les plus grands nombres d'esturgeons jaunes étaient détectés se concentraient près du bassin d'admission, alors que les secteurs où les détections étaient moins nombreuses se concentraient vers l'amont du réservoir. Des analyses démontrent que 66,4 % de la variance de l'utilisation de l'habitat peut être expliquée par des caractéristiques physiques de l'habitat. Les secteurs du réservoir caractérisés par d'amples habitats d'eau profonde, des substrats meubles et fins et une végétation de macrophytes restreinte étaient plus fréquemment occupés et offriraient donc possiblement des conditions d'habitat convenables aux esturgeons jaunes juvéniles. Nous notons que 54,4 % des esturgeons jaunes d'un an et 52,8 % des individus de deux ans ensemencés dans le réservoir Kleber ont été entraînés vers l'aval. La taille du réservoir, sa morphologie et l'emplacement d'habitats convenables par rapport aux infrastructures hydroélectriques pourraient être d'importants facteurs influençant les taux d'entraînement. [Traduit par la Rédaction]

Introduction

Over the past two centuries there has been a marked increase in the number of hydroelectric dams and in the amount of fragmented reservoir habitat. Hydroelectric power development continues at a rapid pace globally, with 3700 hydroelectric dams with a capacity of 1 MW or more planned or under construction as of March 2014 (Zarfl et al. 2015). It is estimated that globally there are over 45 000 large dams (at least 15 m high) and at least 1 000 000 smaller dams that have altered and fragmented river systems that support important fisheries resources (Dynesius and Nilsson 1994; Allan and Castillo 2007; Wang et al. 2011). Within the United States alone there are 45 178 dams that are at least 7.62 m high that impact fish habitat and movements (USACE 2018).

Lake sturgeon (*Acipenser fulvescens*) is a potamodromous, fluvial-dependent species of regulatory and conservation concern that is considered threatened in most states and provinces (Latta 2005; Peterson et al. 2007; Bruch et al. 2016). The historical decline of lake sturgeon populations in the Great Lakes region involved multiple contributing factors, including the expansive development of hydroelectric infrastructure in the late 1800s and early 1900s. In the early 1800s, lake sturgeon were considered a nuisance fish species because they were often caught in and damaged nets (Harkness and Dymond 1961). People also mistakenly believed that lake sturgeon preyed upon more valuable commercial species. Consequently, lake sturgeon were deliberately targeted and removed from many locations (Harkness and Dymond 1961). After around 1850, a lucrative commercial fishery developed for lake sturgeon flesh and caviar (Peterson et al. 2007; Auer and Dempsey 2013). By the early 1900s, most lake sturgeon populations began to decline because of overfishing, as well as habitat degradation, pollution, and fragmentation due to hydroelectric dams (Harkness and Dymond 1961; Brousseau 1987; Hay-Chmielewski and Whelan 1997). For instance, in Lake Michigan the commercial lake sturgeon fishery was closed in 1929 after the commercial catch declined to only one metric ton. Today lake sturgeon are estimated to be at only 1% of their historical abundance (Tody 1974; Haxton et al. 2014), and hydroelectric dams are thought to be one of the major factors limiting the restoration of lake sturgeon in the Great Lakes (Ferguson and Duckworth 1997; Peterson et al. 2007; Coscarelli et al. 2011).

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Recently, interest in using fish passage engineering to reintroduce lake sturgeon above dams or to reconnect fragmented populations disconnected by dams has increased (Coscarelli et al. 2011; Jager et al. 2016; Boothroyd et al. 2018; Koenigs et al. 2019). While information is available on the movement and habitat use characteristics of juvenile sturgeon throughout the species range (Holtgren and Auer 2004; Smith and King 2005; Benson et al. 2005; Trested et al. 2011; Boase et al. 2014) and in reservoirs (McDougall et al. 2013, 2014*a*, 2014*b*; Hrenchuk et al. 2017), less is known about small reservoirs in the Great Lakes. There are approximately 3116 dams in Minnesota, Michigan, and Wisconsin alone that create barriers and reservoir habitat, and 78% of them are less than 7.62 m in height (USACE 2018). Identifying movement patterns and habitat use characteristics is considered vital to lake sturgeon restoration efforts and planning (Holey et al. 2000; Coscarelli et al. 2011). Previous research has shown that juvenile sturgeon use fine sediments and deepwater habitat in rivers and lakes (Benson et al. 2005; Barth et al. 2011; Boase et al. 2014), but other researchers have found that juveniles will use larger substrates (Hrenchuk et al. 2017) or a combination of shallow and deepwater habitats (Holtgren and Auer 2004; Smith and King 2005). Information on entrainment rates of young juveniles and whether juvenile lake sturgeon will use habitat in the vicinity of hydroelectric dams is sparse (Coscarelli et al. 2011; McDougall et al. 2013, 2014*a*). Also, reservoirs contain different types and compositions of habitats, and there is little guidance available to managers concerning how to determine the quality of a reservoir for lake sturgeon reintroduction efforts (McDougall et al. 2017). Young juvenile lake sturgeon are a demographic group of keen interest because they are prone to predation and usually migrate downstream into larger river and lake systems that often have hydroelectric infrastructure (Kynard and Horgan 2001; Pollock et al. 2015; Jager et al. 2016; Pracheil et al. 2016). In addition, in many lake sturgeon populations, the recruitment of juveniles is a major limiting factor to population growth, persistence, and recovery (Coscarelli et al. 2011; Pollock et al. 2015).

To fill these knowledge gaps and to aid sturgeon passage and recovery initiatives, we designed a project to evaluate movements and habitat use characteristics of age-1 and age-2 lake sturgeon stocked into a small hydroelectric reservoir system in northern Michigan. Our specific objectives were to quantify (*i*) movement characteristics, (*ii*) spatial habitat use patterns, (*iii*) environmental factors that influence habitat use, and (*iv*) entrainment characteristics.

Methodology

Study area

This study was conducted on the upper Black River located in Cheboygan County in northern Michigan (Fig. 1). The upper Black River is the largest tributary of Black Lake, and it comprises the spawning grounds for the Black Lake lake sturgeon population (Pledger et al. 2013). The upper Black River is impounded by two hydroelectric dams. Kleber Dam is located 11 km upstream from the river mouth. The dam was built in 1949 with a mean head of 13.4 m, and it forms a reservoir with 370 hectare-metres (1 hectare-metre = 10 000 m^3) of storage capacity. Kleber Dam has two vertical shaft Kaplan turbines, a generating capacity of 1200 kW, and a bottom withdrawal spillway. Kleber Dam is a barrier to upstream movement, limiting access to upstream aquatic habitat formerly suitable for spawning and rearing. Tower Dam is located 5 km upstream of Kleber Dam. Tower Dam was built in 1917, has a mean head of 6.1 m, and forms a small reservoir with 76 hectare-metres of storage capacity. The dam has two vertical shaft Leffel type-z turbine systems, a generating capacity of 560 kW, and a bottom withdrawal spillway.

Transmitter implantation

We used juvenile salmonid acoustic telemetry system (JSATS) transmitters (Lotek Inc., Newmarket, Ontario; transmitter model: L-AMT-5.1B) to tag and track age-1 and age-2 lake sturgeon. We specifically used age-1 and age-2 lake sturgeon because juvenile recruitment continues to be a major problem for a number of populations in the Great Lakes, and there is uncertainty regarding their habitat requirements, movements, entrainment susceptibility, and reservoir residency characteristics (Coscarelli et al. 2011; McDougall et al. 2013, 2014*a*). The dimensions of the transmitters were 5 mm × 7 mm × 13 mm, and they weighed 0.6 g in air. All acoustic transmitters were programmed to have a 10 s transmission rate, with an estimated life expectancy of 180 days. In addition, a 23 mm × 3.65 mm half-duplex PIT-tag (Oregon RFID, Portland, Oregon) was implanted into each lake sturgeon. The transmitters were surgically implanted by performing a standard laparotomy. Before surgery, all sturgeon were anesthetized for approximately 5 min in an anesthetic bath with 125 $mg{\cdot}L^{-1}$ of tricaine methanesulfonate (MS-222; Crossman et al. 2013; Summerfelt and Smith, 1990). Once a sturgeon became fully sedated, weight (g) and total length (mm) measurements were taken. The sturgeon was then placed ventral side up on the operating table and an oxygenated maintenance dose of 100 $mg{\cdot}L^{-1}$ of MS-222 was irrigated across the gills to ensure proper sedation throughout the entire operation. The anesthetic maintenance dose was not recirculated to ensure the efficacy of the anesthetic and to prevent infection. A 12–15 mm incision was made on the ventral surface of the lake sturgeon anterior to the pelvic girdle, which allowed the transmitter to be inserted into the body cavity. The incisions were closed with one to two simple-interrupted sutures made with 4–0 absorbable, monofilament suture material. Some incisions were also closed with surgical adhesive (Vetbond, 3M), as part of a separate experimental tagging study. All juvenile lake sturgeon were held for at least 4 weeks of postoperative observation to ensure proper healing, and all sutures were removed prior to release.

