ASSESSING THE OUTCOMES OF SIMULATED FISH PASSAGE: AN EVALUATION OF SURVIVAL, MOVEMENTS, AND HABITAT USE OF JUVENILE LAKE STURGEON RELEASED ABOVE A HYDROELECTRIC RESERVOIR SYSTEM

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife – Doctor of Philosophy

2023

ABSTRACT

The historical proliferation of hydroelectric dams across North America led to a loss in river system connectivity and alteration of habitat and flow regimes. Fish passage improvements are increasingly being examined as a means to reconnect river systems and restore remnant lake sturgeon (*Acipenser* fulvescens) populations. However, the recruitment benefits of passing adults above dams remains uncertain because limited information is available on the behavior and survival of juvenile lake sturgeon in hydroelectric reservoir systems. We conducted a four year study to assess the behavior, habitat use, movements, and route specific passage survival of juvenile lake sturgeon in two different sized reservoirs on the Black River in northern Michigan. Movements within the river system were tracked through the use of PIT-tag and acoustic telemetry monitoring technology. This involved surgically implanting transmitters within juvenile lake sturgeon to track individual movements. We developed an experiment to refine best surgical practices for this effort by evaluating the effects of incision placement (lateral vs. midline), closure method (suture vs. Vetbond), and tag burden on healing outcomes in age-0 lake sturgeon. Incision dehiscence was low for all treatments, except for midline incisions closed with Vetbond. Incisions closed with suture achieved better healing outcomes initially, but the healing process was 2-3 times more likely to relapse because of severe inflammation compared to lateral incisions closed with Vetbond, indicating that Vetbond is the preferred closure method when sutures are not able to be removed. During the field study, the majority of juveniles out-migrated from the reservoir system in less than 60 days and greater than 90% of movements occurred at night. However, 37% of the age-0 and 27% of the age-1 and age-2 lake sturgeon stayed in the reservoir system for more than 179 days. Also, age-0 lake sturgeon resided within the reservoir system and in the free flowing part of the river for longer periods of time compared with the older lake sturgeon. Outmigration numbers consistently peaked in the spring and fall months and were found to be related to temporal changes in water temperature and discharge levels. Habitat use was higher in areas with more silt habitat and less aquatic vegetation and in areas that had greater mean depth and max depth characteristics. At Kleber Dam the survival rates for passage through the vertical-shaft Kaplan turbine systems were estimated at 70.9% (SE = 0.093) for age-0 and 44.9% (SE = 0.138) for age-1 and age-2 lake sturgeon. At Tower Dam survival through the Leffel type-z vertical-shaft turbine systems was estimated at 86.9% (SE = 0.135) for age-0 and 59.9% (SE = 0.182) for age-1 and age-2 lake sturgeon. Passage survival through the Tower Dam Spillway was estimated at 100% (SE = 0.132) for age-0 and 100% (SE = 0.188) for age-1 and age-2 lake sturgeon. Impingement mortality at Tower Dam differed by age and was 0.4% for age-0, 13.3% for age-1, and 21.8% for age-2 lake sturgeon, while impingement mortality at Kleber Dam was not observed. Our results indicate that the majority of juvenile lake sturgeon will out-migrate rapidly from small reservoir systems in the fall and spring and that movements are nocturnal. However, our data also showed that juveniles can persist within small reservoirs for extended periods of time over multiple years and that reservoir morphology may limit entrainment. Turbine design, bar-rack spacing, and fish length and age at passage are key factors in determining levels of mortality and in forecasting recruitment benefits from lake sturgeon passage improvements. Our results also suggest that spillways can pass lake sturgeon with limited mortality, and operations at dams may be able to be modified to operate spillways at night during peak outmigration times to facilitate safer passage.

This dissertation is dedicated to my mom and dad, Helen and Harwood Hegna.
Thank you for your encouragement and support.

ACKNOWLEDGMENTS

The completion of this dissertation would not be possible without the support and assistance of many people. I want to thank my major advisor, Dr Kim Scribner, for his invaluable guidance and instruction throughout my program. I would also like to thank my committee members, Edward Baker, Dana Infante, and Michael Wagner, for their guidance, feedback, and assistance with my dissertation. This study was funded by the Great Lakes Fishery Trust (project No. 2012–1302). Additional funding was also provided by the Michigan Department of Natural Resources through the State Wildlife Grant Program. I also would like to thank Douglas Larson, John Bauman, and Nathan Barton for their invaluable work managing hatchery production and operations throughout the years of this study. I would also like to thank the seasonal staff at the Black River Sturgeon Rearing Facility, including Shaley Valentine, Zachary Witzel, Andrew Lockwood, Dillon Ross, Ryan Walquist, Jenna Ruzich, Jason Lyons, Rebecca Colby, Garret Johnson, Stefan Tucker, and Adam Chaston for their valuable assistance with the project and with the production and management of the juvenile lake sturgeon. Thanks to Jill Cruth and all MSU support staff for their assistance and guidance. Finally, thanks to my family for their support and encouragement.

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Chapter 1:
Introduction and Summary of Dissertation

Background, Purpose, and Need for the Research

Over the past 150 years the connectivity of our riverine systems in North America has been dramatically altered at the landscape level by the development of dams for hydroelectric power, water storage, and flood control (Cooper et al., 2017; Wang et al., 2011a). Across the United States there are approximately 91,807 dams that fragment river systems, alter habitat, and create barriers that migratory fish must encounter and negotiate over the course of their life history (USACE, 2023). These barriers can delay migration movements, disconnect populations and limit gene flow, reduce access to spawning and rearing habitat, and lead to additional mortality within a system (Barnthouse, 2013; Holbrook et al., 2011; Nyqvist et al., 2017a; Piper et al., 2013; Pracheil et al., 2016). Moreover dams can alter macroinvertebrate and plankton communities, disrupt sediment and nutrient transport, and affect water chemistry and temperature characteristics (Van Looy et al., 2014; Ward and Stanford, 1983). Given that almost every watershed is impacted by dams, research on impacted populations and ways to improve connectivity is imperative and fundamental to the effort to restore imperiled species to our river systems.

Lake sturgeon (*Acipenser fulvescens*) is an adfluvial, potamodromous species that makes annual spring migrations up rivers to spawn and reproduce. Juvenile lake sturgeon rear within their natal river system for a variable amount of time before out-migrating downstream into lakes, reservoirs, or larger rivers to feed and grow (Peterson et al., 2007). The lake sturgeon's migratory life history often brings it into conflict with civil infrastructure and human resource needs across the species' range. Consequently, in most states and provinces the lake sturgeon is now considered to be threatened and is of regulatory and conservation concern (Bruch et al., 2016; Latta, 2005; Peterson et al., 2007).

The rapid development of hydroelectric infrastructure in the late 1800's and early 1900's is one of the major factors that contributed to the historical decline of lake sturgeon populations (Auer and Dempsey, 2013; Peterson et al., 2007). The species was also decimated by overfishing. A valuable commercial fishery developed for lake sturgeon flesh and caviar around 1850, and by the early 1900's many populations began to decline because of over exploitation (Auer and Dempsey, 2013; Peterson et al., 2007). In Lake Michigan the commercial lake sturgeon fishery was closed in 1929 and currently lake sturgeon are estimated to be at only 1% of their historical abundance (Haxton et al., 2014; Tody, 1974). The lethal combination of overfishing, a decline in water quality, habitat loss, and habitat fragmentation is thought to have brought about rapid declines in abundance and extirpation of many lake sturgeon populations (Brousseau, 1987; Harkness and Dymond, 1961; Hay-Chmielewski and Whelan, 1997).

The loss and fragmentation of important riverine habitats by dams is one of the major factors limiting the restoration of lake sturgeon in the Great Lakes (Bruch et al., 2016; Coscarelli et al., 2011; Peterson et al., 2007). Where hydroelectric dams were built they obstructed the migratory movements of lake sturgeon, leading to the loss of spawning and rearing habitat and fragmentation of river systems that once supported the species (Ferguson and Duckworth, 1997; Harkness and Dymond, 1961). In particular, dams were built in areas with the greatest hydraulic head that contained natural rapids, and dams flooded this important spawning habitat and converted it from lotic into lentic habitat (Aadland, 2015; Bruch et al., 2016; Zhong and Power, 1996). Dams can also delay migration movements and cause increased energy expenditure as fish search for passage routes (Holbrook et al., 2011; Nyqvist et al., 2017b; Piper et al., 2013).

Downstream passage through turbine systems and spillways can also cause physical trauma and barotrauma, which can lead to direct mortality and delayed mortality through sublethal effects (Brown et al., 2013; Ferguson et al., 2006; Kynard and Horgan, 2001; Pracheil et al., 2016; Schilt, 2007). Protective bar rack structures meant to protect fish and prevent passage through turbine systems can also inadvertently impinge fish and cause mortality (Barnthouse, 2013; Rytwinski et al., 2017). Furthermore, passage through reservoir systems can subject fish to increased levels of predation due to disorientation in the tailrace, sublethal effects of passage, and changes in habitat caused by dams (Ferguson et al., 2006; Rieman et al., 1991; Ruggerone, 1986). The net result of these impacts is that population recruitment and carrying capacity of river system is often significantly reduced (Huang and Wang, 2018; Pess et al., 2008).

Fish passage engineering has emerged as a possible tool to help reintroduce lake sturgeon above dams and to reconnect fragmented populations disconnected by dams (Boothroyd et al., 2018; Coscarelli et al., 2011; Jager et al., 2016; Koenigs et al., 2018). The spatial extent of the effects of dams on river systems is immense with at least 2,139 dams in Michigan and Wisconsin alone that create barriers and obstruct the movements of migratory fish species (USACE, 2023). Thus, passage solutions are needed to help address wide spread habitat fragmentation and barriers to movement. Most studies and information on fish passage is focused on surface oriented species like salmonids (Cooke et al., 2020; Jager et al., 2016). Limited information is available on route specific passage survival, post-stocking behavior, movements, and entrainment characteristics of juvenile benthic species like lake sturgeon, especially at smaller run-of-the-river hydroelectric dams that are common across the Great Lakes (Bruch et al., 2016; FERC, 2017; Ganus et al., 2018; Hrenchuk et al., 2017; Jager, 2006; Kynard, 1998; Kynard and Horgan, 2001; McDougall et al., 2014a, 2013; Parsley et al., 2007).

Identifying sources and levels of mortality in hydroelectric reservoir systems is vital to lake sturgeon recovery efforts. Young juvenile lake sturgeon are a demographic group of keen interest because they migrate downstream and will often encounter hydroelectric infrastructure and man-made reservoir habitat. In addition, this demographic group is prone to predation (Waraniak et al., 2019, 2018), and many populations suffer from a lack of juvenile recruitment (Coscarelli et al., 2011; Peterson et al., 2007; Pollock et al., 2015). Hydroelectric dams without fish passage systems offer migrating lake sturgeon two passage routes: spillways and turbine systems. A thorough understanding of the mortality characteristics for spillways and different turbine systems that are common in the Great Lakes is necessary to evaluate the potential recruitment benefits of fish passage engineering efforts and reintroduction programs (Coscarelli et al., 2011; Jager et al., 2016; McDougall et al., 2014a). Furthermore, it is important to understand the behavior of juvenile lake sturgeon within reservoirs, how they interact with hydroelectric infrastructure, and the habitats that they use or avoid because this information can guide hatchery supplementation programs and fish passage improvement efforts (Goodwin et al., 2014; Pracheil et al., 2016).

Identifying juvenile lake sturgeon residency and outmigration characteristics and patterns in reservoirs is also vital for determining connectivity between reservoir systems, average age and size at outmigration, suitability of reservoir habitat, and the potential recruitment benefits from supplemental stocking programs or reintroduction efforts (Coscarelli et al., 2011). Also, knowledge of outmigration patterns may be useful in guiding hydroelectric project operations to allow for more efficient and safer passage of out-migrating juveniles (Cooke et al., 2020; Jager et al., 2016). Furthermore, data on age-classes most likely to out-migrate from reservoirs is needed to inform the design of size-class specific downstream passage systems for lake sturgeon (Jager et al., 2016; Kynard et al., 2006; Kynard and Horgan, 2001). Reservoirs also contain different types and compositions of habitats, and there is little long-term monitoring information available on how long juvenile lake sturgeon may use habitat within different sized reservoirs (Coscarelli et al., 2011; Ganus et al., 2018; McDougall et al., 2017, 2014a).

Fisheries research projects that seek to evaluate habitat use, spatial movements, and passage survival at hydro-projects are dependent upon the surgical implantation of acoustic transmitters, radio transmitters, and passive integrated transponders (PIT). Intrinsic to these projects is the assumption that transmitters are not lost and that surgically tagged fish behave and survive similarly compared to un-tagged conspecifics. However, surgical incisions disrupt hemostasis and elicit a whole series of interconnected immune responses (Broughton et al., 2006; Fontenot and Neiffer, 2004). Surgical incisions also involve the direct cutting of connective tissue, muscle tissue, and associated nerves and blood vessels. In addition, the surgically implanted transmitters themselves can add significant weight and can put pressure on internal organs and the incision site (Brown et al., 2010, 1999). This represents a significant physiological impairment that can affect growth, behavior, and survival, which can confound research results (Benson et al., 2005; Panther et al., 2011; Wagner et al., 2011). Unfortunately, most existing research has focused on salmonids and limited clinical information is available on optimal incision placement and closure methods for surgeries on small age-0 juvenile lake sturgeon (Ashton et al., 2017; Crossman et al., 2013; Liss et al., 2018; Miller et al., 2014). Therefore, additional clinical research is warranted to validate and optimize surgical procedures to ensure that study results are accurate.

Dissertation Research Objectives

Chapter 2: Evaluation of Optimal Surgical Incision Placement, Closure Methods, and Transmitter Burden on Surgical Outcomes for Intracoelomic Transmitter Implantation in Age-0 Lake Sturgeon:

1. Determine optimal incision placement (midline vs. lateral) for age-0 lake sturgeon.
2. Assess the suitability of single suture incision closure.
3. Determine the efficacy of surgical adhesive for closing incisions.
4. Evaluate the effects of tag burden (PIT-tag only vs. PIT-tag and acoustic transmitter) on incision healing outcomes.
5. Determine the importance of genetic effects in relation to incision healing characteristics.

Chapter 3: Movements, Habitat Use, and Entrainment of Stocked Age-1 and Age-2 Lake Sturgeon in a Hydroelectric Reservoir System:

1. Assess the movement characteristics of age-1 and age-2 lake sturgeon in a hydroelectric reservoir.
2. Evaluate the spatial habitat use patterns within the reservoir.
3. Determine environmental factors that can influence habitat use patterns.
4. Evaluate entrainment susceptibility of age-1 and age-2 lake sturgeon.

Chapter 4: Juvenile Lake Sturgeon Forebay Behavior and Route-Specific Passage Survival at Two Hydroelectric Dams on the Black River, MI:

1. Quantify passage survival estimates for Kaplan turbine systems for age-0, age-1, and age-2 lake sturgeon.
2. Quantify passage survival estimates for Leffel turbine systems (similar to a Francis turbine system).
3. Quantify passage survival estimates for spillways at hydroelectric dams.
4. Determine the level of delayed mortality resulting from passage.
5. Quantify survival estimates in the free flowing part of the Black River.
6. Document the behavior and habitat use of lake sturgeon in the forebays of Kleber and Tower dams.

Chapter 5: Residency and Outmigration Characteristics of Juvenile Lake Sturgeon Stocked into a Hydroelectric Reservoir System on the Black River, Michigan:

1. Quantify residency characteristics of age-0, age-1, and age-2 lake sturgeon in a hydroelectric reservoir system.
2. Compare residency characteristics between two different sized reservoirs.
3. Determine juvenile lake sturgeon residency characteristics in the free flowing part of the Black River.
4. Investigate the influence of family effects on outmigration behavior.
5. Evaluate the effects of multiple dams on outmigration behavior.
6. Identify temporal environmental cues associated with juvenile lake sturgeon outmigration patterns and timing.

Overview of Methodology

Study Area:

This study was conducted in the upper Black River located in Cheboygan County in northern Michigan (Figure 1.1). 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 17.6 km upstream from the river mouth. The dam was built in 1949 with an average head of 13.4 meters, and it forms a reservoir with 370 hectares 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 an average head of 6.1 meters, and it forms a small reservoir with 76 hectares 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.

Hatchery Production:

All lake sturgeon were reared at the Black River Sturgeon Rearing Facility between April and September in 2014, 2015, and 2016. Some lake sturgeon were produced artificially (i.e., hatchery produced) through the collection of eggs and milt from spawning adult lake sturgeon in the Black River. Adult lake sturgeon within this system are marked with PIT-tags and floy-tags, which allowed us to keep track of family crosses (Crossman et al., 2011). Other lake sturgeon were naturally produced and collected with drift nets during the spring drift season in the lower part of the Black River below the spawning grounds. Naturally produced lake sturgeon larvae that were caught were then transported back to the hatchery for rearing to the appropriate age. To produce the older age-1 and age-2 lake sturgeon some individuals were seasonally transported over to the Wolf Lake State Fish Hatchery and over-wintered each year until they were released.

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-0, age-1, and age-2 lake sturgeon. The dimensions of the transmitters used for age-1 and age-2 lake sturgeon were 5 x 7 x 13 mm, and they weighed 0.6 grams in air. These acoustic transmitters were programmed to have a 10 second transmission rate, with an estimated life expectancy of 180 days. The dimensions of the transmitters used for age-0 lake sturgeon were 3.7 x 5.5 x 11.1 mm, and they weighed 0.32 grams in air. These acoustic transmitters were programmed to have a 15 second transmission rate, with an estimated life expectancy of 100 days. In addition, a 23 x 3.65 mm half-duplex PIT-tag (Oregon RFID, Portland, Oregon) was implanted into each lake sturgeon. The transmitters and PIT-tags were surgically implanted by performing a standard laparotomy. Before surgery, all sturgeon were anesthetized for approximately 5 minutes in an anesthetic bath with 125 mg/L of tricaine methanesulfonate (MS222). 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/L of MS222 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 8-15 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 1-2 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 age-1 and age-2 lake sturgeon were held for at least 4 weeks of post-operative observation and all age-0 lake sturgeon were held for at least 10 days of post-operative observation to ensure proper healing.

In total 140 age-0, 110 age-1, and 110 age-2 lake sturgeon were surgically implanted with acoustic and PIT transmitters. Additionally, a total of 1,664 age-0, 167 age-1, and 37 age-2 lake sturgeon were implanted with only PIT-tags. All lake sturgeon were produced and reared at the Black River Sturgeon Rearing Facility between April and September. The age-1 and age-2 juvenile lake sturgeon produced were 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#: 03/14-041-00).

Surgical Experiment Design:

Four surgical treatments were evaluated in this experiment, along with a control group. All surgical procedures and animal husbandry practices were reviewed and approved by Michigan State University’s animal care program. Two different incision locations and two different closure methods were assessed. Surgical incisions were made ventrally either at the midline along the linea alba or lateral to the midline in the hypaxial musculature anterior to the pelvic girdle. Incisions were either closed with absorbable monofilament suture or with n-butyl-ester cyanoacrylate surgical adhesive (Vetbond®, 3M). A total of 32 lake sturgeon were evaluated for each surgical treatment, and a total of 16 lake sturgeon were evaluated in the control group. Half of the lake sturgeon in each surgical treatment were surgically implanted with only PIT-tags, while the remaining half were implanted with PIT-tags and acoustic transmitters to assess the influence of tag burden and design. The PIT-tags used were cylindrical in shape, 23 mm long, 3.65 mm in diameter, and weighed 0.6 grams (Oregon RFID, Portland, Oregon). The acoustic transmitters used were part of the line of transmitters developed by the U.S. Army Corps of Engineers for the Juvenile Salmonid Acoustic Telemetry System (JSATS). These transmitters are irregularly shaped with a length of 11.1 mm, a width of 5.5 mm, a height of 3.7 mm, and they weighed 0.32 grams (Lotek Wireless Inc., Newmarket, Ontario, Canada; model: L-AMT-1.421).

A total of sixteen 26.2 liter tanks were utilized to house all of the lake sturgeon used in this experiment. Three different families were also used in the experiment to examine genetic effects. The first family consisted of 36 fish, the second family consisted of 54 fish, and the third family consisted of 54 fish. Two fish from each surgical treatment category were placed in each tank. One fish from each treatment category was surgically implanted with only a PIT-tag, while the other fish from the treatment was surgically implanted with a PIT-tag and an acoustic transmitter. In addition, one control fish was placed in each tank, bringing the total number of fish in each tank to nine. The order in which the tanks were filled was randomized, as was the order in which the families were selected to fill a tank. A given tank was filled with nine fish from the same family. Furthermore, the order in which the surgical treatments were carried out for each tank was also randomized in order to reduce bias. Because the treatment types were all mixed together in each tank, each treatment was proportionately influenced by individual tank conditions, making the design robust against confounding tank effects. In the event that a mortality occurred in a given tank, a replacement fish, which did not undergo surgery, was substituted for the deceased fish in order to maintain equal fish densities in each tank throughout the experiment.

Experimental Release of Lake Sturgeon:

Juvenile lake sturgeon were released in 2014, 2015, and 2016. Age-1 and age-2 lake sturgeon were released in small groups of 10-12 individuals, while age-0 lake sturgeon were released in larger groups of approximately 50 individuals. Smaller release groups were used to avoid possible negative effects associated with high stocking densities, which could alter behavior. A total of 790 age-0, 114 age-1, and 61 age-2 lake sturgeon were released upstream of Tower Reservoir (Figure 1.1). A total of 813 age-0, 118 age-1, and 61 age-2 lake sturgeon were released upstream of Kleber Reservoir. A total of 201 age-0, 45 age-1, and 25 age-2 lake sturgeon were released below Kleber Dam. Age-0 lake sturgeon were released in September of each year, while age-1 and age-2 lake sturgeon were released between July and September of each year.

Passive Movement and Entrainment Monitoring:

To monitor movements and entrainment we used PIT-tag monitoring technology and acoustic telemetry. 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 (Figure 1.1). 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 approximately 300 meters 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 located 0.85 km upstream from the river mouth where the Black River empties into Black Lake. We also installed several RFID PIT-tag detection antennas below Tower Dam. This included two antennas below the powerhouse, two antennas below the spillway, and one large stream-wide antenna approximately 500 meters downstream. Hydrophone arrays were deployed in the forebays of both dams to detect acoustic transmitters, and these arrays were operated during the 2015 and 2016 field seasons.

Active Tracking in Kleber Reservoir:

The active tracking survey was conducted between mid-July and mid-September in 2015 and 2016 in Kleber Reservoir. The shallow depth and abundant macrophyte vegetation precluded us from carrying out an effective acoustic survey on Tower Reservoir. For the survey on Kleber Reservoir, we divided the reservoir into 32 zones that were spaced approximately

100 meters apart (Figure 1.1). 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 minutes between 9:00 – 17:00 hours. Repeat visits to a given census zone were separated by a minimum of 3 days. In total, we surveyed each zone 18 times over the course of the project.

Based on detection range tests that we conducted in the reservoir, the WHS4250 hydrophones can readily detect JSATS transmitters within 100 meters; however, the detection efficiency of the equipment rapidly diminishes beyond 100 meters. Generally, the max detection distance for JSATS transmitters is 200 meters (McMichael et al., 2010). For a detection to be validated, the transmitter's ID had to be detected at least twice in a 40 second time period. In addition to the paired detection requirement, we also required that a total of four detections be registered within a 120 second 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.

Habitat Mapping:

We used a high definition side-scan sonar unit (Humminbird, Eufaula, AL; Model: 999ci HD SI Combo Unit) to record depth, hardness, roughness, and side-scan sonar imaging data of

Kleber Reservoir and Tower Reservoir. 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 order to capture data, the sonar unit's transducer was mounted at the bow of the boat, and we followed pre-planned transect lines that crisscrossed the entire reservoir system. In total, we obtained over 40,000 depth, hardness, and roughness measurements. In order to evaluate the accuracy of our habitat mapping, we conducted a ground-truthing survey. 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.

Dissertation Research Outcomes

Chapter 2: Evaluation of Optimal Surgical Incision Placement, Closure Methods, and Transmitter Burden on Surgical Outcomes for Intracoelomic Transmitter Implantation in Age-0 Lake Sturgeon:

Based on the results of the surgical experiment, the risk of death was 5.17 times higher and the risk of viscera expulsion was 6.21 times higher for age-0 lake sturgeon sturgeon that had midline incisions closed with Vetbond compared to all other treatments. Open incision width and length was minimal for all treatments, except for midline incisions closed with Vetbond. However, incision closure was notably weaker for midline incisions closed with suture. The risk of PIT-tag loss was 6.21 times higher and the risk of acoustic transmitter loss was 3.06 times higher for midline incisions closed with Vetbond compared to all other treatments. Sturgeon with midline incisions closed with Vetbond gained less weight compared to the other treatments, while sturgeon with lateral incisions closed with Vetbond gained similar amounts of weight relative to both suture treatments and the control group. Inflammation was very low and slightly decreased over time for incisions closed with Vetbond, while incisions closed with suture exhibited significant increases in inflammation levels over time. Time to complete healing was shortest for incisions closed with suture followed closely by lateral incisions closed with Vetbond. However, for incisions closed with suture the healing process was 2-3 times more likely to relapse because of severe inflammation compared to lateral incisions closed with Vetbond.

Chapter 3: Movements, Habitat Use, and Entrainment of Stocked Age-1 and Age-2 Lake Sturgeon in a Hydroelectric Reservoir System:

We used acoustic telemetry to track the movements of 47 age-1 and age-2 juvenile lake sturgeon (*Acipenser fulvescens*) throughout Kleber Reservoir in northern Michigan. On average lake sturgeon moved 502 meters (SD = 423.18) between telemetry positions, and they moved an average total distance of 1138 meters (SD = 917.07), with age-2 lake sturgeon making longer distance movements than age-1 lake sturgeon. The spatial analysis showed that 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. Our analyses showed that 66.4% of the variance in habitat use could be explained by physical habitat features. Reservoir areas with ample deep water habitat, fine soft substrates, and limited macrophyte vegetation were the most frequently occupied. We also observed that 54.4% of the age-1 and 52.8% of the age-2 lake sturgeon stocked into Kleber Reservoir were entrained during the study.

Chapter 4: Juvenile Lake Sturgeon Forebay Behavior and Route-Specific Passage Survival at Two Hydroelectric Dams on the Black River, MI:

Our observations showed that juvenile lake sturgeon usually made between 1 – 4 approaches into the forebays of both dams and usually stayed within a forebay for several hours before departing. Detections were primarily clustered in a broad area over the deepest part of the forebay downslope of the spillway at Kleber Dam, while at Tower Dam detections were clustered in the deeper part of the forebay immediately adjacent to the spillway and penstocks. Habitat use at both dams was higher in areas with more silt habitat and less aquatic vegetation and in areas that had greater mean depth and greater max depth characteristics. At Kleber Dam the survival rates for passage through the vertical-shaft Kaplan turbine systems were estimated at 70.9% (SE = 0.093) for age-0 and 44.9% (SE = 0.138) for age-1 and age-2 lake sturgeon. Delayed mortality accounted for approximately 10% of the total mortality observed at the Kleber Dam powerhouse. At Tower Dam survival through the Leffel type-z vertical-shaft turbine systems was estimated at 86.9% (SE = 0.135) for age-0 and 59.9% (SE = 0.182) for age-1 and age-2 lake sturgeon. Passage survival through the Tower Dam Spillway was estimated at 100% (SE = 0.132) for age-0 and 100% (SE = 0.188) for age-1 and age-2 lake sturgeon. Impingement mortality at Tower Dam differed by age and was 0.4% for age-0, 13.3% for age-1, and 21.8% for age-2 lake sturgeon, while impingement mortality at Kleber Dam was not observed.

Chapter 5: Residency and Outmigration Characteristics of Juvenile Lake Sturgeon Stocked into a Hydroelectric Reservoir System on the Black River, Michigan:

We conducted a 4-year study to assess the behavioral response of stocking age-0, age-1, and age-2 lake sturgeon into two different sized reservoirs on the Black River in northern Michigan. The majority of observed juveniles out-migrated from the reservoir system in less than 60 days and greater than 90% of movements occurred at night. However, of the age-0 lake sturgeon observed 37% stayed in the reservoir system for more than 179 days and 11% stayed in the reservoir system for more than 499 days. Of the age-1 and age-2 lake sturgeon observed 27% stayed in the reservoir system for more than 179 days and 10% stayed in the reservoir system for more than 499 days. The age-0 lake sturgeon resided within the reservoir system and in the free flowing part of the river for longer periods of time compared with the older lake sturgeon. We further observed that juveniles had shorter residency times in the smaller reservoir with shallower bathymetry compared with the larger reservoir. We also found that family group and production origin (hatchery produced vs. naturally produced) can have an influence on residency behavior. Outmigration numbers consistently peaked in the spring and fall months and were found to be related to temporal changes in water temperature and discharge levels. Water temperature was specifically found to have a threshold type relationship with outmigration numbers.

Dissertation Research Implications

Chapter 2: Evaluation of Optimal Surgical Incision Placement, Closure Methods, and Transmitter Burden on Surgical Outcomes for Intracoelomic Transmitter Implantation in Age-0 Lake Sturgeon:

In mammals Moncryl absorbable monofilament suture (Ethicon, Somerville, New Jersey) has been shown to lose all of its tensile strength at 28 days post-surgery, but the suture material itself is not fully absorbed until 91-119 days post-surgery (Dunn, 2007). This is a fact that is commonly overlooked in telemetry studies, as inflammation will continue to worsen until either the suture material is removed or it is completely absorbed. The inflammation can directly affect the health and behavior of the fish under study, which can confound the results of important research (Bridger and Booth, 2003; Deters et al., 2012; Guo and DiPietro, 2010). The advantage of Vetbond is that the adhesive provides short-term approximation and rapidly dissolves from the tissue over 7 days, largely averting the harmful effects of inflammation that can reverse the healing process (Petering and Johnson, 1991).

Collectively, our results suggest that Vetbond can be safely used to close small lateral incisions (≤ 8 mm) as effectively as sutures, with a much lower risk of severe inflammation. For transmitter implantation, we recommend using a lateral incision through the hypaxial musculature and either closing the incision with suture or Vetbond. If the suture material is not able to be removed before the fish is released, then Vetbond would be the preferred closure method. Our maximum tag burden (0.92 g) was relatively small and the juvenile lake sturgeon tested were sufficiently large (mean weight: 30 g), which likely contributed to the small effect of tag burden in our analyses. Larger tag burdens on smaller fish will likely lead to further complications, as other researchers have noted (Ashton et al., 2017; Brown et al., 2010, 1999).

Chapter 3: Movements, Habitat Use, and Entrainment of Stocked Age-1 and Age-2 Lake Sturgeon in a Hydroelectric Reservoir System:

Our research clearly showed that juvenile lake sturgeon used deep water habitat in areas with fine sediments and limited aquatic vegetation. Consequently, reservoirs with ample deep water 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. Reservoirs lacking this type of habitat may not be able to support juvenile lake sturgeon for long periods of time, which may result in greater entrainment rates. In Kleber Reservoir the highest quality habitat was located adjacent to the dam, making juvenile lake sturgeon susceptible to entrainment. The spatial layout of optimal habitat within a reservoir in relation to hydroelectric infrastructure should be assessed when planning reintroduction programs and in the design of downstream passage systems. The abundance and location of aquatic macrophytes may modify and restrict juvenile lake sturgeon movements, which may be useful in purposely directing movements to bypass systems and in limiting entrainment susceptibility and mortality. Based on our results, the stocking of juvenile lake sturgeon into small reservoir systems will likely result in a significant proportion being entrained, and reintroduction efforts should take into account the morphology of the reservoir and the location of high quality habitats in relation to hydroelectric infrastructure during planning.

Chapter 4: Juvenile Lake Sturgeon Forebay Behavior and Route-Specific Passage Survival at Two Hydroelectric Dams on the Black River, MI:

Forebay characteristics like bathymetry and aquatic vegetation may be key factors that can influence forebay movements, residency time, entrainment susceptibility, and the success of fish passage engineering efforts. The apparent aversion that lake sturgeon have for aquatic vegetation could be used to help guide juveniles toward safer passage routes at hydroelectric dams. The fact that juvenile lake sturgeon of all ages spent a considerable amount of time using habitat in front of the dams, may be promising for the design of passage systems that can engage juvenile lake sturgeon to pass through safer routes.

The older and larger lake sturgeon had much higher turbine passage mortality rates, indicating that age and size at passage are key variables that can influence survival and recruitment. The Kaplan turbine system was observed to cause higher levels of mortality compared with the Leffel turbine system. River systems that have similar Leffel turbine systems on them would likely have higher net juvenile recruitment rates compared with river systems with similar Kaplan turbine systems and may require less fish passage engineering efforts to achieve acceptable project survival rates. Our results also showed that spillways are associated with very little mortality and are the preferred passage route. Operations at dams may be able to be modified to increase passage through spillways at certain times of the years to enhance survival. Passage engineering efforts should focus on behavioral guidance mechanisms within the forebay that can guide juveniles safely into spillways or bypass systems.