In 2015, we surgically implanted transmitters into 49 age-1 and 50 age-2 lake sturgeon. In 2016, we implanted transmitters into 61 age-1 and 56 age-2 lake sturgeon. Age-1 lake sturgeon had a mean mass of 135 g (SD = 31.6 g) and a mean total length (TL) of 348 mm (SD = 40.0 mm). Age-2 lake sturgeon had a mean mass of 479 g (SD = 87.8 g) and a mean TL of 486 mm (SD = 35.3 mm). All lake sturgeon were produced and reared at the Black River Sturgeon Rearing Facility between April and September. The juvenile lake sturgeon were then over-wintered at the Wolf Lake State Fish Hatchery. All surgical procedures and animal husbandry practices were reviewed and approved by Michigan State University's animal care program (IACUC No. 03/14-041-00) in accordance with the Guide for the Care and Use of Laboratory Animals (NAS 2011).

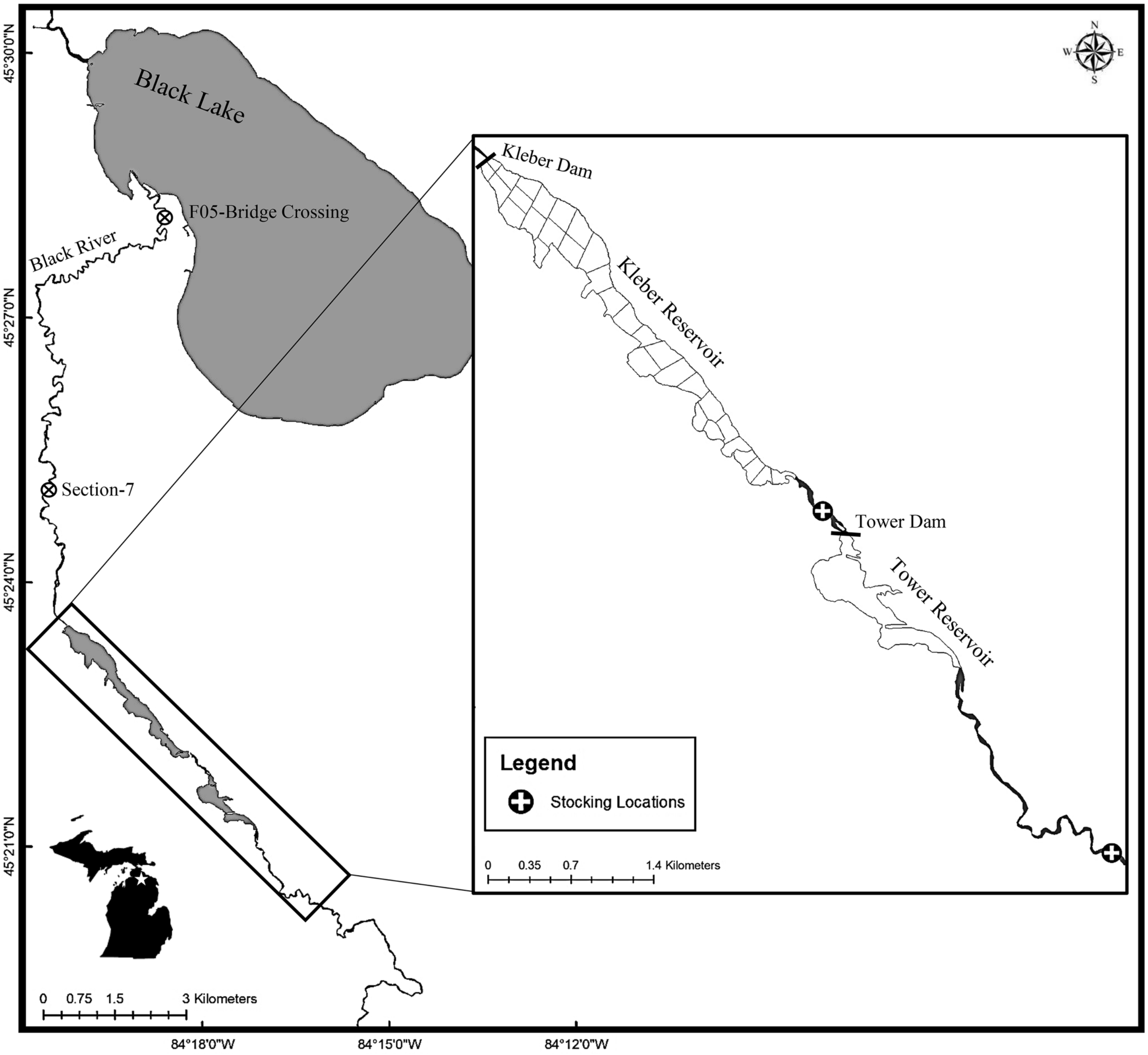
Experimental release of lake sturgeon

In 2015 and 2016, the juvenile lake sturgeon were released in small groups of 10–12 into either Tower or Kleber reservoirs between mid-July and late August (Fig. 1). A total of 53 age-1 and 53 age-2 lake sturgeon were released into Tower Reservoir ~4.7 km upstream of Tower Dam. A total of 57 age-1 and 53 age-2 lake sturgeon were released into Kleber Reservoir ~4.4 km upstream of Kleber Dam. Small release groups were used to avoid possible negative effects associated with high stocking densities, which could alter behavior. Releases at stocking locations were separated by 3–7 days.

Active tracking

The active tracking survey was conducted between mid-July and mid-September of each project year in Kleber Reservoir. The survey time period was based around the operating time frame of our seasonal hatchery on the Black River. While lake sturgeon were stocked upstream of Tower Reservoir, no survey was conducted on Tower Reservoir. Fifteen lake sturgeon from Tower Reservoir

Fig. 1. Map of Black Lake and the upper Black River system located in Cheboygan County, Michigan. The inset map highlights Kleber Dam, Kleber Reservoir, Tower Dam, and Tower Reservoir, along with the lake sturgeon stocking locations used for the research project. In the inset map, Kleber Reservoir is divided into the 32 census zones that were surveyed during the project. Radio frequency identification (RFID) antennas were located at the F05-bridge crossing, section-7, 300 m below Kleber Dam, and at the Kleber Dam powerhouse. Map data are from the United States Geological Survey National Hydrography Dataset.



did succeed in passing Tower Dam, and they were detected and tracked within Kleber Reservoir as part of the survey.

To survey Kleber Reservoir, we divided the reservoir into 32 zones that had midpoints spaced ~100 m apart from midpoints of adjacent zones (Fig. 1). The size, shape, and location of the different zones were based on the morphology of the reservoir and the specifications of the acoustic telemetry system. Each zone was then surveyed from a boat at its central observation point with a JSATS compatible WHS4250 hydrophone data-logger (Lotek Inc., Newmarket, Ontario) to listen for acoustic transmitters that were in the vicinity. Starting at one end of the reservoir, we slowly worked our way across to the other end of the reservoir, surveying each zone for 10 min between 0900–1700 h. Repeat visits to a given census zone were separated by at least 2 days. In total, we surveyed each zone 18 times over the course of the project. This included 16 survey days in 2015 and 19 survey days in 2016 during the two field seasons.

Based on detection range tests that we conducted in the reservoir, the WHS4250 hydrophones can readily detect JSATS transmitters within 100 m; however, the detection efficiency of the equipment rapidly diminishes beyond 100 m. Generally, the maximum detection distance for JSATS transmitters is 200 m (McMichael et al. 2010). For a detection to be validated, the transmitter's ID had to be detected at least twice in a 40 s time period. In addition to the paired detection requirement, we also required that a total of four detections be registered within a 120 s time period (McMichael et al. 2010). We quantified the number of unique individuals detected in each zone, as well as the total number of detections in each zone. Individual lake sturgeon could not be detected more than once in a zone during a given survey day.

Entrainment monitoring

To monitor entrainment, we installed a number of different radio frequency identification (RFID) antennas below Kleber Dam that could detect the half-duplex PIT-tags that were implanted within the juvenile lake sturgeon (Fig. 1). Six vertically oriented antennas were installed at the Kleber Dam powerhouse to monitor outflow from the two turbine units. One stream-wide antenna was installed ~300 m downstream of the Kleber Dam powerhouse. Two seasonal stream-wide RFID antennas were operated between April and August at the entrance to the adult lake sturgeon spawning grounds at a location termed section-7. Lastly, three stream-wide RFID antennas were installed at the F05-bridge crossing 15.3 km downstream from Kleber Dam where the Black River empties into Black Lake (Fig. 1).