The smaller 2.5 cm vertical bar-rack spacing at Tower Dam and possible hydraulic flow differences may have contributed to the higher observed impingement mortality compared with Kleber Dam, which has 7.6 cm vertical bar-rack spacing. Past research has shown that lake sturgeon are poor swimmers compared to salmonids (Peake et al., 1997). Specifically, the geometry of the lake sturgeon tail generates 18% less thrust compared to trout over sustained and prolonged swimming speeds, and the body of a sturgeon generates approximately 3.5 times more drag compared with trout (Webb, 1986). This makes lake sturgeon uniquely vulnerable to impingement, as observed in our study, and provides engineering challenges. Our results clearly indicate that bar-rack spacing and structure design has the potential to greatly impact impingement mortality and the net recruitment of juveniles (Rytwinski et al., 2017). Flow rates around bar-rack structures must be a major consideration in the evaluation and design of lake sturgeon passage systems.

Chapter 5: Residency and Outmigration Characteristics of Juvenile Lake Sturgeon Stocked into a Hydroelectric Reservoir System on the Black River, Michigan:

In summary, our results indicate that the majority of juvenile lake sturgeon will out-migrate rapidly from small reservoir systems in the fall and spring after stocking and that outmigration movements are nocturnal. However, our data also showed that lake sturgeon can persist within and rely upon resources in small reservoirs for extended periods of time over multiple years. Outmigration from reservoirs was largely initiated by seasonal changes in water temperatures and discharge during the spring and fall. Therefore, through the monitoring of water temperature and discharge dynamics hydroelectric projects can identify peak outmigration time periods over which operations may be able to be modified. Specifically, operations at dams may be able to be modified to take advantage of outmigration behavior through the selective operation of spillways at night during these peak outmigration time periods to facilitate safer passage and improve recruitment of juvenile lake sturgeon. The bathymetry characteristics of a reservoir may also heavily influence the level of residency and entrainment in a system. Reservoirs that are smaller and shallower are expected to have lower long-term residency rates compared with larger reservoirs. As reservoir size and habitat quality increases the length of residency is expected to also increase. As residency time increases the greater the number of age cohorts within a reservoir, which would result in larger juveniles inhabiting the reservoir and encountering hydroelectric dam infrastructure during outmigration. Therefore, age and size related factors need to be considered based on the characteristics of the reservoir system when engineering passage systems for juvenile lake sturgeon.

Figures

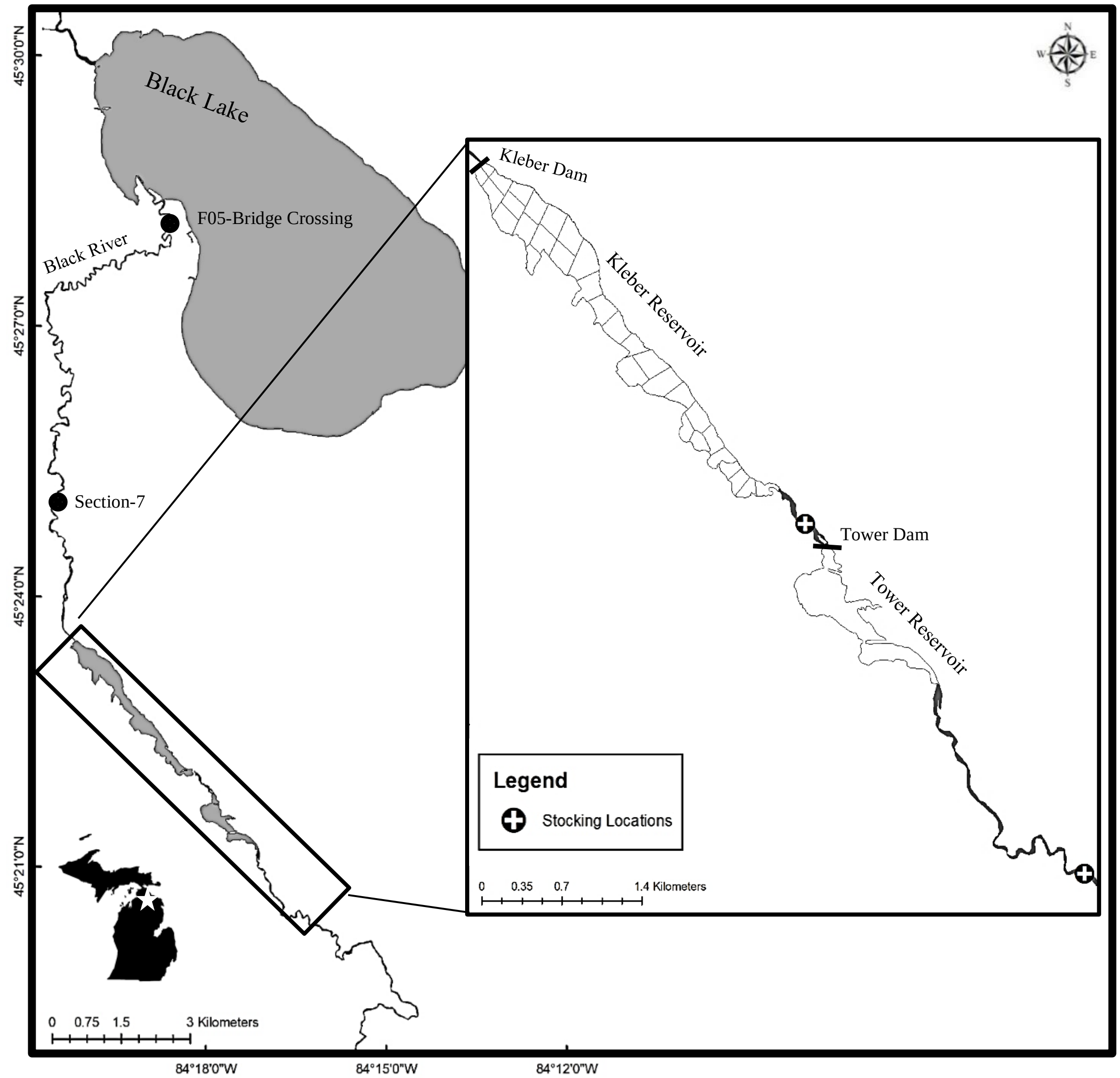

Figure 1.1: Map of Black Lake and the upper Black River system located in Cheboygan County, Michigan. The inset map highlights Kleber Dam, Kleber Reservoir, Tower Dam, and Tower Reservoir, along with the lake sturgeon stocking locations used for the research project. PIT-tag antennas were located at the F05-bridge crossing, section-7, Kleber Dam, and at Tower Dam.

Chapter 2:
Evaluation of Optimal Surgical Techniques for Intracoelomic Transmitter Implantation in Age-0 Lake Sturgeon

Reprinted with permission from Hegna, J., Scribner, K., Baker, E., 2019. Evaluation of optimal surgical techniques for intracoelomic transmitter implantation in age-0 lake sturgeon. Fish. Res. 218, 198–208. https://doi.org/10.1016/J.FISHRES.2019.05.017.

Abstract

We evaluated the effects of incision placement (midline vs. lateral), closure method (absorbable monofilament suture vs. n-butyl-ester cyanoacrylate adhesive, Vetbond®, 3M), and tag burden (PIT-tag only vs. PIT-tag and acoustic transmitter) on survival, post-operative complications (i.e., viscera expulsion, necrosis), incision dehiscence, incision apposition, transmitter retention, incision healing, inflammation, and growth for intracoelomic transmitter implantation in age-0 lake sturgeon (*Acipenser fulvescens*). The risk of death was 5.17 times higher and the risk of viscera expulsion was 6.21 times higher for sturgeon that had midline incisions closed with Vetbond compared to all other treatments. Incision dehiscence probabilities were low for all treatments, except for midline incisions closed with Vetbond. Time to complete incision apposition occurred most quickly in the lateral suture treatment followed closely by the midline suture and lateral vetbond treatment groups. Tissue strength was notably weaker in the midline region. Transmitter retention was 100% for all treatments except for midline incisions closed with Vetbond. Inflammation was low and slightly decreased over time for incisions closed with Vetbond, while incisions closed with suture exhibited significant increases in inflammation levels over time. Incisions closed with suture achieved better healing outcomes initially, but the healing process was 2-3 times more likely to relapse

because of severe inflammation compared to lateral incisions closed with Vetbond. Sturgeon with midline incisions closed with Vetbond gained less weight compared to the other treatments, while sturgeon with lateral incisions closed with Vetbond gained similar amounts of weight relative to both suture treatments and the control group. Collectively, results suggest that Vetbond can be effectively used to close small lateral incisions (≤ 8 mm), with a lower risk of severe inflammation compared with sutures. For transmitter implantation, we recommend using a lateral incision through the hypaxial musculature and either closing the incision with suture or Vetbond.

Introduction

In telemetry and long-term monitoring studies the surgical implantation of acoustic transmitters, radio transmitters, and passive integrated transponder (PIT) tags is vital to fisheries research projects that seek to evaluate habitat use, spatial movements, and passage survival at hydroelectric projects. Intrinsic to these projects is the assumption that transmitters are not lost and that surgically tagged fish behave and survive similarly compared to un-tagged conspecifics. However, surgical incisions disrupt homeostasis and elicit a whole series of interconnected immune responses (Broughton et al., 2006; Fontenot and Neiffer, 2004). The process through which incisions are healed is intricate and dynamic, and it involves four stages in vertebrates: hemostasis, inflammation, proliferation, and remodeling (Guo and DiPietro, 2010). Surgical incisions involve the cutting of connective tissue, muscle tissue, and associated nerves and blood vessels. In addition, the surgically implanted transmitters themselves can add significant weight and can put pressure on internal organs and the incision site (Brown et al., 2010, 1999). This represents a significant physiological impairment that can affect growth, behavior, and survival, which can confound research results (Benson et al., 2005; Panther et al., 2011; Wagner et al., 2011). Thus, significant clinical evidence is required to validate and optimize surgical procedures.

There are many factors that can delay incision healing, but the primary factors usually are dehiscence, poor apposition, and inflammation (Boyd et al., 2011; Guo and DiPietro, 2010; Miller et al., 2014; Petering and Johnson, 1991). Dehiscence and poor apposition cause incisions to heal through a longer process termed secondary intention instead of through primary intention (Barbul, 2005; Panther et al., 2011). In secondary intention the gap between the incised tissues must be filled with fibrous granulation tissue. This granulation tissue is then able to contract and close the incision opening via myofibroblasts (Barbul, 2005; Panther et al., 2011). Inflammation is a natural part of the incision healing process, but prolonged inflammation can cause the healing process to relapse (Guo and DiPietro, 2010; Miller et al., 2014). Inflammation may be prolonged because of the inefficient removal of microbes and decontamination of the wound site, which leads to elevated levels of pro-inflammatory cytokines (Guo and DiPietro, 2010; Koh and DiPietro, 2011). In telemetry studies inflammation can also be prolonged by suture material, which elicits a foreign body immune response. Unless the suture material is promptly removed the inflammation can persist for long periods of time, as most suture material takes longer than 90 days to be completely absorbed (Dunn, 2007). In addition, prolonged inflammation results in higher levels of metalloproteases at the incision site, and these proteases degrade the newly forming extracellular matrix of the wound, reversing healing progress (Guo and DiPietro, 2010). Over time this can lead to the complete dehiscence of the incision, thereby, completely reversing the healing process (Miller et al., 2014). Many researchers are not able to hold their tagged fish for post-operative evaluations and suture removal. Consequently, researchers may be unaware that their study fish are exhibiting severe inflammation that is harming the healing process and potentially affecting health and behavior.

There are two main incision locations that have been used for intracoelomic transmitter implantation in fishes. Incisions can be made along the midline linea alba, which is composed of less perfused connective tissue, in both salmonids (Panther et al., 2011; Wagner et al., 2011) and sturgeon (Murray, 2002; Smith and King, 2005). In humans this is the preferred incision location because it is associated with quicker healing, stronger closure, and less muscle and nerve damage (Rath et al., 1996; Tera and Aberg, 1977). Alternatively, incisions can be made parallel and lateral to the midline through the hypaxial musculature in both salmonids (Wagner et al., 2011) and sturgeon (Crossman et al., 2013; Liss et al., 2018; Miller et al., 2014). Lateral incisions can cause both muscle and nerve damage, which can take longer to heal (Burger et al., 2002; Tera and Aberg, 1977; Wagner et al., 2011). One commonly cited benefit of lateral incisions in salmonids is that the incision is located in an anatomic region that is less vulnerable to contact with bottom substrate and debris; however, in dorsal-ventrally flattened fish, like lake sturgeon (*Acipenser fulvescens*), there is no such benefit (CCAC, 2005; Wagner et al., 2011). While studies have compared optimal incision site location in salmonids (Panther et al., 2011; Wagner and Stevens, 2000), to our knowledge only one study has evaluated the subject matter on age-0 white sturgeon (Liss et al., 2018) and no comparable studies have examined optimal incision placement in age-0 lake sturgeon.

Incisions can be closed with a variety of methods. Absorbable monofilament suture material is commonly used for closing incisions in salmonids (Deters et al., 2010; Wagner et al., 2011) and sturgeon (Boone et al., 2013; Hondorp et al., 2015; Liss et al., 2018). The simple interrupted closure pattern is also routinely used to close incisions in salmonids (Deters et al., 2012; Wagner et al., 2011) and sturgeon (Hondorp et al., 2015; Liss et al., 2018), as it provides high closure strength and requires less suture material than mattress patterns, which are often associated with more inflammation (Deters et al., 2012; Wagner et al., 2011). Transmitters have continued to decrease in size and this has subsequently led to a reduction in incision length. Traditionally at least two sutures have been used to close incisions, but the reduction in incision length now makes single suture closure and even self-closure (i.e., no suture or closure method) possible (Deters et al., 2012; Liss et al., 2018; Wagner et al., 2011). Using less suture material is advantageous because less foreign material in tissues results in less problematic inflammation and better incision healing (Deters et al., 2012; Liss et al., 2018; Miller et al., 2014).

Surgical grade adhesives (i.e., n-Butyl cyanoacrylate and octyl cyanoacrylate) are another option for closing increasingly smaller incisions, and surgical grade adhesives are generally bactericidal, dissolve rapidly, and do not illicit a strong inflammatory response (Bhagat and Becker, 2017; Bruns and Worthington, 2000; Elmasalme et al., 1995; Romero et al., 2009). To our knowledge there are only two studies that have evaluated the efficacy of a surgical grade adhesive for incision closure in fish (Jepsen et al., 2017; Lowartz et al., 1999). The few other studies available on the subject have examined household superglue, ethyl 2-cyanoacrylate (Baras and Jeandrain, 1998; Kaseloo et al., 1992; Nemetz and Macmillan, 1988;

Petering and Johnson, 1991). Some studies examining adhesives have found that it is associated with poor closure and tissue inflammation, while other studies have observed strong closure and minimal inflammation. Household superglue was once used in medical procedures, but it is now considered medically contraindicated because it is severely cytotoxic (Sohn et al., 2016; Toriumi et al., 1990). No studies that we are aware of have evaluated the efficacy of adhesives for closing incisions on sturgeon.

Over the past two decades there has been increased research interest and regulatory concern regarding juvenile lake sturgeon passage behavior and survival at hydroelectric dams (Coscarelli et al., 2011; Jager et al., 2016). In regulatory survival studies it is imperative that surgical procedures do not affect survival or behavior. The significant lack of information on optimal surgical incision placement and closure methods for age-0 lake sturgeon led to the development of this project. In this study our objectives were to evaluate (1) optimal incision placement (midline vs. lateral), (2) the suitability of single suture incision closure, (3) the efficacy of surgical adhesive for closing incisions, (4) the influence of tag burden (PIT-tag only vs. PIT-tag and acoustic transmitter), and (5) the importance of family genetic effects in relation to incision dehiscence characteristics, incision apposition quality, inflammation, incision healing, transmitter retention, and mortality.

Methodology

Surgical Treatments:

Four surgical treatments were evaluated, along with a control group. All surgical procedures and animal husbandry practices were reviewed and approved by Michigan State University's animal care program (IACUC#: 03/14-041-00). Two different incision locations and two different closure methods were assessed. Surgical incisions were made ventrally either at the midline along the linea alba or lateral and parallel to the midline in the hypaxial musculature anterior to the pelvic girdle. Incisions were either closed with a single interrupted absorbable monofilament suture or with n-butyl-ester cyanoacrylate surgical adhesive (Vetbond®, 3M). A total of 32 lake sturgeon were evaluated for each surgical treatment, and a total of 16 lake sturgeon were evaluated in the control group. Half of the lake sturgeon in each surgical treatment were surgically implanted with only PIT-tags, while the remaining half were implanted with PIT-tags and acoustic transmitters to assess the influence of tag burden and design. The PIT-tags used were cylindrical in shape, 23 mm long, 3.65 mm in diameter, and weighed 0.6 grams (Oregon RFID, Portland, Oregon; Figure 2.1b). The acoustic transmitters used were developed by the U.S. Army Corps of Engineers for the Juvenile Salmonid Acoustic Telemetry System (JSATS). These transmitters are irregularly shaped with a length of 11.1 mm, a width of 5.5 mm, a height of 3.7 mm, and they weighed 0.32 grams (Lotek Wireless Inc., Newmarket, Ontario, Canada; model: L-AMT-1.421; Figure 2.1a).

The different treatments have been abbreviated to facilitate discussion. The MS (midline-suture) treatment consisted of a midline incision closed with suture; the LS (lateral-suture) treatment consisted of a lateral incision closed with suture; the MV (midline-Vetbond) treatment consisted of a midline incision closed with Vetbond; the LV (lateral-Vetbond) treatment consisted of a lateral incision closed with Vetbond; and the CA (control anesthetic only) or control group treatment consisted of the group of control fish that did not receive an incision, but did undergo general anesthesia and were placed on the operating table for five minutes as though they were having a surgery.

Experimental Design:

A total of sixteen 26.2 liter tanks were utilized to house all lake sturgeon used in this experiment. Three different families were also used in the experiment to examine family genetic effects. The first family consisted of 36 fish, the second family consisted of 54 fish, and the third family consisted of 54 fish. Two fish from each surgical treatment category were placed in each tank. One fish from each treatment category was surgically implanted with only a PIT-tag, while the other fish from the treatment was surgically implanted with a PIT-tag and an acoustic transmitter. In addition, one control fish was placed in each tank, bringing the total number of fish in each tank to nine. The order in which the tanks were filled was randomized, as was the order in which the families were selected to fill a tank. A given tank was filled with nine fish from the same family. Furthermore, the order in which the surgical treatments were carried out for each tank was also randomized in order to reduce bias. Because the treatment types were all mixed together in each tank, each treatment was proportionately influenced by individual tank conditions, making the design robust to confounding tank effects. In the event that a mortality occurred in a given tank, a replacement fish, which did not undergo surgery, was substituted for the deceased fish in order to maintain equal fish densities in each tank throughout the experiment.

Fish Husbandry:

The 16 experimental tanks were housed at the Black River Sturgeon Rearing Facility along the Black River in Cheboygan County, Michigan. The Black River Sturgeon Rearing Facility is a streamside hatchery that uses continuously pumped river water from Kleber Reservoir (~680 L/min). Water entered each tank from above at a uniform flow rate and no water was recirculated. The lake sturgeon in each tank were fed approximately 10% of their body weight in bloodworms per day over three daily feeding times (Aloisi et al., 2006). Tanks were cleaned and maintained on a daily basis, and uneaten food was removed to ensure a healthy environment. Water temperature was recorded every hour with the use of an Onset Hobo temperature logger (Bourne, Massachusetts), and the average water temperature over the study was 20.47 °C (SD = 1.809, Range: 16.13 – 24.31 °C) . All lake sturgeon were kept and monitored within the tanks for a total of 21 days.

Surgical Procedures:

Surgical procedures were carried out in 2016 between September 1st and September 6th by one experienced surgeon (Jonathan Hegna) in order to avoid the confounding effects of using multiple surgeons. All of the lake sturgeon used had been raised in the stream-side hatchery and were previously acclimated to the water conditions. Before surgery, sturgeon were anesthetized for approximately 5 minutes in an anesthetic bath with 125 mg/L of tricaine methanesulfonate (MS222). Once a sturgeon became fully sedated based on visually observing a loss of reflexes, slow heart rate, and slow opercular movements, wet weight and total length measurements were taken. On average the age-0 lake sturgeon weighed 30.23 g (SD = 4.308, Range: 20.3 – 43.6) and were 205.47 mm in total length (SD = 10.451, Range: 168 – 231). Average tag burden as a percent of total body weight was 1.99% (SD = 0.290, Range: 1.38 – 2.67%) for sturgeon implanted with only PIT-tags and 3.15% (SD = 0.450, Range: 2.44 – 4.53%) for sturgeon implanted with a PIT-tag and an acoustic transmitter. The sturgeon was then placed ventrally on the operating table and an oxygenated maintenance dose of 100 mg/L of MS222 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. Protective padding was used on the operating table to prevent abrasions and injury. The randomized surgical treatment type was then carried out with the appropriate incision location and closure method. Sturgeon in the control group underwent the anesthetic bath and were put on the operating table with the maintenance dose for a total of five minutes, but they did not receive a surgical incision or transmitter. However, sturgeon in the control group did receive a small dorsal fin clip for identification.

Incision sites were disinfected with a 10% betadine solution prior to making the incision. Surgical incisions were either made ventrally at the midline along the linea alba or lateral to the midline anterior to the pelvic girdle with a size 15 surgical blade. Surgical incisions were measured to 8 mm in length with the use of a caliper. Incisions were either closed with one simple interrupted absorbable monofilament suture or with Vetbond. The suture was pre-sterilized with ethylene oxide and consisted of absorbable, monofilament polyglycolide-cocaprolactone 5-0 suture material (PGCL Unify®, AD-Surgical, Sunnyvale, California; comparable to Monocryl, Ethicon®) with pre-attached 3/8ths curvature, reverse-cutting suture needles. Olsen-hegar needle holders and small soft tissue forceps were also used during the operation. In order to apply the Vetbond, the two edges of the incision were firmly apposed by hand. Then one drop of Vetbond was applied and allowed to air dry for approximately 15 seconds, forming a thin coating over the incision. A second drop was subsequently added to the incision forming an additional adhesive coat that was allowed to air dry for an additional 20-30 seconds. Only a thin coating of the adhesive is recommended by the manufacturer (3M Health Care, 2016), and attention was given to avoid pooling of the adhesive on the skin. After the incision was securely closed, the sturgeon was then placed in its experimental tank and monitored until motor control was regained. We recorded the total time of the surgery starting from when the sturgeon were placed on and removed from the operating table. On average the MS treatment took 3.55 minutes (SD = 0.645, Range: 2.38 – 5.08 mins), the LS treatment took 4.00 minutes (SD = 1.009, Range: 2.13 – 7.67 mins), the MV treatment took 3.46 minutes (SD = 0.948, Range: 2.23 – 6.41 min), and the LV treatment took 3.35 minutes (SD = 0.743, Range: 2.32 – 5.08 mins). Between surgeries the surgical table and maintenance dose tubing was disinfected with a 10% betadine solution. All surgical instruments were disinfected with 95% ethanol for a minimum of ten minutes.

Post-Operative Evaluations:

Post-operative evaluations were conducted every seven days for three weeks. Sturgeon were placed in an anesthetic bath for five minutes until they were completely sedated prior to evaluation. At each evaluation we noted surgical complications and irregularities with the healing process. Surgical complications mainly included viscera expulsion and tissue necrosis (Figure 2.2k). We also recorded how long Vetbond remained at the incision site and whether it caused severe inflammation or delayed healing. Each tank was also monitored multiple times each day for mortalities.

A number of different measurements were also taken during each evaluation, including open incision width and length (i.e., dehiscence characteristics; Figure 2.2j). We also measured un-apposed incision width and length (Figure 2.2i). Open incision width and un-apposed incision width were measured at the location where the width was greatest. Incision apposition refers to how closely aligned the two edges of the incision are. Some closure methods are not as effective at apposition and may result in scar tissue forming between the two incision edges, which ultimately closes the incision through secondary intention. In other cases, extremely poor apposition leads to dehiscence of the incision resulting in open incision width and length. Each tank was monitored multiple times each day for transmitters that may have fallen out of open incisions.

We also scored inflammation characteristics using a point-based rating system adapted from Wagner and Stevens (2000). Inflammation was rated from 1 to 4 along the margin of the incision, with a higher number indicating more inflammation along the incision. A rating of 1 indicated that no inflammation was present, a rating of 2 indicated that there was little inflammation along the incision site (i.e., less than 10% of incision site inflamed), a rating of 3 indicated that there was little to moderate inflammation along the incision site (i.e., 10-50% of incision site inflamed), and a rating of 4 indicated that there was moderate to high inflammation (i.e., up to 100% of incision site inflamed; Figure 2.2a,b,c,e). Suture entrance and exit sites were rated on a binary basis regarding whether they exhibited inflammation or not. Furthermore, each suture site was also rated on a binary basis regarding whether it exhibited severe inflammation or not (Figure 2.2f,g,h). The rating scores for incision inflammation, suture site inflammation, and severe suture site inflammation were then summed together to determine the total level of inflammation.

In addition, we scored the incision healing process using a rating index adapted from Wagner and Stevens (2000) that ranged from 1 to 8 (Table 1; Figure 2.2). The rating scale takes into account incision dehiscence, incision apposition, scar tissue formation, and inflammation. A rating of 1 indicates that the incision has healed, is completely secure, and that there is little to no inflammation, while a rating of 8 indicates that the incision is completely open. On the final post-operative evaluation on day 21 the sturgeon were weighed and their total length was measured again. This allowed total weight gain (g) and total length increase (mm) for the three week experimental time period to be determined.

Statistical Analyses:

Restricted maximum likelihood (REML) based mixed effects models were used to evaluate initial weight and length differences among treatments, along with incision healing scores and inflammation scores by treatment and week. In all relevant analyses fixed factors included surgical treatment group, tag burden (PIT-tag only vs. PIT-tag and acoustic tag), and family. Covariates included initial length, initial weight, average water temperature, and surgery time. The REML mixed model approach was used because it is robust to correlated variables, unequal variances, and can handle both balanced and unbalanced designs. Covariance structure in repeated-measures mixed model analyses was determined through comparing corrected Akaike information criterion (AICc) values for different structures.

Multivariate analysis of variance (MANOVA) was used to evaluate weight gain and length increase over the course of the experiment. Firth generalized binomial regression was used to evaluate the probability of acoustic transmitter loss, probability of PIT-tag loss, probability of incision healing relapse, probability of mortality, probability of tissue necrosis, probability of viscera expulsion, probability of complete healing, and probability of incision dehiscence. For the probability analyses we were usually only able to evaluate the main surgical treatment effects, as the low incidence rate of the phenomena made more complex models with interactions infeasible. Parametric Weibull time-to-event analysis was used to evaluate time to complete apposition. All statistical analyses were carried out with the JMP Pro version 14 statistics software package (SAS Institute, Cary, NC, USA).

Results

Mortality Rates and Surgical Complications:

No mortalities were observed in fish from the MS, LS, LV, and CA treatments over the 21 day observation period. In the MV treatment a total of three mortalities (9.4%) were documented. Two deaths occurred on day 7 and one death occurred on day 10. The Firth generalized binomial regression model showed differences in mortality risk between treatments (LR-Chi square: 8.28, DF: 1, $p = 0.004$). Fish in the MV treatment were 5.17 times more likely (95% CI: 1.58 – 60.23, $p = 0.004$) to die compared to the other treatments. Tag burden (PIT-tag only vs. PIT-tag and acoustic transmitter) was not predictive of mortality (LR-Chi square: 0.00, DF: 2, $p = 1.000$).

Viscera expulsion was not observed in fish from the MS, LS, and LV treatments. In the MV treatment, at total of five fish (15.6%) exhibited some level of viscera expulsion (Figure 2.2k). Three of these fish presented with the complication at day 7, one at day 14, and one at day 21. The Firth generalized binomial regression model found that the risk of viscera expulsion for fish in the MV treatment was 6.21 times higher (LR-Chi-square: 13.51, DF: 1, $p < 0.001$; 95% CI: 2.04 – 71.52, $p < 0.001$) compared to the MS, LS, and LV treatments. Tag burden was not predictive of viscera expulsion (LR-Chi-square: 0.072, DF: 1, $p = 0.788$). Additionally, three fish developed tissue necrosis over the course of the experiment. Two fish (6.2%) exhibiting tissue necrosis were in the MS treatment group and the other fish (3.1%) was in the MV treatment group.

Vetbond was associated with a low incidence rate of surgical complications. At 21 days post-operatively, we observed that the Vetbond only caused inflammation that delayed the healing process in two fish (3.3%) treated with the adhesive (groups pooled together; inflammation score ≥ 4). Both affected fish were in the LV treatment, accounting for 6.2% of the treatment group. The inflammation associated with the Vetbond was caused by remnants of the surgical adhesive, which managed to stay adhered to the incision area eliciting a foreign body immune response. At the conclusion of the experiment, the Vetbond that was causing inflammation in the two fish was easily excised with a scalpel and forceps.

Incision Dehiscence Probability by Week:

The probability of an incision being open or dehisced varied significantly by treatment at 7 days post-surgery based on the Firth generalized binomial regression model (L-R Chi-Square:

33.27, DF: 3, p < 0.001). By day 7, three fish from the MS treatment (9.4%), one fish from the LS treatment (3.1%), fifteen fish from the MV treatment (46.9%), and zero fish from the LV treatment had an incision that was dehisced. Fish in the MV treatment were 9.44 times more likely than fish in the MS treatment (95% CI: 3.90 – 36.38, p < 0.001), 9.45 times more likely than fish in the LS treatment (95% CI: 3.89 – 36.34, p < 0.001), and 9.49 times more likely than fish in the LV treatment (95% CI: 3.89 – 36.23, p < 0.001) to have a dehisced incision at 7 days post-surgery. Average open incision length at 7 days post-surgery was 1.82 mm (SE = 0.279) for the MV treatment, 0.19 mm (SE = 0.275) for the MS treatment, 0.05 mm (SE = 0.272) for the LS treatment, and open incision length was non-existent for the LV treatment. At 14 and 21 days post-surgery, only four fish (12.5%) had dehisced incisions documented in the MV treatment group, while no fish had dehisced incisions documented in the other treatment groups. Fish in the MV treatment were 5.73 times more likely (95% CI: 1.55 – 32.79, p = 0.003) than fish in the other treatments to have a dehisced incision. Fish in the MV treatment still had on average 0.20 mm (SE = 0.244) of open incision length by day 21

Time to Complete Incision Apposition:

Time until complete apposition varied significantly by treatment according to the parametric Weibull time-to-event model (Wald Chi-Square: 193.80, DF: 3, p < 0.001; Figure 2.3). Fish in the MV treatment took 1.72 times longer than fish in the MS treatment (95% CI = 1.51 – 1.93, p < 0.001), 2.17 times longer than fish in the LS treatment (95% CI = 1.90 – 2.48, p < 0.001), and 1.64 times longer than fish in the LV treatment (95% CI = 1.41 – 1.90, p < 0.001) for complete and sustained incision apposition to occur. Fish in the MS treatment took 1.24 times longer (95% CI = 1.13 – 1.35, $p < 0.001$) and fish in the LV treatment took 1.35 times longer (95% CI = 1.22 – 1.48, $p < 0.001$) for complete apposition to occur compared to fish in the LS treatment group.

We also found evidence that there was a significant interaction between treatment and tag burden with regards to time to complete apposition (Wald Chi-Square: 10.77, DF: 3, p = 0.013), indicating that within the LV treatment group those fish implanted with PIT-tags and acoustic transmitters took 1.15 times longer (95% CI = 1.01 – 1.31, p = 0.0331) to reach complete incision apposition compared to those fish implanted with only PIT-tags. Greater initial total length prior to surgery was also associated with a marginal decrease in time to complete apposition (ETR = 0.98, 95% CI = 0.97 – 0.99, p = 0.014), while the other covariates were not significant ($p > 0.200$).

Transmitter Retention:

We did not observe transmitter losses in fish from the MS, LS, and LV treatments over the 21 day experiment. In the MV treatment group a total of five PIT-tags (15.6%) and one acoustic transmitter (6.2%) were lost. One PIT-tag was lost on day 2, one on day 5, two on day 6, and one on day 7 of the experiment. The one acoustic transmitter was lost on day 5. The Firth generalized binomial regression model showed that fish in the MV treatment were 6.21 times more likely (LR-Chi-square: 13.51, DF: 1, $p < 0.001$; 95% CI: 2.04 – 71.52, $p < 0.001$) to lose a PIT-tag compared to fish in the MS, LS, and LV treatments. Fish in the MV treatment were also marginally 3.06 times more likely (LR-Chi-square: 1.87, DF: 1, p = 0.172; 95% CI: 0.69 – 37.34, p = 0.172) to lose an acoustic transmitter compared to fish in the MS, LS, and LV treatments. Tag burden was not predictive of PIT-tag loss (LR-Chi-square: 0.000, DF: 1, $p = 1.000$).