Each RFID PIT-tag antenna system consisted of a half-duplex RFID reader (Oregon RFID, Portland, Oregon) to power the antenna and log data, a tuner board to achieve proper electromagnetic resonance, and a power source to power the system. At all sites we used regular grid power to run the antennas, except for the two seasonal antennas at section-7, which were powered by two 200 W solar panels (Zamp Solar, Bend, Oregon). Half-duplex RFID antenna systems constantly switch their electromagnetic fields on and off to wirelessly charge and subsequently listen for PIT-tags in the vicinity. Antennas that were in close proximity at each site were synchronized to prevent charge–listening cycle interference. RFID monitoring started in May 2015 and continued through September 2018.

Habitat mapping

We used a Humminbird 999ci HD SI side-scan sonar unit (Humminbird, Eufaula, Alabama) to record depth, hardness, roughness, and side-scan imaging data, and ReefMaster (version 2.0) software (West Sussex, UK) to extract and view this multichannel sonar data of Kleber Reservoir. The sonar unit used a 200/83 kHz dual beam system to collect down imaging data and a 800 kHz side-imaging beam to collect side-scan sonar imaging data. To capture data, we mounted the sonar unit's transducer at the bow of the boat, and we followed preplanned transect lines spaced 30.5 m apart that crisscrossed the entire reservoir system at a speed of 3.2 km·h^{-1}. Hardness measurements were based on data from the integral of the second sonar echo return (E2), while roughness measurements were based on data from the integral of the first sonar echo return (E1; Venteris and May 2014). In total, we obtained over 40 000 depth, hardness, and roughness measurements.

The bathymetry, hardness, and roughness data were then imported into ArcGIS for further processing. The depth data were interpolated by using ordinary exponential kriging (mean error (ME) = 0.005, root mean squared error (RMSE) = 0.469, standardized RMSE = 0.844) to produce a complete bathymetry map of the reservoir. The hardness and roughness data were also interpolated by using inverse distance weighting (hardness: ME = –0.002, RMSE = 18.012; roughness: ME = 0.006, RMSE = 18.847) to produce two more habitat maps. The sonar imaging data were digitally mosaicked together in the Reef Master software to produce several different sonar imaging maps with different scan angles. We then delineated the bottom substrate by constructing shapefiles based on the distinct sonar signatures of different substrate types (Kaeser and Litts 2010).

To evaluate the accuracy of our mapping, we conducted a ground-truthing survey. Thirty-five points were randomly chosen throughout the reservoir. Scuba divers were then sent to the bottom at each randomly selected point and recorded the dominant substrate type and depth in the surrounding 10 m^2 area. Substrate size was classified based on a modified Wentworth scale (Bain et al. 1985). Based on the survey, we found that our bathymetric map was 95% percent accurate ±1.2 m, while our substrate map was 97% percent accurate. The water level in the reservoir was very stable during the months of the active tracking survey, based on data collected in 2016 (mean reservoir head level = 213.73 m above sea level, SD = 0.026 m, range: 213.64–213.80 m). Owing to a data logging error problem, water level information is not available for this time period in 2015.

Statistical analyses

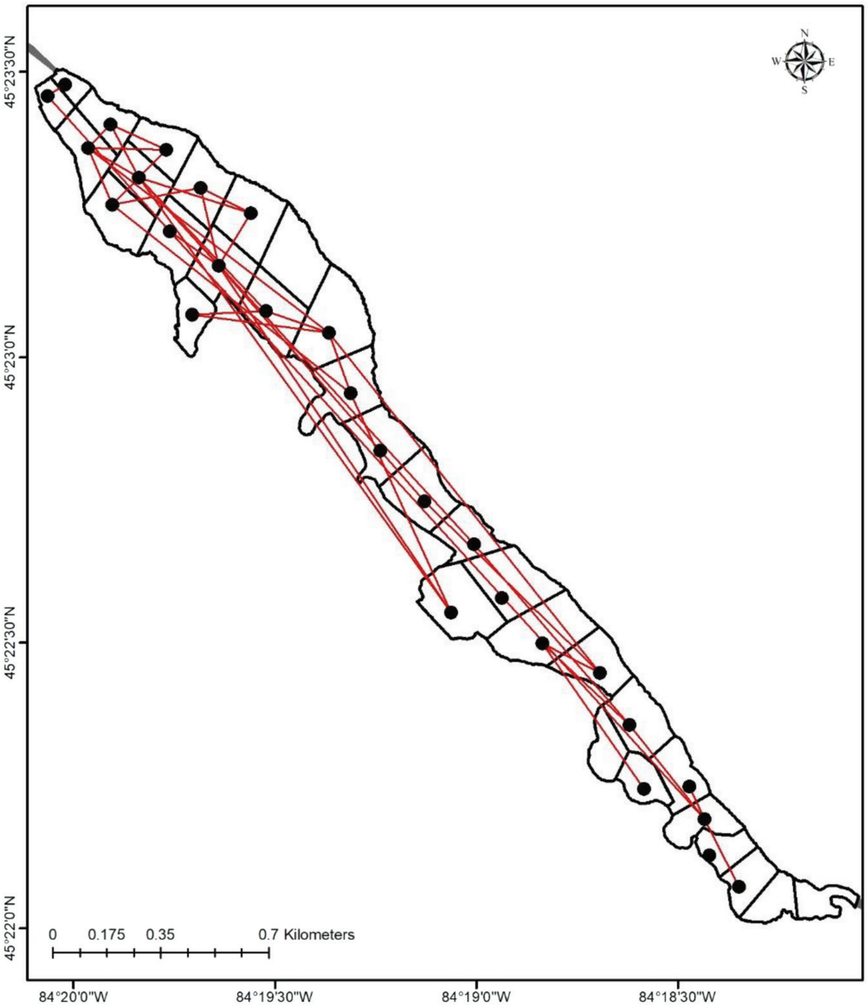
The distance moved by individual lake sturgeon, based on repeated detections, was calculated by measuring the direct line distance between the designated centers of the respective census zones. We calculated total distance traveled, maximum distance traveled between observation points, and mean distance traveled between observation points. We used a restricted maximum likelihood (REML) based general linear model to evaluate differences between the two age groups with respect to the movement metrics. Entrainment probabilities between age groups and stocking locations were compared with statistical odds ratios.

The number of unique lake sturgeon detected and the total number of detections were summarized by census zone. We used the Getis–Ord general G analysis to evaluate the global clustering characteristics of the two datasets (Getis and Ord 1992; Ord and Getis 1995). We conducted repeated analyses on both datasets using different neighborhood distances to determine the distance at which the clustering was strongest based on G_i Z scores. We also used the Getis–Ord G_i^* hot spot analysis to evaluate the local clustering characteristics of both datasets (Getis and Ord 1992; Ord and Getis 1995).

In the spatial analyst package within ArcGIS, we summarized descriptive habitat statistics by using 150 m radius zones that overlapped by 50 m. Semi-overlapping zones were used to account for the uncertainty in transmitter locations. Descriptive habitat statistics for each zone included hectares of silt, hectares of aquatic vegetation, percent silt, percent vegetation, mean depth, maximum depth, mean hardness, mean roughness, hectares of low hardness habitat (i.e., habitat less than or equal to 60 hardness units), hectares of water ≥ 2.1 m deep, hectares of water ≥ 3.1 m deep, hectares of water ≥ 6.1 m deep, and channel width.

We used the computed habitat variables to investigate habitat associations with the observed level of habitat use determined from the active tracking survey. We evaluated the two response variables, number of unique individuals and total detections in each zone, separately. Because of problems with high outliers in two census zones located near the forebay of Kleber Dam (i.e., zone 5: 15 detections; zone 6: 18 detections), we used a rating scale to meaningfully recategorize the total detections data for all analyses. The rating scale classified zero detections as 1, one detection as 2, two to three detections as 3, four to six detections as 4, and more than six detections as 5. The habitat predictor variables showed strong signs of multicollinearity, which could not be remedied by selectively removing variables from the analysis. Consequently, a standard spatial autoregressive model could not be reliably used to evaluate the data. Therefore, we used projection to latent structures regression (PLSR; a.k.a. partial least squares regression) based on the SIMPLS algorithm (De Jong 1993), which is robust against multicollinearity and small samples sizes (Wold 1966; Abdi 2010). We used leave-one-out cross-validation to determine the number of components needed to maximize the predictive ability of the model based on the amount of X and Y variance explained. X variance refers to the variance in the predictor variables, while Y variance refers to the variance in the response variable accounted for by the predictor variables (Abdi 2010). Variable selection was performed by evaluating variable importance in projection (VIP) scores, standardized coefficients, component weights, examining x residuals versus the predictors, by

Fig. 2. Map illustrating the coarse-scale movements of 24 juvenile lake sturgeon between census zones in Kleber Reservoir. The red lines represent movements between census zones, and the black circles represent the central observation point for each zone. The more red lines that are adjacent or overlap with each other, the more movement that was measured between the given zones based on telemetry data. The red lines only represent direct linear movements between different zones and do not represent the actual movement route. Map data are from the United States Geological Survey National Hydrography Dataset. [Colour online.]



assessing cross-validation performance (e.g., PRESS, predictive R^2) and biological importance (Wold et al. 2001; Carrascal et al. 2009; Mehmood et al. 2012).