Incision Inflammation by Week:

Inflammation by week was found to vary significantly by treatment (F-Ratio: 17.52, DF: 6, $p < 0.001$; Figure 2.4). The interaction between treatment, family, and week was marginally significant (F-Ratio: 1.63, DF: 12, $p = 0.087$), while the interaction between treatment and family was significant (F-Ratio: 3.81, DF: 6, $p = 0.002$). However, the interaction between tag burden and treatment was not significant (F-Ratio: 0.66, DF: 3, $p = 0.577$). All covariates were not significant ($p > 0.340$), except for average temperature (F-Ratio: 48.49, DF: 1, $p < 0.001$). At 7 days post-operatively, the level of inflammation experienced by fish was relatively uniform across the MS (mean = 2.81, SE = 0.154), LS (mean = 2.52, SE = 156), MV (mean = 2.63, SE = 157), and LV (mean = 2.26, SE = 0.155; Tukey HSD, $p > 0.800$) treatment groups. By day 14 the level of inflammation that fish in the MS (mean = 3.39, SE = 0.220) and LS (mean = 3.83, SE = 0.221) treatment groups exhibited had greatly increased and was substantially higher than the level of inflammation observed in the MV (mean = 1.42, SE = 0.227) and LV (mean = 1.58, SE = 0.221) treatment groups (Tukey HSD, $p < 0.001$).

At 21 days post-operatively, inflammation continued to increase among fish in the MS (mean = 4.13, SE = 0.2216) and LS (mean = 4.18, SE = 0.2229) treatment groups causing inflammation levels to become significantly higher compared to fish in the MV (mean = 0.78, SE = 0.2296) and LV (mean = 1.14, SE = 0.2221; Tukey HSD, $p < 0.0001$) treatment groups. For comparison, at 21 days post-operatively 65.6% of the MS treatment group and 68.7% of the LS treatment group had significant inflammation that was delaying the healing process (inflammation score ≥ 4), while no fish from the MV treatment group and only 6.3% of the LV treatment group displayed a similar level of detrimental inflammation. Fish in the MS treatment were 10.07 times more likely (95% CI: 4.09 – 35.87, $p < 0.0001$) and fish in the LS treatment were 11.47 times more likely (95% CI: 4.66 – 41.26, $p < 0.0001$) to experience severe inflammation compared to fish in the LV treatment group. Fish in the MS and LS treatment groups exhibited a marked increase in inflammation over time between day 7 and day 21 (Tukey HSD, $p < 0.0001$), while fish in the MV and LV treatment groups exhibited a slight decrease in inflammation over time between day 7 and day 21 (Tukey HSD, $p \leq 0.0014$).

Incision Healing Scores by Week:

The mixed model analysis revealed significant differences in healing scores (Table 2.1) among the surgical treatments (F-Ratio: 34.64, DF: 3, $p < 0.001$; Figure 2.5). There was also a significant interaction between treatment and examination week (F-Ratio: 8.46, DF: 6, $p < 0.001$) and between family and treatment (F-Ratio: 3.37, DF: 6, $p = 0.004$) with regards to incision healing. Seven days post-surgery we observed significant differences in healing between fish in the MV treatment group (mean = 4.85, SE = 0.330) and the MS (mean = 3.61, SE = 0.325), LS (mean = 2.65, SE= 0.320), and LV (mean = 2.94, SE = 0.329) treatment groups (Tukey HSD, $p < 0.001$). Fish in the MV treatment group exhibited poor healing characteristics. The level of healing experienced by fish in the LV treatment group was intermediate to that experienced by the MS (Tukey HSD, T-Ratio: 2.90, $p = 0.149$) and LS (Tukey HSD, T-Ratio: -1.23, $p = 0.986$) treatment groups.

Incision healing by day 14 improved drastically in all treatments compared to measurements taken on day 7 (Tukey HSD, $p < 0.001$). Fish in the MV treatment group (mean = 3.28, SE = 0.330) continued to experience the poorest level of healing, especially compared to the LS (mean = 2.06, SE = 0.179; Tukey HSD, T-Ratio: $p < 0.001$) and MS (mean = 1.49, SE = 0.184; Tukey HSD, $p < 0.001$) treatment groups. The observed improvement in the MV treatment group was largely due to three fish within the treatment dying and, thus, measurements were no longer taken. Fish in the LS treatment group experienced somewhat better healing than fish in the LV treatment group at 14 days post-operatively (Tukey HSD, T-Ratio: -5.14, $p < 0.001$).

Incision healing by day 21 improved significantly for fish in the LV treatment group (Tukey HSD, T-Ratio = 4.10, $p < 0.003$), but no improvements were observed for fish in the MS (Tukey HSD, T-Ratio: 1.18, $p = 0.990$), MV (Tukey HSD, T-Ratio: 1.70, $p = 0.866$), and LS (Tukey HSD, T-Ratio: -0.92, $p = 0.999$) treatment groups relative to measurements taken on day 14. Fish in the MV treatment (mean = 2.86, SE = 0.285) displayed a significantly poorer level of healing compared to fish in the MS (mean = 1.77, SE = 0.281), LS (mean = 1.71, SE = 0.288), and LV (mean = 1.72, SE = 0.278; Tukey HSD, $p < 0.001$) treatments. The fish in the MS, LS, and LV treatments comparatively all displayed similar levels of healing by day 21 (Tukey HSD, $p = 1.000$). However, fish in the MS treatment were 2.58 times (15.6% incidence rate) more likely (95% CI: 1.09 – 10.31, $p < 0.001$), and fish in the LS treatment were 3.16 times (18.8% incidence rate) more likely (95% CI: 1.17 – 12.51, $p < 0.001$) to experience a healing relapse event compared to fish in the LV treatment group between day 14 and day 21. The healing relapse events observed in the MS and LS treatment groups largely arose because of severe inflammation that developed between day 14 and day 21 from the prolonged immune response to suture material. Fish in the MV (3.1% incidence rate) and LV (0.0% incidence rate) treatments had similar low to non-existent rates of healing relapse ($p = 1.000$).

Probability of Complete Healing by Day 21:

The Firth generalized binomial regression model showed that there were significant differences in complete healing probabilities at the end of the experiment (LR-Chi square: 21.55, DF: 3, $p < 0.001$). At 21 days post-operatively, fish that had undergone the MS treatment were 5.62 times (95% CI 1.92 – 16.45, $p = 0.002$), those that underwent the LS treatment were 4.20 times (95% CI 1.48 – 11.94, $p = 0.007$), and those that underwent the LV treatment were 7.86 times (95% CI 2.56 – 24.15, $p < 0.001$) more likely to be completely healed compared to fish in the MV treatment group. Probabilities of complete healing at 21 days post-operatively were similar among fish from the MS, LS, and LV treatment groups ($p > 0.260$). There was not a significant interaction between treatment and tag burden (LR-Chi square: 1.40, DF: 3, $p = 0.706$), but there was a significant interaction with family (LR-Chi square: 35.52, DF: 6, $p < 0.001$). All covariates were not significant ($p > 0.16$).

Weight Gain:

There were no significant differences in weight among the treatment groups at the beginning of the study (F-Ratio: 0.61, DF: 4, $p = 0.656$). The MANOVA analysis showed differences among treatment groups with respect to weight gain and total length increase at the end of the study (Pillai's Trace: 0.18, F-Ratio: 3.86, DF: 6, $p = 0.001$; Figure 2.6). There was also no significant interaction between treatment and tag burden (Pillai's Trace: 0.07, F-Ratio: 1.36, DF: 6, $p = 0.231$) or with family (Pillai's Trace: 0.06, F-Ratio: 0.428, DF: 16, $p = 0.974$). All covariates were not significant ($p > 0.110$), except for initial total length (Pillai's Trace: 0.06, F-Ratio: 3.475, DF: 2, $p = 0.034$). Fish in the MS (mean weight gain = 15.84 g, SE = 0.837), LS (mean weight gain = 17.34 g, SE = 0.837), LV (mean weight gain = 17.40 g, SE = 0.837), and control (mean weight gain = 15.63 g, SE = 1.184) treatment groups gained similar amounts of weight over the course of the 21 day experiment (Tukey HSD, $p > 0.600$). The fish in the MV treatment group gained significantly less weight than the fish in the MS (Tukey HSD, T-Ratio: 3.00, $p = 0.026$), LS (Tukey HSD, T-Ratio: 4.27, $p < 0.001$), and LV (Tukey HSD, T-Ratio: -4.32, $p < 0.001$) treatment groups. However, the fish in the MV treatment group gained a comparable amount of weight relative to the control group (Tukey HSD, T-Ratio: -2.30, $p = 0.150$).

Total Length Increase:

There were no significant differences in total length among the treatment groups at the beginning of the study (F-Ratio: 0.59, DF: 4, $p = 0.669$). Fish in the LS (mean length increase = 31.00 mm, SE = 0.986) and LV (mean length increase = 31.81 mm, SE = 0.986) treatment groups grew in length similarly over the course of the 21 day experiment (Tukey HSD, T-Ratio: -0.58, $p > 0.977$), as did fish in the MS (mean length increase = 27.91 mm, SE = 0.986) and LS (Tukey HSD, T-Ratio: -2.22, $p = 0.179$) treatment groups (Figure 2.6). However, fish in the MS treatment group grew marginally less in length compared to fish in the LV treatment group (Tukey HSD, T-Ratio: -2.80, $p = 0.045$). Fish in the MV treatment group (mean length increase = 25.79 mm, SE = 1.036) grew significantly less in length than fish in the LS (Tukey HSD, T-Ratio:

3.64, p = 0.003) and LV (Tukey HSD, T-Ratio: -4.21, p < 0.001) treatments, but grew comparably relative to the control group (mean length increase = 29.62 mm, SE = 1.395; Tukey HSD, T-Ratio: -2.21, p = 0.184) and the MS treatment group (Tukey HSD, T-Ratio: 1.48, p = 0.579).

Discussion

Mortality and Surgical Complications:

We examined optimal incision placement and the efficacy of using Vetbond surgical adhesive for closing incisions in age-0 lake sturgeon. Mortality was only associated with sturgeon in the MV treatment group. The three mortalities that occurred in the experiment were associated with viscera expulsion, which was the most likely cause of death. During viscera expulsion internal organs may be damaged by the external environment, osmoregulation capability is severely degraded, the risk of infection greatly increases, and the incision is generally not able to close (Boyd et al., 2011; Panther et al., 2011). Boyd et al. (2011) noted that viscera expulsion was more common in smaller fish and for midline incisions closed with a single suture than for incisions closed with two sutures when Chinook salmon smolts were exposed to simulated turbine passage.

The occurrence of tissue necrosis was very low, only occurring along midline incisions of sturgeon in the MS (6.25%) and MV (3.1%) treatment groups. The tissue necrosis observed in the sturgeon in the MS treatment group likely resulted from the suture material causing the tissue to become ischemic (Whipple et al., 1938). The tissue necrosis observed in the sturgeon in the MV treatment group was associated with dehiscence of the incision. The lower perfusion of the tissues along the midline linea alba (Panther et al., 2011) makes tissue necrosis more of a concern in this region compared to lateral incisions made along the hypaxial musculature. However, lateral incisions can damage vascular muscle tissue (Tera and Aberg, 1977) and nerve axons (Burger et al., 2002), which can result in greater blood loss (Nygaard, 1996) and longer healing times (Anderson and Roberts, 1975; Wagner et al., 2011).

Incision Dehiscence and Apposition:

Our experimental results clearly demonstrate that Vetbond was not able to adequately close midline incisions, while it was efficient at closing lateral incisions. The LS and LV surgical treatments were the most robust against incision dehiscence, and they provided the highest level of closure. Midline incisions closed with sutures experienced lower apposition quality and a higher rate of dehiscence compared to lateral incisions closed with suture. Tissue in the midline region was also more fragile, and the incisions tended to close with delicate scar tissue. The higher level of dehiscence and poorer apposition quality in the MV and MS treatment groups would cause incisions to heal through the much longer process of secondary intention. This ultimately delays the reepithelialization process, increases susceptibility to infection, reduces osmoregulatory performance, and requires more energy (Guo and DiPietro, 2010).

The lower apposition quality and higher incidence rate of dehiscence observed in the midline region can likely be explained by several factors. The midline region is the connection point for the abdominal muscles used during locomotion, which makes the midline region more vulnerable to higher levels of lateral tension that could lead to poor apposition and dehiscence (Boyd et al., 2011; Panther et al., 2011). Transmitters are also more likely to rest on and apply pressure to the midline incision area. Furthermore, the midline linea alba region is poorly vascularized, which may result in weaker fibrin clot formation and slower healing compared with lateral incisions made through the hypaxial musculature (Panther et al., 2011). Histological results reported by Panther et al. (2011) showed that midline incisions for Chinook salmon smolts healed poorly with less fibrotic tissue at the incision site, the edges of the incision curled inward, and the incision was only connected by a thin layer of epithelial cells compared to lateral incisions.

Transmitter Retention:

Incision closure and apposition characteristics are directly linked to transmitter retention. PIT-tag loss was only observed by sturgeon in the MV treatment group (15.6%). Sturgeon in the MV treatment group were 6.21 times more likely to lose a PIT-tag compared to fish in the other treatments. Acoustic transmitter loss was rare, with only one transmitter lost in the MV treatment group (3.1%). The irregular shape of the JSATS transmitter may have contributed to the low level of loss observed. LS, MS, and LV surgical treatments were all robust to transmitter loss, indicating that comparable tag retention can be achieved when Vetbond is used to close lateral incisions. This also indicates that only one suture is necessary to ensure high transmitter retention in lateral or midline incisions. Similar research on juvenile Chinook salmon found that only one simple interrupted suture was required for closing midline incisions, maintaining apposition, and achieving high transmitter retention (Deters et al., 2012).

Studies on juvenile sturgeon transmitter retention have generally focused on larger juveniles than the size range we evaluated (mean weight: 30 g). Miller et al. (2014) reported

93.75% transmitter retention for lateral incisions closed with suture in juvenile green sturgeon (mean weight: 347 g; *A. smedirostris*), although the sample size was low (N = 16). Conversely, Crossman et al. (2013) found that transmitter retention of relatively large transmitters (length: 2.7 cm, diameter: 0.9 cm) inserted through lateral incisions was only 25% for non-anchored transmitters and 88% for transmitters anchored to the peritoneum in juvenile shortnose sturgeon (mean weight: 318 g; *A. brevirostrum*). Smith and King (2005) also experienced poor transmitter retention with midline incisions in a telemetry study, reporting 40% transmitter loss with yearling lake sturgeon (mean weight: 207 g). More recently, Liss et al., (2018) observed 100% transmitter retention for ventral-lateral and dorsal-flank incisions in age-0 white sturgeon (weight: ~ 69 g). Similarly, Ashton et al., (2017) noted 100% transmitter retention in age-0 white sturgeon for un-sutured dorsal-flank incisions for a variety of weight classes (weight: 26 – 126 g).

Incision Healing and Inflammation:

While lake sturgeon in the MS and LS treatment groups generally attained complete healing first, their healing process began to relapse and deteriorate significantly by day 21 compared with the LV treatment group because of severe inflammation generated by the immune response to the suture material. In contrast, inflammation associated with the Vetbond surgical adhesive was very low, and healing was robust in the LV treatment group. However, lake sturgeon in the MV treatment group exhibited poor healing throughout the entire experiment.

To avoid the detrimental effects of inflammation, absorbable monofilament suture material should be promptly removed once incisions have become securely closed, usually 7-14 days post-surgery. Sutures cease to be beneficial after incisions are securely closed and will quickly become harmful to the healing process (Deters et al., 2012; Dunn, 2007; Liss et al., 2018). Miller et al. (2014) reported that severe inflammation in response to suture material caused lateral incisions to reopen by the third week in green sturgeon, and they recommended using the least amount of suture material possible. Liss et al., (2018) also found that suture material impaired the healing process in age-0 white sturgeon, and they recommended not using sutures to close small 7-9 mm incisions. In mammals Moncryl absorbable monofilament suture (Ethicon, Somerville, New Jersey) has been shown to lose all of its tensile strength at 28 days post-surgery, but the suture material itself is not fully absorbed until 91-119 days post-surgery (Dunn, 2007). This is a fact that is commonly overlooked in studies, as inflammation will continue to worsen until either the suture material is removed or it is completely absorbed. The inflammation can potentially affect the health and behavior of the fish under study, which can confound the results of important research (Bridger and Booth, 2003; Deters et al., 2012; Guo and DiPietro, 2010).