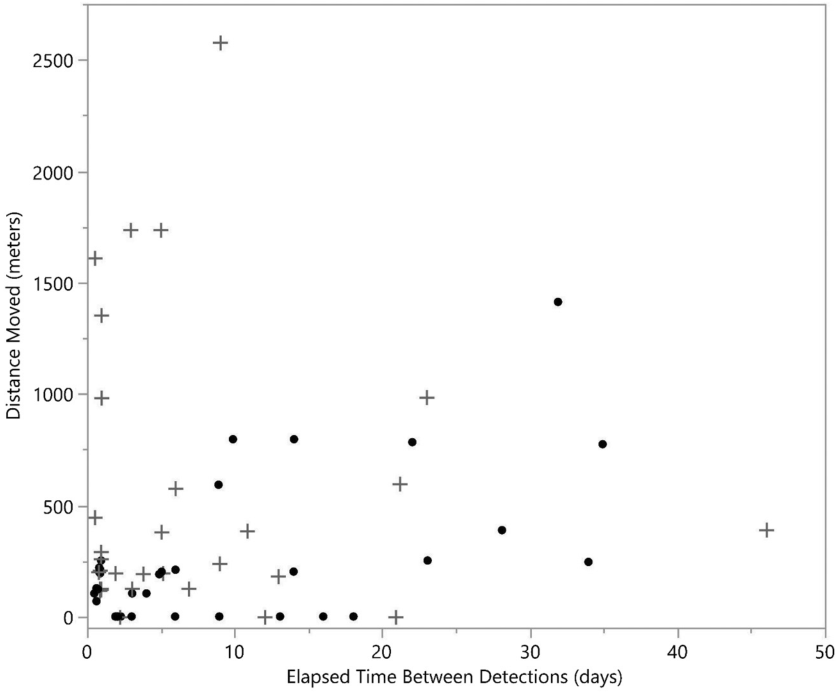
We used geographically weighted regression (GWR) to examine how habitat variables affected habitat use spatially across Kleber Reservoir (Brunsdon et al. 1998). As a prerequisite for the analysis, we assessed spatial autocorrelation in the data by using both global and local Moran's *I*. Because of strong multicollinearity, GWR models were run separately for each significant predictor identified in the PLSR analysis. All GWR analyses were accomplished using an adaptive kernel based on corrected Akaike information criterion (AIC_c). Spatial statistical analyses and all mapping were conducted in ArcGIS Desktop 10.5.1 (ESRI, Redlands, California). Movement metrics were calculated with the use of the ArcMET software package in ArcMap. All other statistical analyses were accomplished with JMP Pro version 14 software package (SAS Institute, Cary, North Carolina, USA) and Minitab version 18 software package (Pennsylvania State University, State College, Pennsylvania).

Results

Detections and movement characteristics

Over the course of the project between late July and mid-September of 2015 and 2016, we obtained validated detections from a total of 44 unique lake sturgeon. This included detections from 26 age-1 and 18 age-2 lake sturgeon, and we logged a total of 117 nonrepetitive detections around Kleber Reservoir. Thirteen age-1 and seven age-2 lake sturgeon were only detected once, while 13 age-1 and 11 age-2 lake sturgeon were detected two or more times (mean number of detections = 4.1, SD = 2.63). The lake sturgeon with multiple detections on average moved a total of 1138 m (SD = 917.1 m) in direct linear distance over the course of the sampling period (Fig. 2). The mean distance moved between observation points was 502 m (SD = 423.2 m), and the mean maximum distance moved between observation points was 765 m (SD = 628.1 m). The elapsed time between detections was highly variable and averaged 10.54 days (SD = 10.38 days; Fig. 3). Statistical tests showed that there were differences in movement characteristics between the two age groups. Age-2 lake sturgeon (mean total distance = 1545 m, SE = 261.8 m) moved more in total distance than age-1 lake sturgeon (mean total distance = 764 m, SE = 250.7 m; *F* ratio: 4.64, df: 1, $p = 0.043$). Maximum distance moved between observation points also marginally differed between the two age groups, with age-2 lake sturgeon (mean maximum distance = 1013 m, SE = 183.4 m) making somewhat longer movements than age-1 lake sturgeon (mean maximum distance = 537 m, SE = 175.6 m; *F* ratio: 3.53, df: 1, $p = 0.074$).

Fig. 3. Scatterplot showing linear distance moved (m) versus elapsed time between detections (days) for 73 different movement segments from 24 unique lake sturgeon that were detected on two or more occasions. Age-1 lake sturgeon are represented by black circles, while age-2 lake sturgeon are represented by grey crosses.



Spatial hotspot analysis

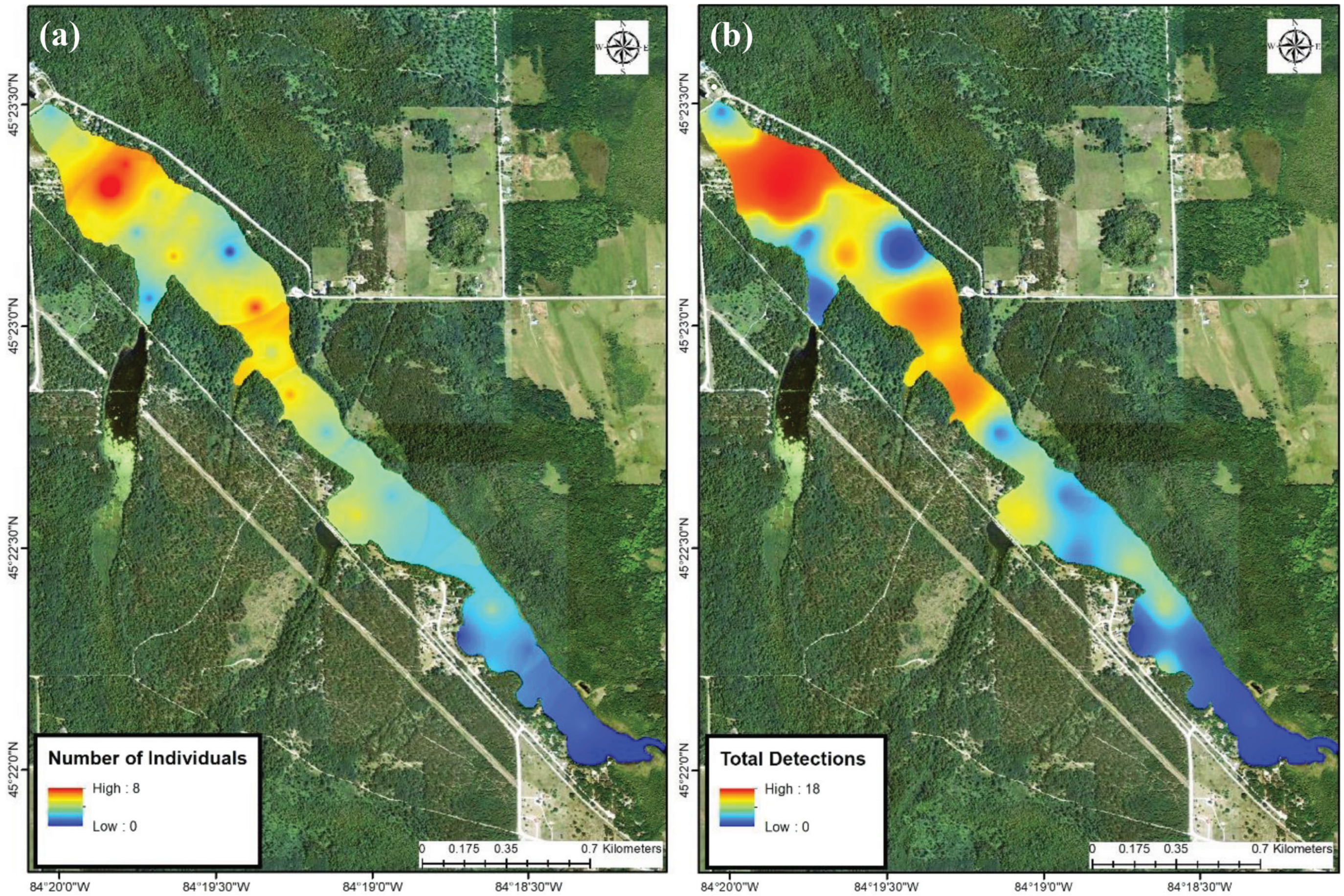
Most lake sturgeon detections were located near the forebay of Kleber Dam and in the middle of the reservoir (Fig. 4). Detections were sparse toward the shallow, channelized head of the reservoir. Similarly, the number of unique lake sturgeon detected was highest near the forebay of Kleber Dam and in the middle of the reservoir, while few lake sturgeon were detected toward the head of the reservoir (Fig. 4). The Getis–Ord general *G* analysis showed that on a global scale there was statistically significant clustering of high values across the reservoir, with regards to both the number of unique lake sturgeon detected (observed *G*: 0.293, expected *G*: 0.216, *Z* score: 4.004, $p < 0.001$) and total detections (observed *G*: 0.251, expected *G*: 0.216, *Z* score: 3.611, $p < 0.001$). We found that in both cases the level of significant clustering peaked at a neighborhood size of 450 m, which was subsequently used as the optimal distance band in the local spatial analyses. The local scale Getis–Ord G_i^* hotspot analysis indicated a very significant clustering of high values near the forebay of Kleber Dam, significant clustering of high values toward the middle of the reservoir, and a significant clustering of low values toward the head of the reservoir, with regards to both the number of unique individuals detected and total detections (Fig. 5).