Growth Characteristics:

Lake sturgeon in the MV treatment group gained significantly less weight than sturgeon in the other treatment groups. Sturgeon in the MV treatment group also grew less in length compared to sturgeon in the LS and LV treatments. In contrast, sturgeon in the LV treatment grew similarly compared to sturgeon in the LS treatment and control group. This provides additional evidence that Vetbond can be safely used to close lateral incisions, without causing adverse health impacts. It seems likely that the poor incision healing and incision dehiscence experienced by the MV treatment group resulted in poorer growth compared to the other treatments (Boyd et al., 2011; Guo and DiPietro, 2010).

Transmitter burden was not linked to differences in growth characteristics likely because the level of tag burden tested relative to body weight was very low (mean: 1.99% vs. 3.15%). Some researchers have found that fish can be robust against the effects of tag burden (Ammann et al., 2013; Brown et al., 1999; Miller et al., 2014), while others have found clear deleterious effects on growth (Brown et al., 2010; Chittenden et al., 2009; Robertson et al., 2003). Sutton and Benson (2003) found that larger external radio transmitter burdens (Range: 1.25% - 6%) on juvenile lake sturgeon caused significantly lower growth, and they recommended that transmitter weight should not exceed 1.25% of body weight. Ashton et al., (2017) observed that transmitter burden (0.6 – 2.6%) only had a small effect on the growth of age-0 white sturgeon, and the sturgeon were able to regain their growth potential by 28 days post-implantation.

Prior Research on Cyanoacrylate Adhesives for Incision Closure in Fishes:

To our knowledge, only two studies have examined the efficacy of a surgical grade adhesive (e.g., Vetbond) for intracoelomic transmitter implantation. Jepsen et al., (2017) found that 10-15 mm incisions on brown trout (*Salmo* trutta) closed with histo-glue (chemically identical to Vetbond) presented with the best healing characteristics (i.e., limited inflammation and necrosis), but 30% of the transmitters were lost in the treatment group. Lowartz et al., (1999) observed that 5 mm incisions on larval sea lamprey closed with Vetbond were associated with more inflammation and higher mortality compared with suture treatments.

The other studies on the subject matter have all examined the efficacy of household superglue. Petering and Johnson (1991) examined the efficacy of a gel based superglue for closing 20 – 25 mm incisions on black crappies (*Pomoxis nigromaculatus*), and they found that incisions closed with superglue healed slower, there was a much higher frequency of incision dehiscence, and at 21 days post-operatively 70% of the transmitters had been expelled. The researchers also observed that the superglue caused less inflammation than sutures, took 38% less time to apply compared to sutures, and at 3 days post-operatively the superglue began to fall off. Other researchers have similarly noted poor closure characteristics with household superglue (Kaseloo et al., 1992; Raoult et al., 2012). In contrast, Baras and Jeandrain (1998) noted good closure performance, better survival, and considerably less inflammation than sutures when a biological bandage was used in conjunction with superglue to close 20 mm incisions on yellow eels (*Anguilla Anguilla*), and Nemetz and Macmillan (1988) similarly noted limited inflammation and good closure quality with minor mesentery adhesions when superglue was used to close 15 mm incisions on channel catfish (*Ictalurus punctatus*).

In the present study we found that Vetbond surgical adhesive was effective at closing lateral incisions, but was not effective at closing midline incisions. We also did not observe severe tissue inflammation or necrosis associated with the adhesive. The differences observed among the studies presented in this section are likely the result of multiple factors, including incision length, incision location, surgical technique, surgical experience, structural tissue differences, immune response differences, surgical site infection, and the amount of tension that the incision is exposed to. The characteristics of the adhesive itself are also a vital factor.

Surgical grade adhesives have limited cytotoxicity, while household superglue is severely cytotoxic and medically contraindicated (Sohn et al., 2016; Toriumi et al., 1990). In addition, most of the studies that evaluated the efficacy of household superglue applied a thick superglue gel to the incision cites, which is not recommended, as you should only apply a very thin coating of surgical adhesive that is in liquid format (usually only 1-2 drops), making sure to avoid the pooling of the adhesive on the skin (3M Health Care, 2016).

Surgical Recommendations:

We found that midline and lateral incisions 8 mm in length on age-0 lake sturgeon can be safely closed with a single suture, while achieving high survival and transmitter retention. However, the midline linea alba tissue is more delicate and our results showed poorer apposition and closure characteristics in this area. Therefore, we recommend using a minimum of two simple interrupted sutures to close midline incisions. We also found that Vetbond was not able to safely close midline incisions, while it was effective at closing lateral incisions. Consequently, small lateral incisions can be safely and effectively closed with either a single interrupted suture or with Vetbond surgical adhesive. If the sutures are not able to be removed within 7-14 days post-surgery, then we recommend that Vetbond be used because it is associated with significantly less inflammation and better incision healing in the long-term. Our research also showed that PIT-tags can be safely inserted into the body cavity of age-0 lake sturgeon with high retention and fewer problems than what has been reported for the traditional dorsal musculature insertion region (Damon-Randall et al., 2010; Hamel et al., 2012; Moser et al., 2000). In order to minimize potential family genetic effects on incision healing, care should also be taken to ensure adequate diversity (Blankenhorn et al., 2009; Liaw et al., 1998; McBrearty et al., 1998). Future simulated turbine passage research is needed to evaluate the reliability of these closure methods and incision locations for lake sturgeon that may rapidly out-migrate through hydroelectric infrastructure (Boyd et al., 2011).

Acknowledgements

We thank the 2016 hatchery staff at the Black River Sturgeon Rearing Facility, including Douglas Larson, Shaley Valentine, Zachary Witzel, Andrew Lockwood, Stefan Tucker, Jason Lyons, and Rebecca Colby for their valuable assistance with the surgical experiment and the production and management of the lake sturgeon. This study was funded in part by the Great Lakes Fishery Trust (project # 2013.1302). Additional Funding was also provided by the Michigan Department of Natural Resources through the State Wildlife Grant Program.

Tables

Table 2.1: Description of the incision healing scoring system used to assess the healing process, adapted and modified from Wagner and Stevens (2000).

Incision Healing Score	Rating Description
1	Incision is closed and completely secure. There is little to no inflammation and healing is essentially complete.
2	Incision is closed and completely secure, but inflammation is evident and is impeding the healing process.
3	Incision is closed and relatively secure, although the closure is not overtly strong and healing is not complete. Inflammation may or may not be evident.
4	Incision is closed, but only with thin fragile tissue or a fragile scab. Inflammation may or may not be evident.
5	Incision is held in proximity, but not completely closed, as edges still slide. Inflammation may or may not be evident.
6	Incision is partially open at one end or in the middle (<50% open). Inflammation may or may not be evident.
7	More than 50% of incision is open. Inflammation may or may not be evident.
8	Incision is completely open. Inflammation may or may not be evident.

Figures

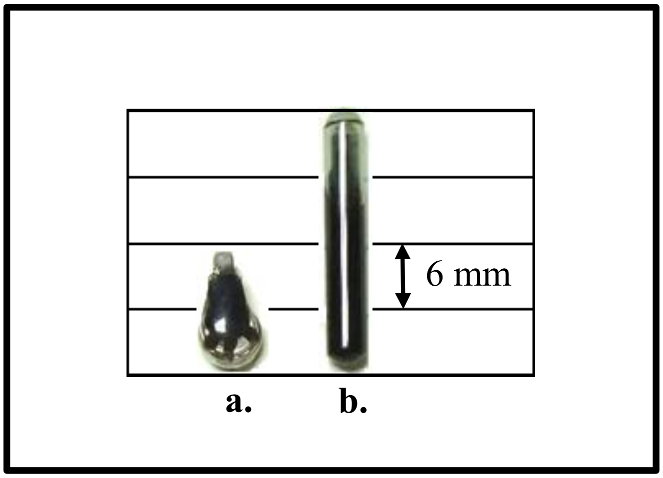

Figure 2.1: Picture displaying the (a.) 0.32 gram JSATS L-AMT-1.421 acoustic transmitter with dimensions of 11.1 x 5.5 x 3.7 mm manufactured by Lotek Wireless and (b.) the 0.6 gram PIT-tag with dimensions of 3.65 x 23 mm manufactured by Oregon RFID (b).

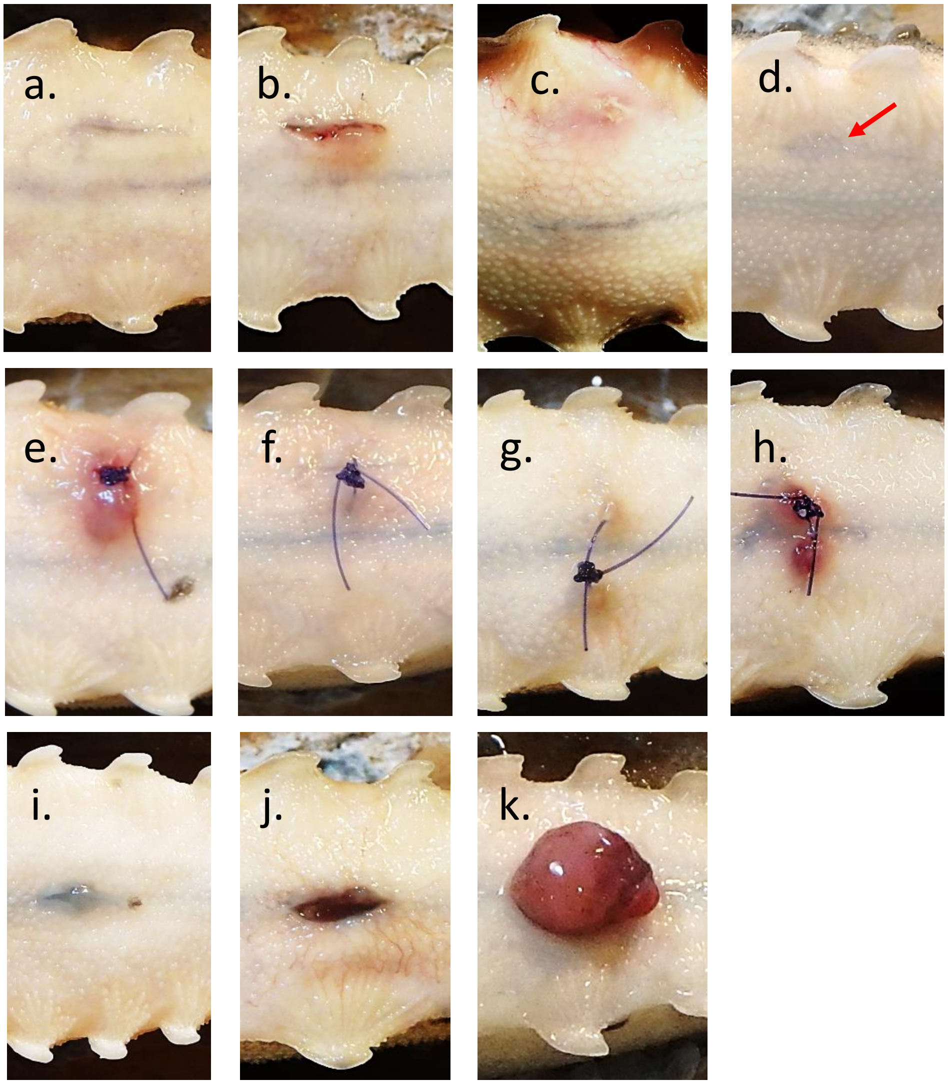

Figure 2.2: Surgical pictures representing key incision healing characteristics and surgical complications for lateral and midline incisions closed with absorbable monofilament suture and Vetbond on age-0 lake sturgeon. Well approximated lateral incision closed with Vetbond; incision closure is secure, but relatively weak with no inflammation evident at 7 days post-surgery (a.). Lateral incision closed with Vetbond with significant inflammation evident at 7 days post-surgery (b.). Lateral incision closed with Vetbond exhibiting inflammation because remnants of the adhesive were still adhered to the skin at 21 days post-surgery (c.). Lateral incision (location of red arrow) closed with Vetbond showing reepithelialization and the relative completion of the healing process at 21 days post-surgery; approximation is excellent, incision closure is very strong, and no inflammation is evident (d.). Lateral incision closed with suture exhibiting comprehensive severe inflammation and fibrosis at 21 days post-surgery (e.). Lateral incision closed with suture displaying no inflammation at suture sites at 7 days post-surgery (f.). Midline incision closed with suture displaying moderate inflammation at suture sites at 14 days post-surgery (g.). Midline incision closed with suture displaying severe inflammation at suture sites at 21 days post-surgery (h.). Midline incision closed with Vetbond; incision edges are not completely approximated, as the incision edges are separated by blue-colored fibrous scar

Figure 2.2 (cont'd)
tissue that has sealed the incision opening at 14 days post-surgery (i.). Midline incision closed with Vetbond with complete dehiscence of the surgical incision; moderate inflammation is evident around the margins of the incision at 7 days post-surgery (j.). Midline incision closed with Vetbond displaying severe viscera expulsion through the incision site at 14 days post-surgery (k.).

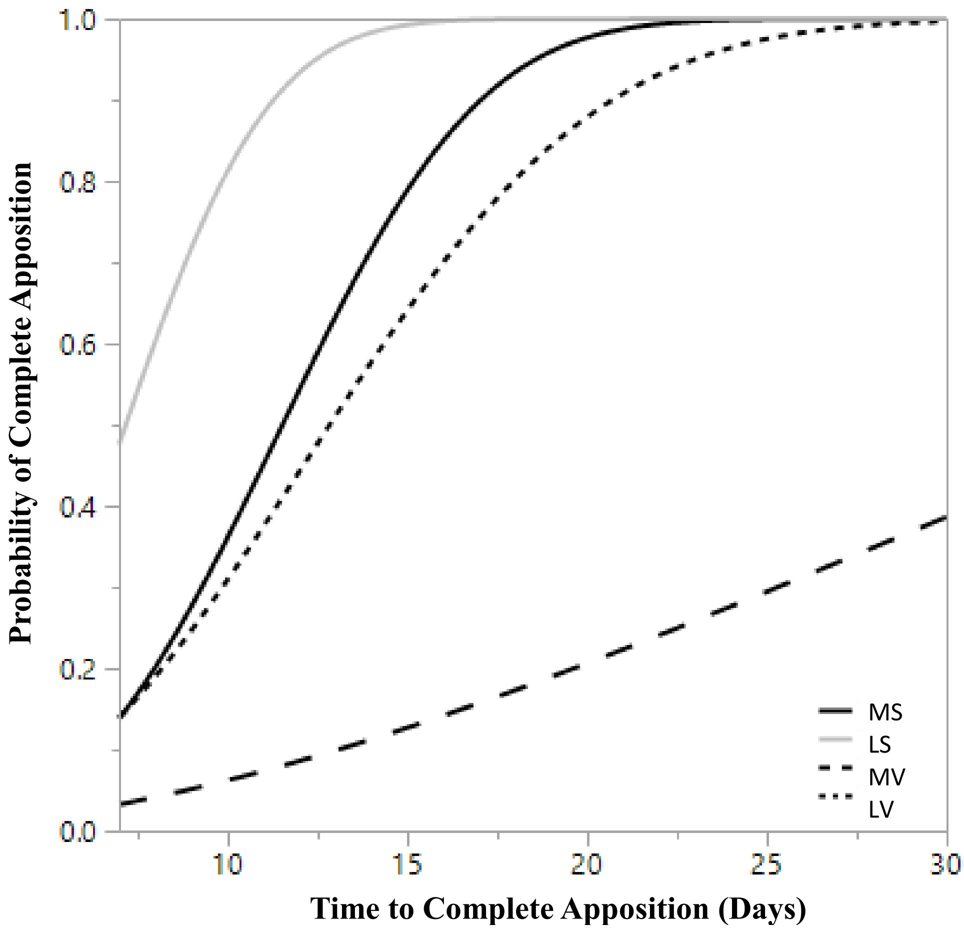

Figure 2.3: Parametric Weibull time-to-event analysis showing observed and projected probabilities for time until complete incision apposition for each surgical treatment group of lake sturgeon. Treatment groups: MS = midline incision closed with suture, LS = lateral incision closed with suture, MV = midline incision closed with Vetbond, LV = lateral incision closed with Vetbond.

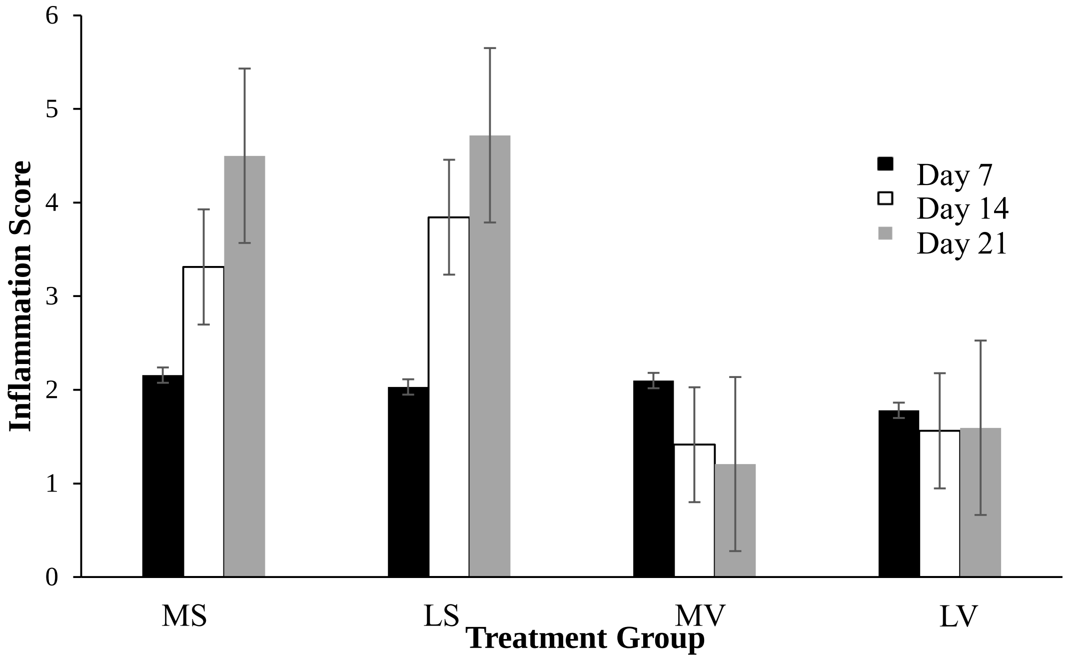

Figure 2.4: Average inflammation score by week for each surgical treatment group of lake sturgeon. Means are shown (± SE). Treatment groups: MS = midline incision closed with suture, LS = lateral incision closed with suture, MV = midline incision closed with Vetbond, LV = lateral incision closed with Vetbond.

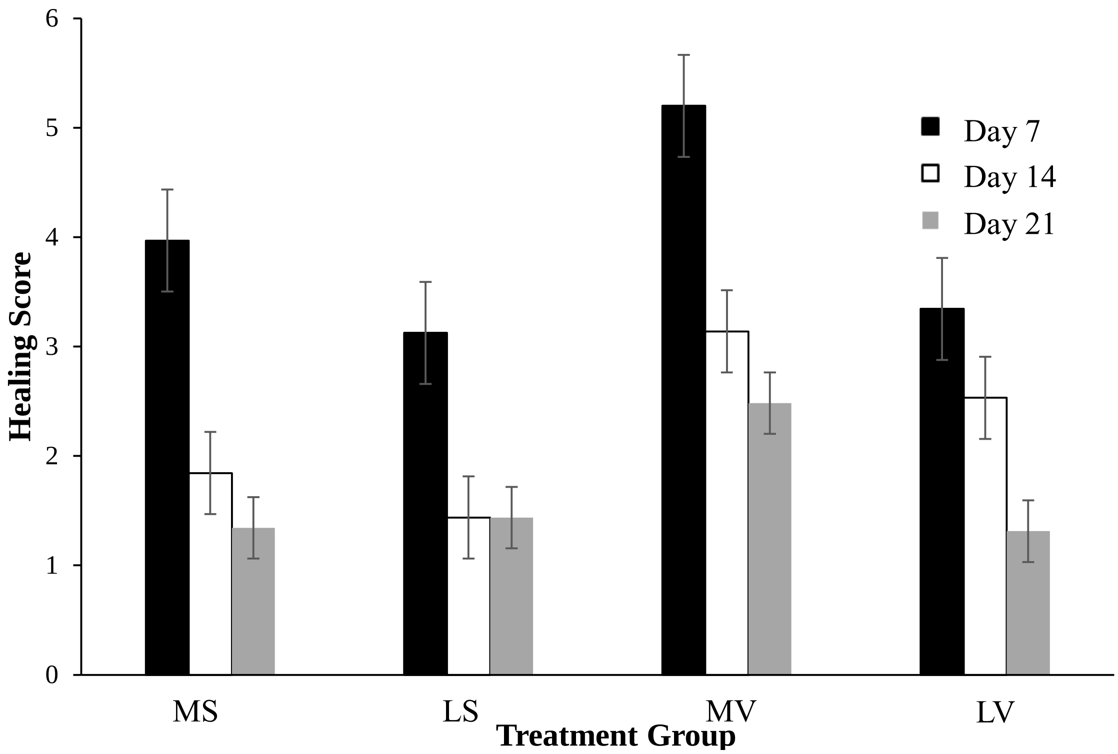

Figure 2.5: Average healing score by week for each surgical treatment group of lake sturgeon. Means are shown (± SE). Treatment groups: MS = midline incision closed with suture, LS = lateral incision closed with suture, MV = midline incision closed with Vetbond, LV = lateral incision closed with Vetbond.

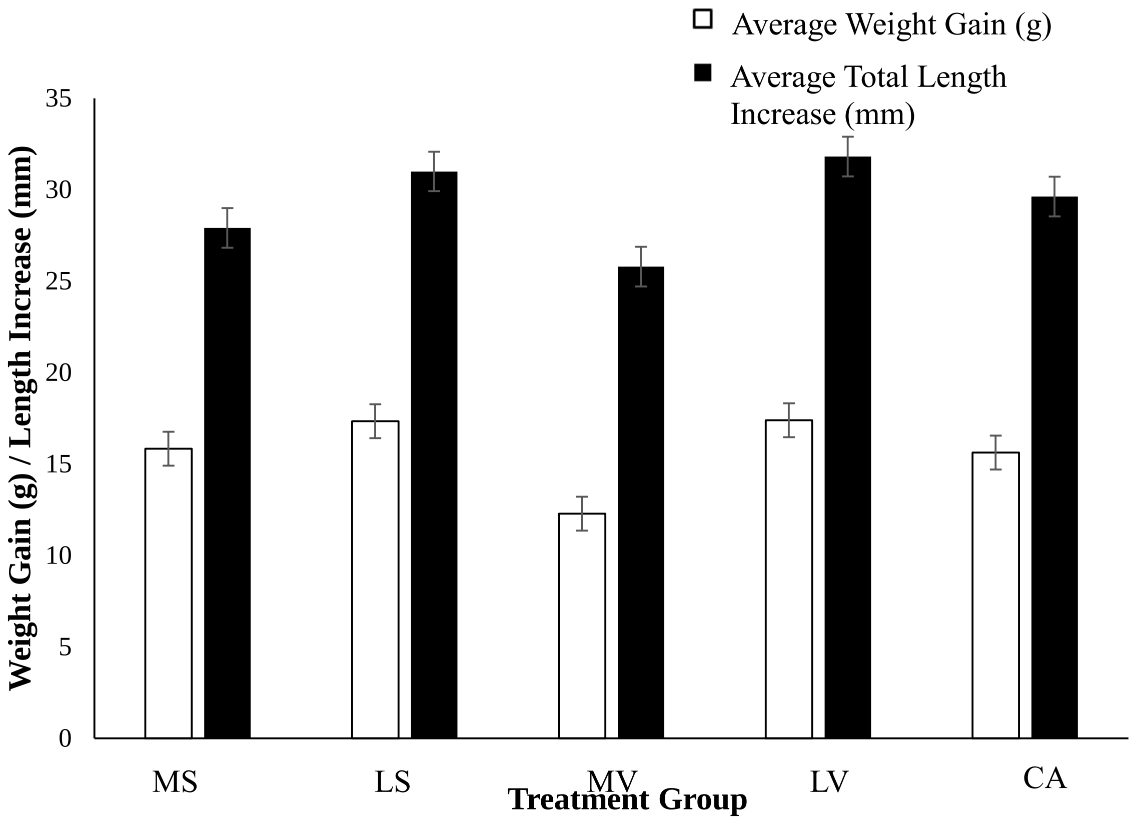

Figure 2.6: Average weight gain (grams; white bars) and total length increase (mm; black bars) over the 21 day experimental time period for each surgical treatment group of lake sturgeon. Means are shown (± SE). Treatment groups: MS = midline incision closed with suture, LS = lateral incision closed with suture, MV = midline incision closed with Vetbond, LV = lateral incision closed with Vetbond, CA = control group treated with anesthetic only.

Chapter 3:
Movements, Habitat Use, and Entrainment of Stocked Juvenile Lake Sturgeon in a Hydroelectric Reservoir System.

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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 meters between telemetry positions, with age-2 lake sturgeon making longer distance movements 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 deep water 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.

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 meters high) and at least 1 000 000 smaller dams that have altered and fragmented river systems that support important fisheries resources (Allan and Castillo, 2007; Dynesius et al., 2005; Wang et al., 2011b). Within the United States alone there are 45 178 dams that are at least 7.62 meters high that impact fish habitat and movements (USACE, 2023).

Lake sturgeon (*Acipenser fulvescens*) is a potamodromous, fluvial-dependent species of regulatory and conservation concern that is considered threatened in most states and provinces (Bruch et al., 2016; Latta, 2005; Peterson et al., 2007). 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 1800's and early 1900's. Originally in the early 1800's 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 (Auer and Dempsey, 2013; Peterson et al., 2007). By the early 1900's most lake sturgeon populations began to decline because of overfishing, as well as habitat degradation, pollution, and fragmentation due to hydroelectric dams (Brousseau, 1987; Harkness and Dymond, 1961; 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 (Haxton et al., 2014; Tody, 1974), and hydroelectric dams are thought to be one of the major factors limiting the restoration of lake sturgeon in the Great Lakes (Coscarelli et al., 2011; Ferguson and Duckworth, 1997; Peterson et al., 2007).

Recently interest in using fish passage engineering to reintroduce lake sturgeon above dams or to reconnect fragmented populations disconnected by dams has increased (Boothroyd et al., 2018; Coscarelli et al., 2011; Jager et al., 2016; Koenigs et al., 2018). While information is available on the movement and habitat use characteristics of juvenile sturgeon throughout the species range (Benson et al., 2005; Boase et al., 2014; Holtgren and Auer, 2004; Smith and King, 2005; Trested et al., 2011) and in reservoirs (Hrenchuk et al., 2017; McDougall et al., 2014a, 2014b, 2013), less is known about small reservoirs in the Great Lakes. There are approximately 3,116 dams in Minnesota, Michigan, and Wisconsin alone that create barriers and reservoir habitat, and 78% of them are less than 7.62 meters in height (USACE, 2023). Identifying movement patterns and habitat use characteristics is considered vital to lake sturgeon restoration efforts and planning (Coscarelli et al., 2011; Holey et al., 2000). Previous research has shown that juvenile sturgeon use fine sediments and deep water habitat in rivers and lakes (Barth et al., 2011; Benson et al., 2005; 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 deep water 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., 2014a, 2013). 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 (Jager et al., 2016; Kynard and Horgan, 2001; Pollock et al., 2015; 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 (1) movement characteristics, (2) spatial habitat use patterns, (3) environmental factors that influence habitat use, and (4) entrainment characteristics.

Methodology

Study Area:

This study was conducted on the upper Black River located in Cheboygan County in northern Michigan (Figure 3.1). 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 17.6 km upstream from the river mouth. The dam was built in 1949 with an average head of 13.4 meters, and it forms a reservoir with 370 hectare-meters 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 an average head of 6.1 meters, and it forms a small reservoir with 76 hectare-meters 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., 2014a, 2013). The dimensions of the transmitters were 5 x 7 x 13 mm, and they weighed 0.6 grams in air. All acoustic transmitters were programmed to have a 10 second transmission rate, with an estimated life expectancy of 180 days. In addition, a 23 x 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 minutes in an anesthetic bath with 125 mg/L of tricaine methanesulfonate (MS222; 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/L of MS222 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 1-2 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 four weeks of post-operative 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 grams (SD = 31.6) and a mean total length (TL) of 348 mm (SD = 40.0). Age-2 lake sturgeon had a mean mass of 479 grams (SD = 87.8) and a mean TL of 486 mm (SD = 35.3). 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#: 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 (Figure 3.1). A total of 53 age-1 and 53 age-2 lake sturgeon were released into Tower Reservoir approximately 4.7 km upstream of Tower Dam. A total of 57 age-1 and 53 age-2 lake sturgeon were released into Kleber Reservoir approximately 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 timeframe 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 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 approximately 100 meters apart from midpoints of adjacent zones (Figure 3.1). 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 minutes between 9:00 – 17:00 hours. 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 meters; however, the detection efficiency of the equipment rapidly diminishes beyond 100 meters. Generally, the max detection distance for JSATS transmitters is 200 meters (McMichael et al., 2010). For a detection to be validated, the transmitter's ID had to be detected at least twice in a 40 second time period. In addition to the paired detection requirement, we also required that a total of four detections be registered within a 120 second 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 (Figure 3.1). 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 approximately 300 meters 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 located 0.85 miles upstream from the river mouth where the Black River empties into Black Lake (Figure 3.1).

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 batteries connected to two 200 watt solar panels (Zamp Solar, Bend, Oregon). Half-duplex RFID antenna systems constantly switch their electromagnetic fields on and off in order 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 sidescan sonar unit (Humminbird, Eufaula, AL) to record depth, hardness, roughness, and side-scan imaging data, and ReefMaster (version 2.0) software (West Sussex, UK) to extract and view this multi-channel 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. In order to capture data, the sonar unit's transducer was mounted at the bow of the boat, and we followed pre-planned transect lines spaced 30.5 meters apart that crisscrossed the entire reservoir system at a speed of approximately 3.2 kilometers per hour. 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 (ME = 0.005, 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).

In order 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 meters, 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 = 701.21 ft above sea level, SD = 0.085, Range: 700.91 – 701.45). Due 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, max 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 GiZscores. We also used the Getis-Ord Gi* 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-meter radius zones that overlapped by 50 meters. Semi-overlapping zones were used to take into account 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, max 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 meters deep, hectares of water ≥ 3.1 meters deep, hectares of water ≥ 6.1 meters 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 re-categorize the total detections data for all analyses. The rating scale classified zero detections as 1, one detection as 2, 2-3 detections as 3, 4-6 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 (Abdi, 2010; Wold, 1966). 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 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 pre-requisite 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, NC, USA) and Minitab version 18 software package (Pennsylvania State University, State College, PA).

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 non-repetitive detections around Kleber Reservoir. Thirteen age-1 and 7 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 meters (SD = 917.1) in direct linear distance over the course of the sampling period (Figure 3.2). The average distance moved between observation points was 502 meters (SD = 423.2), and the average max distance moved between observation points was 765 meters (SD = 628.1). The elapsed time in-between detections was highly variable and averaged 10.54 days (SD = 10.38; Figure 3.3). 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) moved more in total distance than age-1 lake sturgeon (mean total distance = 764 m, SE = 250.7; F-Ratio: 4.64, DF: 1, $p = 0.043$). Max distance moved between observation points also marginally differed between the two age groups, with age-2 lake sturgeon (mean max distance = 1013 m, SE = 183.4) making somewhat longer movements than age-1 lake sturgeon (mean max distance = 537 m, SE = 175.6; F-Ratio: 3.53, DF: 1, $p = 0.074$).

Spatial Hotspot Analysis:

Most lake sturgeon detections were located near the forebay of Kleber Dam and in the middle of the reservoir (Figure 3.4). 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 (Figure 3.4). 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 meters, which was subsequently used as the optimal distance band in the local spatial analyses. The local scale Getis-Ord Gi* 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 (Figure 3.5).

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 (Figure 3.6). These variables include the amount of silt habitat, amount of deep water 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 (Figure 3.7). 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 3.1). 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 Y-variance was explained by the first component (Table 3.1). 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 3.1). The second component was almost exclusively explained by the amount of low hardness habitat (50.9%) and by the amount of deep water habitat (49.7%). The third component was dominated by the amount of deep water 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 (Figure 3.8). These variables include the amount of silt habitat, amount of deep water habitat (≥ 6.1 m), mean depth, amount of low hardness habitat (≤ 60 hardness units), max depth, the interaction between mean depth and the amount of silt habitat, and the interaction between the amount of silt habitat and deep water habitat (Figure

3.7). 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 3.2). 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 3.2). 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 depth and silt habitat (16.2%; Table 3.2). 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 max depth (44.2%), amount of deep water habitat (30.0%), and by the interaction between silt and deep water habitat (28.7%).