PLSR habitat associations

Based on our variable removal criteria and PLSR model diagnostics, we identified five variables that were significantly positively associated with the number of unique lake sturgeon detected in each zone within the reservoir (Fig. 6). These variables include the amount of silt habitat, amount of deepwater habitat (≥6.1 m), mean depth, amount of low hardness habitat (≤60 hardness units), and the interaction between mean depth and the amount of silt habitat (Fig. 7). Cross-validation showed that the optimal number of components for the analysis was three. With three components the PLSR model was able to explain 97.6% of the *X* variance and 66.4% of the *Y* variance (van der Voet T^2: 0.313, p = 0.639, PRESS: 53.04, prediction R^2: 53.2; Table 1). The more conservative PLSR model with only one component explained 71.5% of the *X* variance and 47.5% of the *Y* variance (van der Voet T^2: 1.235, p = 0.272, PRESS: 69.57, prediction R^2: 38.69%), indicating that the majority of the variance was explained by the first component (Table 1). The amount of silt habitat was the most important variable with respect to the first component, explaining 24.5% of the variance, followed closely by the amount of low hardness habitat (22.9%), mean depth (18.1%), and the interaction between mean depth and silt habitat (23.3%; Table 1). The second component was almost exclusively explained by the amount of low hardness habitat (50.9%) and by the amount of deepwater habitat (49.7%). The third component was dominated by the amount of deepwater habitat, which explained 78.7% of the variance of that component.

The results of the second PLSR analysis examining habitat associations with the total number of lake sturgeon detections in each zone was very similar to the first analysis. Based on our variable removal criteria and PLSR model diagnostics, we identified seven variables that were significantly positively associated with the total number of detections observed in each zone within the reservoir (Fig. 8). These variables include the amount of silt habitat, amount of deepwater habitat (≥6.1 m), mean depth, amount of low hardness habitat (≤60 hardness units), maximum depth, the interaction between mean depth and the amount of silt habitat, and the interaction between the amount of silt habitat and deepwater habitat (Fig. 7). Cross-validation showed that the optimal number of components for the analysis was three. With three components the PLSR model was able to explain 96.6% of the *X* variance and 64.4% of the *Y* variance (van der Voet T^2: 0.245, p = 0.890, PRESS: 19.01, prediction R^2: 54.2%; Table 2). The more conservative PLSR model with only one component explained 79.0% of the *X* variance and 45.0% of the *Y* variance (van der Voet T^2: 1.129, p = 0.321, PRESS: 25.515, prediction R^2: 38.52%), indicating that the majority of the *Y* variance was explained by the first component (Table 2). The most important variables that explained the most amount of *Y* variance on the first component included the amount of silt habitat (19.4%), amount of low hardness habitat (20.1%), mean depth (13.3%), and the interaction between mean

Fig. 4. (*a*) Interpolated map showing where the highest number of unique lake sturgeon were detected across Kleber Reservoir. (*b*) Interpolated map showing where the most lake sturgeon detections were located across Kleber Reservoir. Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program. [Colour online.]



depth and silt habitat (16.2%; Table 2). The second component was almost exclusively explained by the amount of low hardness habitat, which explained 69.2% of the *Y* variance on that component. The third component was principally explained by maximum depth (44.2%), amount of deepwater habitat (30.0%), and by the interaction between silt and deepwater habitat (28.7%).

Geographically weighted regression (GWR)

The GWR results analyzing the number of unique lake sturgeon detected in each zone showed that the magnitude of the influence of silt habitat (R^2: 48.3%, R^2 adj.: 44.1%, AIC$_c$: 119) and low hardness habitat (R^2: 47.7%, R^2 adj.: 42.53%, AIC$_c$: 121) varied spatially across the reservoir (Fig. S1[1]). In both cases the effect size (i.e., local R^2) of silt and low hardness habitat quantity was greatest toward the more confined, shallow head of the reservoir. The influence of mean depth and deepwater habitat did not vary spatially across the reservoir.

The GWR results analyzing the total number of lake sturgeon detections in each zone showed that the magnitude of the influence of silt habitat (R^2: 53.6%, R^2 adj.: 49.34%, AIC$_c$: 84.34), low hardness habitat (R^2: 54.8%, R^2 adj.: 50.4%, AIC$_c$: 83.92), and maximum depth (R^2: 44.2%, R^2 adj.: 38.6%, AIC$_c$: 90.67) varied spatially across the reservoir (Fig. S2[1]). In all three cases the effect size (i.e., local R^2) of silt habitat, low hardness habitat, and maximum depth was greatest toward the more confined, shallow head of the reservoir. The influence of mean depth and deepwater habitat did not vary spatially across the reservoir.

Entrainment observations

We detected a minimum of 79 (percent entrained = 36.6%, 79 of 216) lake sturgeon that were entrained over the course of the study. A total of 41 (37.3%, 41 of 110) age-1 lake sturgeon were entrained, of which 31 (54.4%, 31 of 57) were originally stocked into Kleber Reservoir and 10 (18.9%, 10 of 53) into Tower Reservoir. In addition, a total of 38 (35.8%, 38 of 106) age-2 lake sturgeon were entrained, of which 28 (52.8%, 28 of 53) were originally stocked into Kleber Reservoir and 10 (18.9%, 10 of 53) into Tower Reservoir. The age-1 and age-2 lake sturgeon stocked into Kleber Reservoir had equivalent entrainment probabilities (odds ratio (OR) = 1.06, 95% CI = 0.50–2.25, z = 0.16, p = 0.870), as did the age-1 and age-2 lake sturgeon that were stocked into Tower Reservoir (OR = 1.00, 95% CI = 0.37–2.64, z = 0.00, p = 1.000). However, the age-1 lake sturgeon stocked into Kleber Reservoir were 5.13 times more likely to be entrained through Kleber Dam compared with the age-1 lake sturgeon stocked into Tower Reservoir (95% CI = 2.16–12.15, z = 3.71, p < 0.001). Similarly, the age-2 lake sturgeon stocked into Kleber Reservoir were 4.82 times more likely to be entrained through Kleber Dam compared with the age-2 lake sturgeon stocked into Tower Reservoir (95% CI = 2.01–11.54, z = 3.52, p < 0.001).

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0407.

Fig. 5. (*a*) Getis–Ord G_i^* hot spot analysis probability map for the number of unique lake sturgeon detected in each zone. (*b*) Getis–Ord G_i^* hot spot analysis probability map for the total number of lake sturgeon detections in each zone. A cold spot indicates a statistically significant cluster of low values, while a hot spot indicates a statistically significant cluster of high values. Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program. [Colour online.]

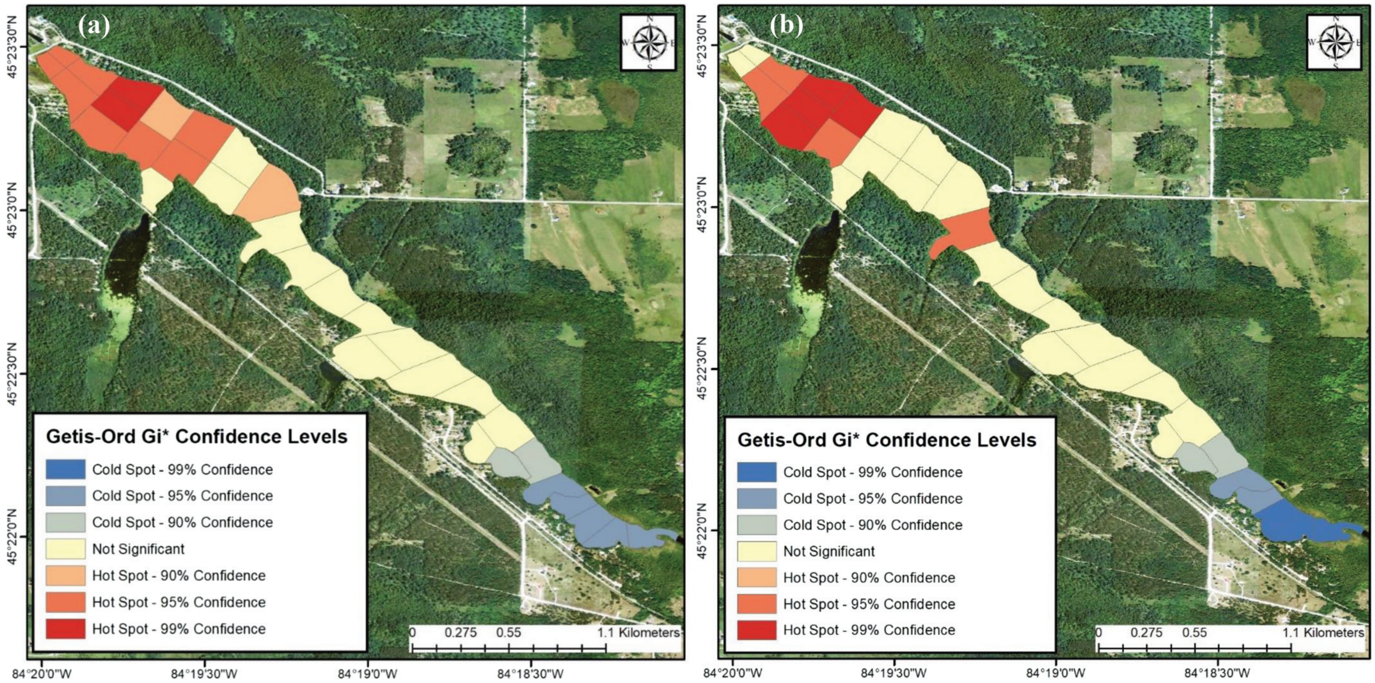
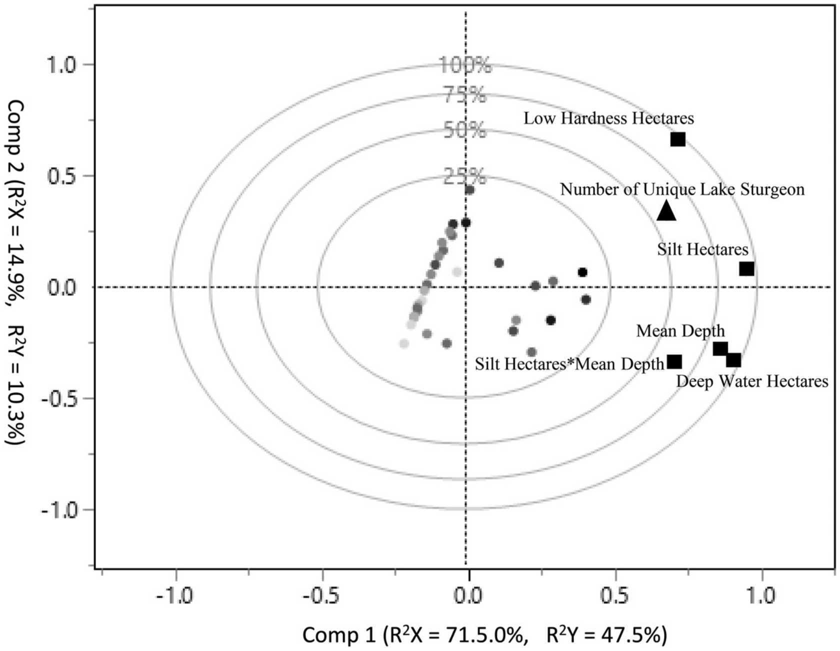


Fig. 6. Correlation loading plot for the projection to latent structures regression (PLSR) analysis examining habitat associations with the number of unique lake sturgeon detected in each census zone. The small shaded circles represent the scores for the different census zones, and the shading level represents the number of individuals detected in each zone, with darker shading indicating more individuals detected. The black squares indicate the loadings for the different predictor habitat variables, and the black triangle indicates the loading value for the response variable: the number of unique lake sturgeon detected. The concentric circles in the background labeled 25%–100% indicate the relative amount of variation explained by the two components for the predictor variables and the response variable.



Most sturgeon were entrained through Kleber Dam relatively quickly following release (Fig. 9). The median number of days until a lake sturgeon was entrained was 42.25 days. There was a considerable amount of variability in observed entrainment times, ranging between 0.43 and 1038.02 days (mean = 164.8 days, SD = 263.28 days). Overall, 55.7% (44 of 79) of the observed entrainment events occurred within 60 days following release. For the lake sturgeon that were just stocked into Kleber Reservoir, 66.1%

Fig. 7. (*a*) Interpolated bathymetry map of Kleber Reservoir. (*b*) Substrate habitat map of Kleber Reservoir based on side-scan sonar imaging. (*c*) Interpolated bottom hardness map of Kleber Reservoir. Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program. [Colour online.]

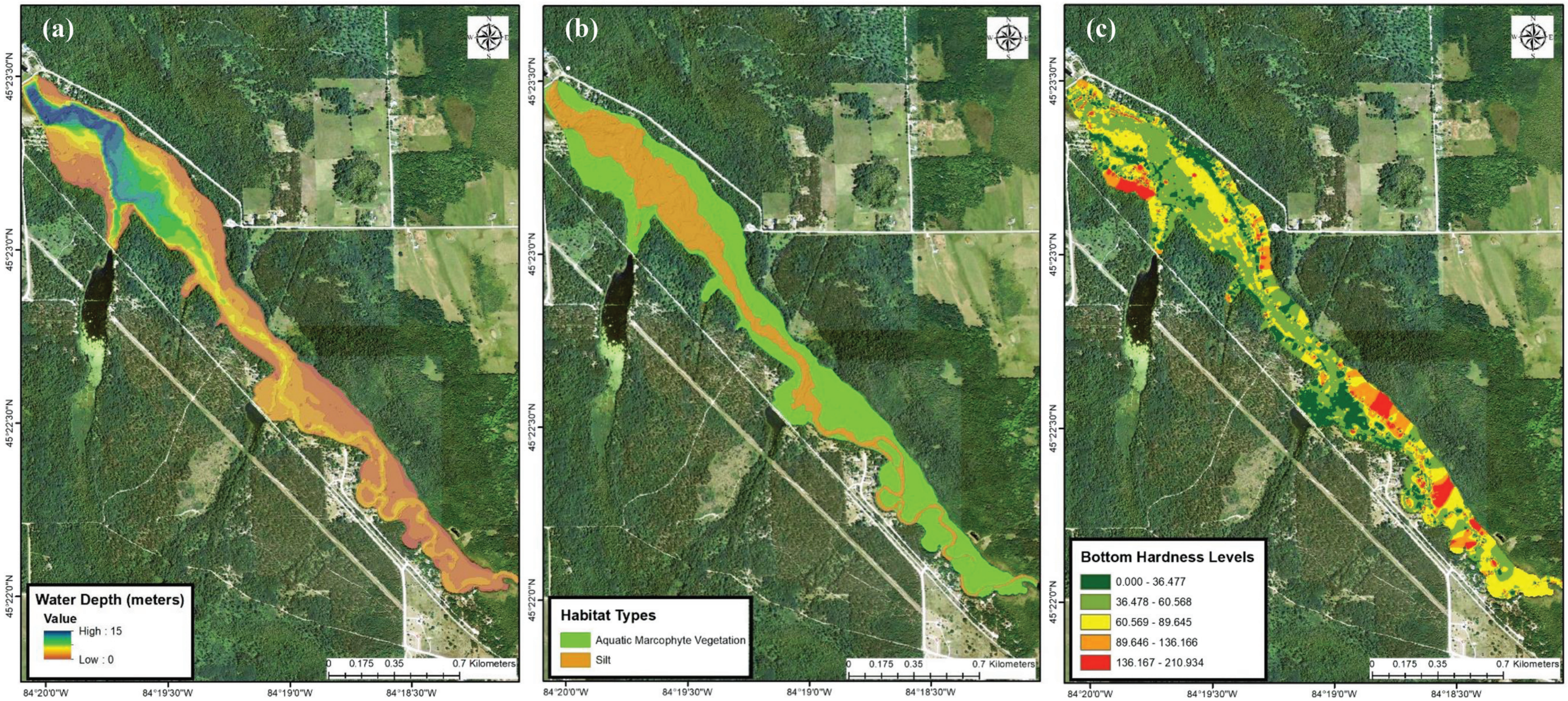


Table 1. Results of the projection to latent structures regression (PLSR) analysis for the number of unique lake sturgeon observed in each zone.

PLSR model components

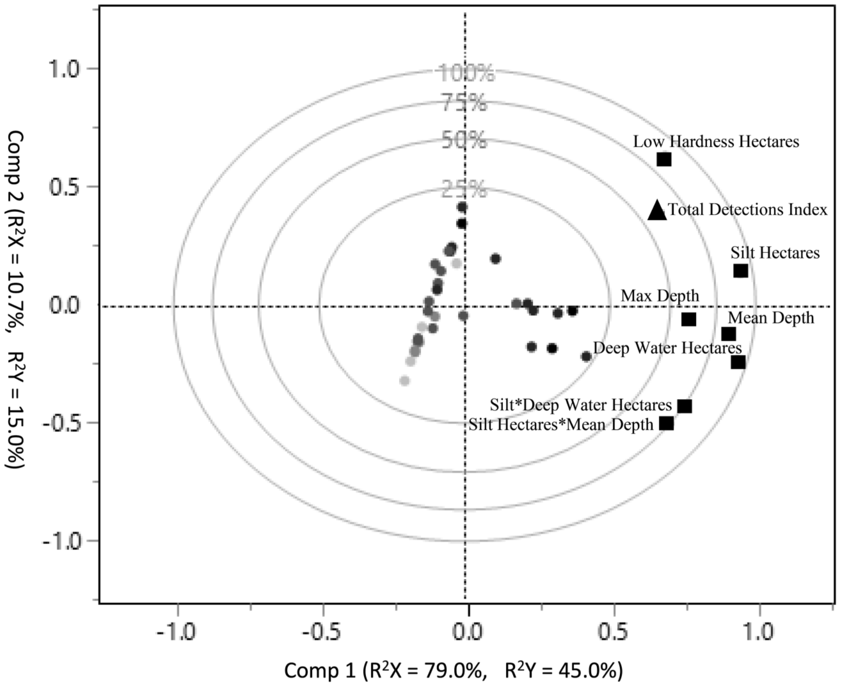
Components	PRESS	Voet T^2	p	R^2 X	R^2 Y
1	69.568	1.235	0.272	0.715	0.475
2	61.593	0.725	0.491	0.149	0.103
3	53.044	0.313	0.639	0.074	0.086

Variable component weights

	Weights			Pearson correlation	
Habitat variables	Comp. 1	Comp. 2	Comp. 3	r	p
Silt hectares	0.495	0.115	−0.029	0.675	0.000
Silt hectares × mean depth	0.483	0.067	0.508	0.659	0.000
Low hardness hectares	0.479	0.714	−0.108	0.655	0.000
Mean depth	0.426	−0.067	0.482	0.582	0.000
Deepwater hectares (≥6.1 m)	0.332	−0.705	−0.887	0.454	0.009

Note: The component model comparisons section compares predicted residual error sum of squares (PRESS), van der Voet T^2, X variance explained, and Y variance explained for each component. van der Voet T^2 is a randomization test that tests whether the model differs significantly from the optimum model. The variable weights section shows the weights obtained for each predictor variable for each component, along with Pearson correlation coefficients. The squared sum of the weights for each component sums to one, which allows the percent Y variance explained by each variable to be determined for each component.

Fig. 8. Correlation loading plot for the projection to latent structures regression (PLSR) analysis examining habitat associations with the total number of lake sturgeon detections in each zone. The small shaded circles represent the scores for the different census zones, and the shading level represents the number of detections, with darker shading indicating more detections. The black squares indicate the loadings for the different predictor habitat variables, and the black triangle indicates the loading value for the response variable: total detections index. The concentric circles in the background labeled 25%–100% indicate the relative amount of variation explained by the two components for the predictor variables and the response variable.



(39 of 59) of the entrainment events occurred within 60 days following release. However, 16.5% (13 of 79) of all observed lake sturgeon entrainment events occurred more than 300 days after release.

Discussion

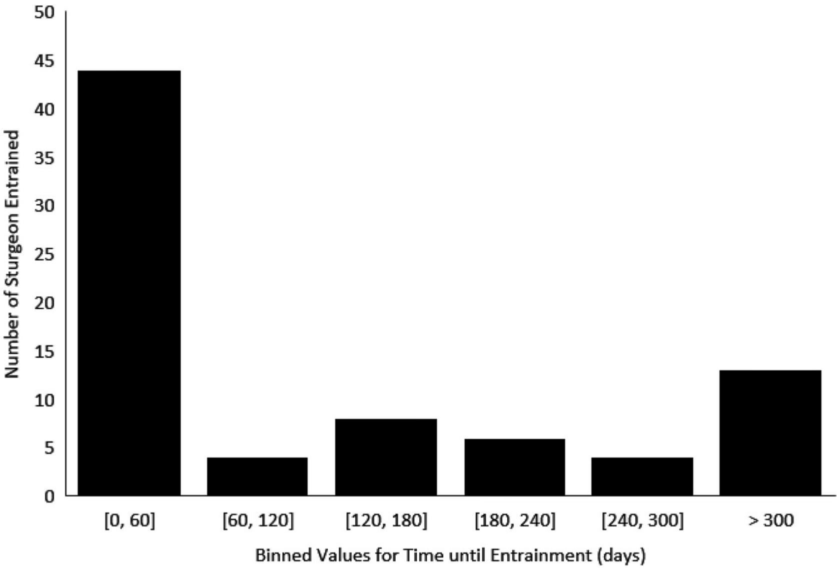
Identifying movement patterns and habitat use characteristics is essential for the conservation and management of imperiled species like lake sturgeon (Holey et al. 2000). Based on our acoustic telemetry study, we found that movements of age-1 and age-2 lake sturgeon within Kleber Reservoir were relatively limited, with total movement distance averaging 1138 m. On average, the lake sturgeon moved just over 500 m in direct linear distance between successive telemetry positions. Similar to our findings, Holtgren and Auer (2004) showed that lake sturgeon movements between telemetry positions in the larger Portage Lake system ranged between 260 and 1630 m. Smith and King (2005) also observed that juvenile lake sturgeon movements between telemetry locations in Black Lake were relatively limited, ranging between 330 and 800 m. They also noted that home range size was relatively small, ranging between 0.74 and 5.98 km². Even in large river systems like the Winnipeg River, Peshtigo River, and the St. Clair River,

Table 2. Results of the projection to latent structures regression (PLSR) analysis for the total number of detections of lake sturgeon observed in each zone.

PLSR model components					
Components	PRESS	Voet T^2	p	R^2 X	R^2 Y
1	25.515	1.129	0.321	0.790	0.450
2	20.098	0.000	1.000	0.107	0.150
3	19.006	0.245	0.890	0.069	0.044
Variable component weights					
	Weights			Pearson correlation	
Habitat variables	Comp. 1	Comp. 2	Comp. 3	r	p
Silt hectares	0.440	0.217	0.005	0.683	0.000
Silt hectares × mean depth	0.402	−0.003	0.209	0.625	0.000
Low hardness hectares	0.448	0.832	0.013	0.695	0.000
Max. depth	0.333	0.006	0.665	0.516	0.002
Silt hectares × deepwater hectares	0.324	−0.332	−0.536	0.503	0.004
Mean depth	0.365	−0.082	0.291	0.567	0.001
Deepwater hectares (≥6.1 m)	0.309	−0.428	−0.547	0.479	0.006

Note: Data explanation is the same as for Table 1.

Fig. 9. Histogram showing time until entrainment (binned into six categories) for 79 juvenile lake sturgeon that were entrained below Kleber Dam based on radio frequency identification (RFID) detections data.



researchers have noted that the movements of juvenile lake sturgeon are quite modest and localized (Benson et al. 2005; Barth et al. 2011; Boase et al. 2014). We also found that older age-2 lake sturgeon tended to make somewhat longer movements compared with age-1 lake sturgeon. Prior studies have similarly found that larger and older lake sturgeon tend to move longer distances (Smith and King 2005; McDougall et al. 2013).

There are several important limitations of our study that should be noted to provide context for interpretation. The lake sturgeon that we tagged and studied were all hatchery-produced and artificially stocked into the reservoirs. In addition, because of seasonal operating restrictions, we began monitoring their behavior relatively quickly after they were released, which did not give the lake sturgeon much time to acclimate. Therefore, our results largely quantify the post-stocking behavior of age-1 and age-2 lake sturgeon, which may be different from that observed in wild populations. Furthermore, we only conducted active tracking during the daytime because of staffing limitations, so our results only describe diurnal behavior patterns. Multiple researchers have found differences between nocturnal and diurnal behavior (Chiasson et al. 1997; Holtgren and Auer 2004; Benson et al. 2005). For example, Benson et al. (2005) specifically observed that juvenile lake sturgeon were relatively immobile during the daytime and oriented themselves upstream into the current, while at night the lake sturgeon swam continuously close to the river bottom.

Areas of Kleber Reservoir with high levels of habitat use were statistically clustered near the forebay of Kleber Dam and toward the middle of the reservoir, while areas with low levels of habitat use were clustered toward the head of the reservoir. We found that physical habitat characteristics could largely explain the observed spatial variation in habitat use. The amount of silt, amount of low hardness habitat, mean depth, and the amount of deepwater habitat (≥6.1 m) explained between 47.5% and 66.4% of the variation in the number of unique lake sturgeon detected in each reservoir zone. Similarly, the amount of silt, amount of low hardness habitat, mean depth, maximum depth, and the amount of deepwater habitat explained between 45.0% and 64.4% of the variation in the total number of detections in each reservoir zone. In general, lake sturgeon appeared to readily use areas with deep water and soft, fine sediments and tended to not use areas with shallow water or abundant macrophyte vegetation.

Our research and that of others strongly suggests that lake sturgeon movements and habitat use are limited by areas of contiguous deepwater habitat (Holtgren and Auer 2004; Barth et al. 2011; McDougall et al. 2013; Boase et al. 2014). Holtgren and Auer (2004) observed that lake sturgeon usually used water depths greater than 10 m. McDougall et al. (2013) reported that lake sturgeon movement was largely restricted to deepwater habitat greater than 15 m in depth and that shallow river narrows could effectively constrain the movement of lake sturgeon. However, Smith and King (2005) found that some young juveniles tended to use shallower nearshore areas (2–3.5 m deep), while others used deep offshore areas (>9 m deep) in Black Lake. Some authors have suggested that the observed tendency to use deepwater habitat may be a predator avoidance strategy (Holtgren and Auer 2004; Smith and King 2005; Barth et al. 2011). It has also been proposed that deepwater habitats provide better hydraulic conditions and are in depositional areas that accumulate detrital matter and nutrients, making them productive foraging areas (Boase et al. 2014).

We also found that lake sturgeon used areas with soft, fine substrates that lacked abundant vegetation. In Kleber Reservoir, silt and aquatic macrophytes constituted the overwhelming majority of the habitat that was available. Consequently, we were not able to evaluate or describe the use of larger substrates like gravel and cobble by juvenile lake sturgeon. Several authors have comparably noted that lake sturgeon tend to avoid areas with aquatic macrophytes (Kempinger 1996; Holtgren and Auer 2004; Gerig et al. 2011). Sbikin and Bibikov (1988) found that juvenile Russian sturgeon (*Acipenser gueldenstaedtii*), beluga sturgeon (*Huso huso*), sevryuga sturgeon (*Acipenser stellatus*), and ship sturgeon (*Acipenser nudiventris*) avoided aquatic vegetation because it inhibited their ability to move, orient, and feed efficiently.

Other researchers have similarly noted that lake sturgeon use silt habitat (Werner and Hayes 2005; Gerig et al. 2011; Trested et al. 2011), along with sand–clay substrates (Chiasson et al. 1997), organic substrates (Holtgren and Auer 2004; Smith and King 2005), and sand substrates (Peake 1999; Benson et al. 2005). Nilo et al. (2006) suggested that sturgeon are generalists and opportunistic benthic feeders that are quite versatile. Werner and Hayes (2005) noted that 65.4% of juvenile lake sturgeon habitat in the St. Lawrence River was composed of silt. Smith and King (2005) also observed that 84% of the deepwater areas that juvenile and yearling lake sturgeon commonly used in Black Lake were composed of silt. In contrast, Hrenchuk et al. (2017) reported that lake sturgeon in the Stephens Lake reservoir system (Nelson River, Manitoba) used areas with gravel, cobble, and boulder 57.3% of the time and generally avoided downstream areas with fine sediments, despite the fact that more benthic macroinvertebrates resided in the region downstream dominated by silt. The researchers suggested several reasons for this observed use of larger upstream substrates: (*i*) drifting macroinvertebrates might be more abundant farther upstream where currents are faster and substrates are larger, (*ii*) the sturgeon may not be adapted to using the silt habitat available farther downstream because the dam and its associated habitat features are contemporary features, and (*iii*) the lake sturgeon may develop a core-area affinity based on where they settle out as larvae, which would make them less likely to establish residency downstream in the silt-dominated habitat region.

For the age-1 and age-2 lake sturgeon stocked into Kleber Reservoir, we observed high minimum entrainment rates in excess of 50%. In addition, we observed that 66% of the entrained fish that were stocked into Kleber Reservoir were entrained within 60 days following release. This likely accounts for the low observed detection rate in the active tracking survey. Both age-1 and age-2 lake sturgeon stocked into Kleber Reservoir had similar entrainment probabilities, as did the age-1 and age-2 lake sturgeon stocked into Tower Reservoir. The lake sturgeon stocked into Kleber Reservoir were more likely to be entrained below Kleber Dam compared with the lake sturgeon stocked into Tower Reservoir. The reason for this observed difference in entrainment probabilities may be explained by the following two factors: (*i*) high passage mortality at Tower Dam and (*ii*) Tower Reservoir may have characteristics that tended to limit entrainment or promote residency. In Kleber Reservoir, the deepwater habitat that was used the most was located in close proximity to the dam, and this may have made the lake sturgeon quite vulnerable to entrainment in this relatively small reservoir system. In contrast with our findings, McDougall et al. (2013) observed that 0% of juvenile lake sturgeon (339–509 mm TL), 10% of subadult lake sturgeon (516–711 mm TL), and 8.7% of adult lake sturgeon (853–1357 mm TL) were entrained in a larger 10 km long reservoir along the Winnipeg River. Similarly, a fine-scale acoustic positioning study at the same location found that annual downstream passage rates were 0% for juvenile lake sturgeon, 21% for subadult lake sturgeon, and 2.9% for adult lake sturgeon (McDougall et al. 2014*a*). The differences in observed entrainment rates are likely related to reservoir size, reservoir morphology, the location of suitable habitats in relationship to the dams, or rearing origin (i.e., wild versus hatchery-produced and stocked).

With respect to reintroduction and passage programs for lake sturgeon and other species, there is much uncertainty with regards to reservoir residency characteristics. Juvenile lake sturgeon may out-migrate rapidly through a reservoir or they may reside within a reservoir for a number of years, making use of the reservoir's habitat and resources (Smith and King 2005; Peterson et al. 2007; McDougall et al. 2013, 2014*a*; Hrenchuk et al. 2017; McDougall et al. 2017). In our study, we observed a high level of entrainment (>50%) and the majority of entrainment events happened within the first 60 days, but we also observed that 16.5% of the entrainment events occurred more than 300 days after release, indicating that some lake sturgeon did reside within the reservoir system and use the habitat for an extended period of time. In some systems entrainment of juvenile lake sturgeon, especially at high levels, is clearly detrimental to a population because it results in a loss in juvenile recruitment (Jager 2006; Jager et al. 2016; Pracheil et al. 2016). Entrainment through hydroelectric turbine systems is especially detrimental, as it is usually associated with high mortality (Pracheil et al. 2016). However, healthy self-sustaining lake sturgeon populations exist in reservoir systems, despite low levels of entrainment (McDougall et al. 2013, 2014*a*, 2017). In other systems, juvenile lake sturgeon would be expected to become entrained as they out-migrate downstream through a reservoir into larger river and lake systems (Thuemler 1985; Coscarelli et al. 2011; Jager et al. 2016; Koenigs et al. 2019), but juveniles may use reservoirs as nursery habitat for a variable amount of time. Therefore, the quality of reservoir habitat may be key to the success of reintroduction programs and improved juvenile recruitment. Our research clearly showed that juvenile lake sturgeon used deepwater habitat in areas with fine sediments and limited aquatic vegetation. Consequently, reservoirs with ample deepwater habitat, fine soft substrates, and limited macrophyte vegetation may provide suitable habitat conditions to support juvenile lake sturgeon and would be candidate locations for lake sturgeon passage efforts. The abundance and location of aquatic macrophytes may modify and restrict lake sturgeon movements, which may be useful in limiting entrainment susceptibility and in passage engineering. The stocking of juvenile lake sturgeon into small reservoir systems will likely result in a large proportion being entrained, and reintroduction efforts should account for the morphology of the reservoir and the location of high-quality habitats in relation to hydroelectric infrastructure during planning.

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