Geographically Weighted Regression:

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 (Figure S3.1). 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 deep water 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 max depth (R^2: 44.2%, R^2 Adj: 38.6%, AIC_c: 90.67) varied spatially across the reservoir (Figure S3.2). In all three cases the effect size (i.e., local R^2) of silt habitat, low hardness habitat, and max depth was greatest toward the more confined, shallow head of the reservoir. The influence of mean depth and deep water 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 (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 to 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 to the age-2 lake sturgeon stocked into Tower Reservoir (95% CI = 2.01 – 11.54, z =

3.52, $p < 0.001$).

Most sturgeon were entrained through Kleber Dam relatively quickly following release (Figure 3.9). 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, SD = 263.28). 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% (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 meters. On average the lake sturgeon moved just over 500 meters 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 – 1630 meters. Smith and King (2005) also observed that juvenile lake sturgeon movements between telemetry locations in Black Lake were relatively limited, ranging between 330 – 800 meters. They also noted that home range size was relatively small, ranging between 0.74 – 5.98 km^2. Even in large river systems like the

Winnipeg River, Peshtigo River, and the St Clair River, researchers have noted that the movements of juvenile lake sturgeon are quite modest and localized (Barth et al., 2011; Benson et al., 2005; 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 (McDougall et al., 2013; Smith and King, 2005).

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 (Benson et al., 2005; Chiasson et al., 1997; Holtgren and Auer, 2004). 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 deep water 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, max depth, and the amount of deep water 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 deep water habitat (Barth et al., 2011; Boase et al., 2014; Holtgren and Auer, 2004; McDougall et al., 2013). Holtgren and Auer (2004) observed that lake sturgeon usually used water depths greater than 10 meters. McDougall et al. (2013) reported that lake sturgeon movement was largely restricted to deep water habitat greater than 15 meters 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 deep water habitat may be a predator avoidance strategy (Barth et al., 2011; Holtgren and Auer, 2004; Smith and King, 2005). It has also been proposed that deep water 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 (Gerig et al., 2011; Holtgren and Auer, 2004; Kempinger, 1996). Sbikin and Bibikov (1988) found that juvenile Russian sturgeon (*A. guldenstadti*), beluga sturgeon (*Huso huso*), sevryuga sturgeon (*A. stellatus*), and ship sturgeon (*A. 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 (Gerig et al., 2011; Trested et al., 2011; Werner and Hayes, 2005), along with sand-clay substrates (Chiasson et al., 1997), organic substrates (Holtgren and Auer, 2004; Smith and King, 2005), and sand substrates (Benson et al., 2005; Peake, 1999). 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 deep water 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 downstream silt dominated habitat region. The researchers suggested several reasons for this observed use of larger upstream substrates: (1) drifting macroinvertebrates might be more abundant further upstream where currents are faster and substrates are larger, (2) the sturgeon may not be adapted to using the silt habitat available further downstream because the dam and its associated habitat features are contemporary features, and (3) 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 to the lake sturgeon stocked into Tower Reservoir. The reason for this observed difference in entrainment probabilities may be explained by the following two factors: (1) high passage mortality at Tower Dam and (2) Tower Reservoir may have characteristics that tended to limit entrainment or promote residency. In Kleber Reservoir the deep water 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 to 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., 2014a). 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 vs. 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 (Hrenchuk et al., 2017; McDougall et al., 2017, 2014a, 2013; Peterson et al., 2007; Smith and King, 2005). 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., 2017, 2014a, 2013). 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 (Coscarelli et al., 2011; Jager et al., 2016; Koenigs et al., 2018;

Thuemler, 1985), 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 deep water habitat in areas with fine sediments and limited aquatic vegetation. Consequently, reservoirs with ample deep water 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 significant proportion being entrained, and reintroduction efforts should take into account the morphology of the reservoir and the location of high quality habitats in relation to hydroelectric infrastructure during planning.

Acknowledgements

This study was funded by the Great Lakes Fishery Trust (project # 2012-1302). Additional Funding was also provided by the Michigan Department of Natural Resources through the State Wildlife Grant Program. We thank the hatchery staff at the Black River Sturgeon Rearing Facility, including John Bauman, Nathan Barton, Douglas Larson, Shaley Valentine, Zachary Witzel, Andrew Lockwood, Stefan Tucker, Jason Lyons, Rebecca Colby, Garret Johnson, Dillon Ross, Ryan Walquist, Adam Chaston, and Jenna Ruzich for their valuable assistance with the project and with the production of the juvenile lake sturgeon.

Tables

Table 3.1: Results of the projection to latent structures regression (PLSR) analysis for the number of unique lake sturgeon observed in each zone. 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.

PLSR Model Components:

Components	PRESS	Voet T^2	p	R^2X	R^2Y
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
Deep Water Hectares (≥6.1 m)	0.332	-0.705	-0.887	0.454	0.009

Table 3.2: Results of the projection to latent structures regression (PLSR) analysis for the total number of detections of lake sturgeon observed in each zone. 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. 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.

PLSR Model Components:

Components	PRESS	Voet T^2	p	R^2X	R^2Y
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*Deep Water Hectares	0.324	-0.332	-0.536	0.503	0.004
Mean Depth	0.365	-0.082	0.291	0.567	0.001
Deep Water Hectares (≥6.1 m)	0.309	-0.428	-0.547	0.479	0.006

Figures

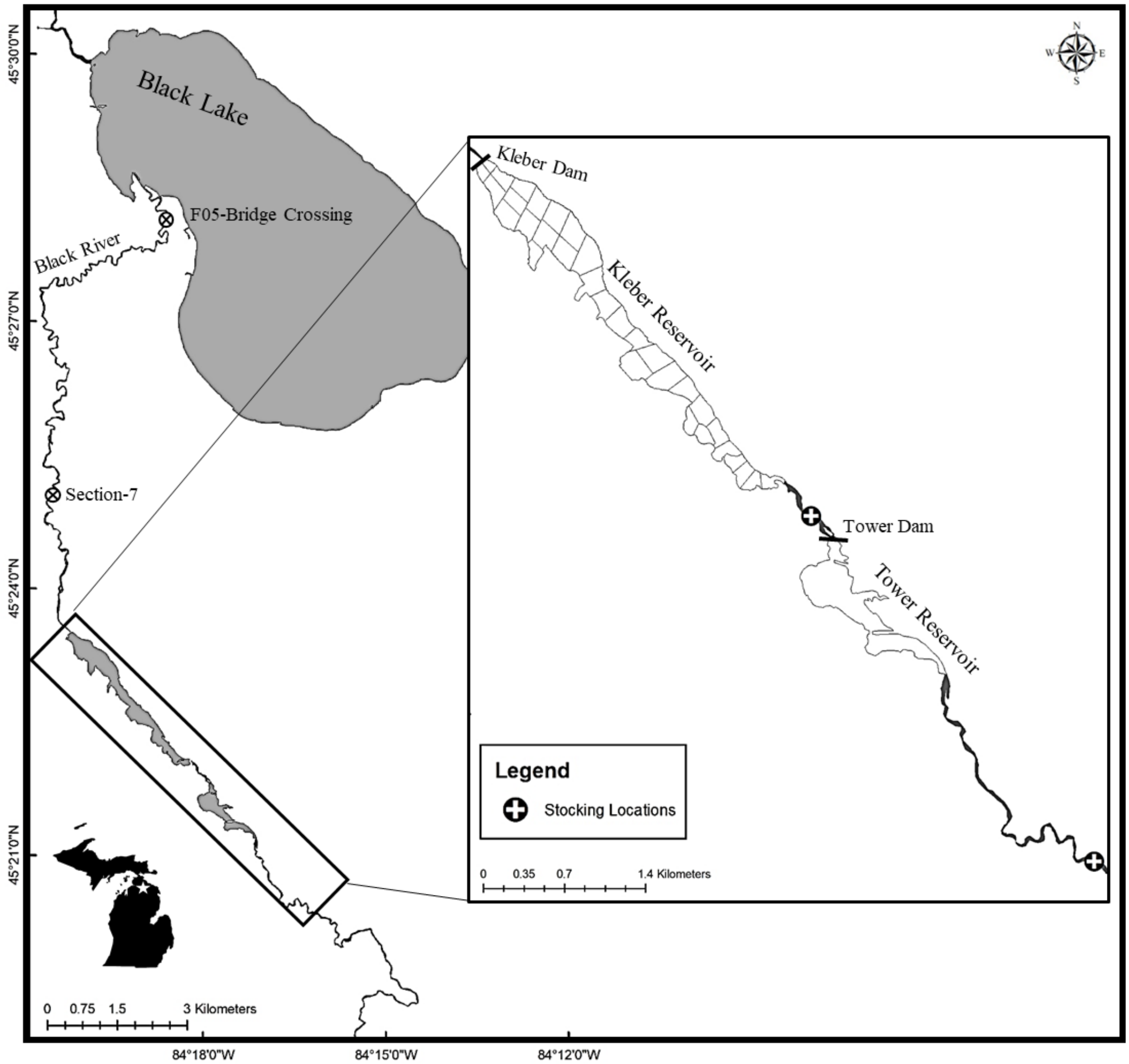

Figure 3.1: Map of Black Lake and the upper Black River system located in Cheboygan County, Michigan. The inset map highlights Kleber Dam, Kleber Reservoir, Tower Dam, and Tower Reservoir, along with the lake sturgeon stocking locations used for the research project. In the inset map Kleber reservoir is divided into the 32 census zones that were surveyed during the project. RFID antennas were located at the F05-bridge crossing, section-7, 300 meters below Kleber Dam, and at the Kleber Dam powerhouse. Map data is from the United States Geological Survey National Hydrography Dataset.

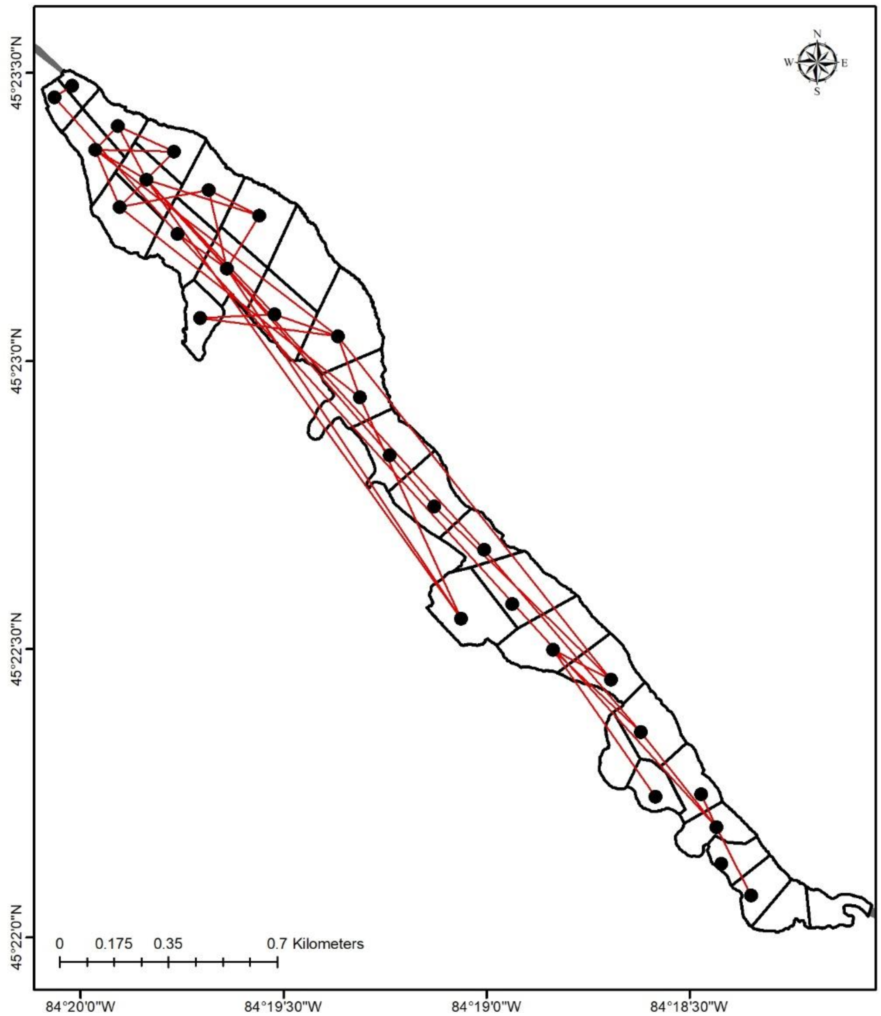

Figure 3.2: Map illustrating the coarse-scale movements of 24 juvenile lake sturgeon between census zones in Kleber Reservoir. The red lines represent movements between census zones, and the black circles represent the central observation point for each zone. The more red lines that are adjacent or overlap 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 is from the United States Geological Survey National Hydrography Dataset.

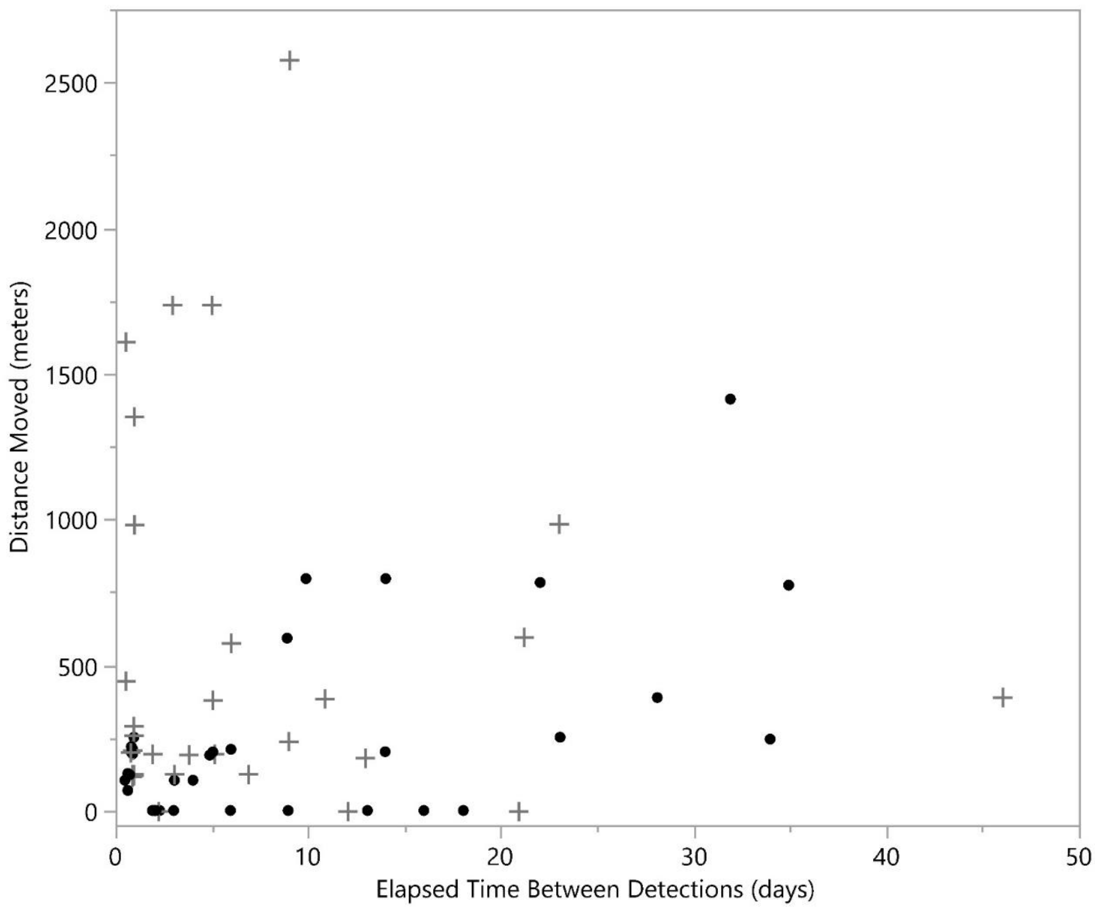

Figure 3.3: Scatterplot showing linear distance moved (meters) vs. elapsed time between detections (days) for 73 different movement segments from 24 unique lake sturgeon that were detected on two or more occasions. Age-1 lake sturgeon are represented by black circles, while age-2 lake sturgeon are represented by grey crosses.

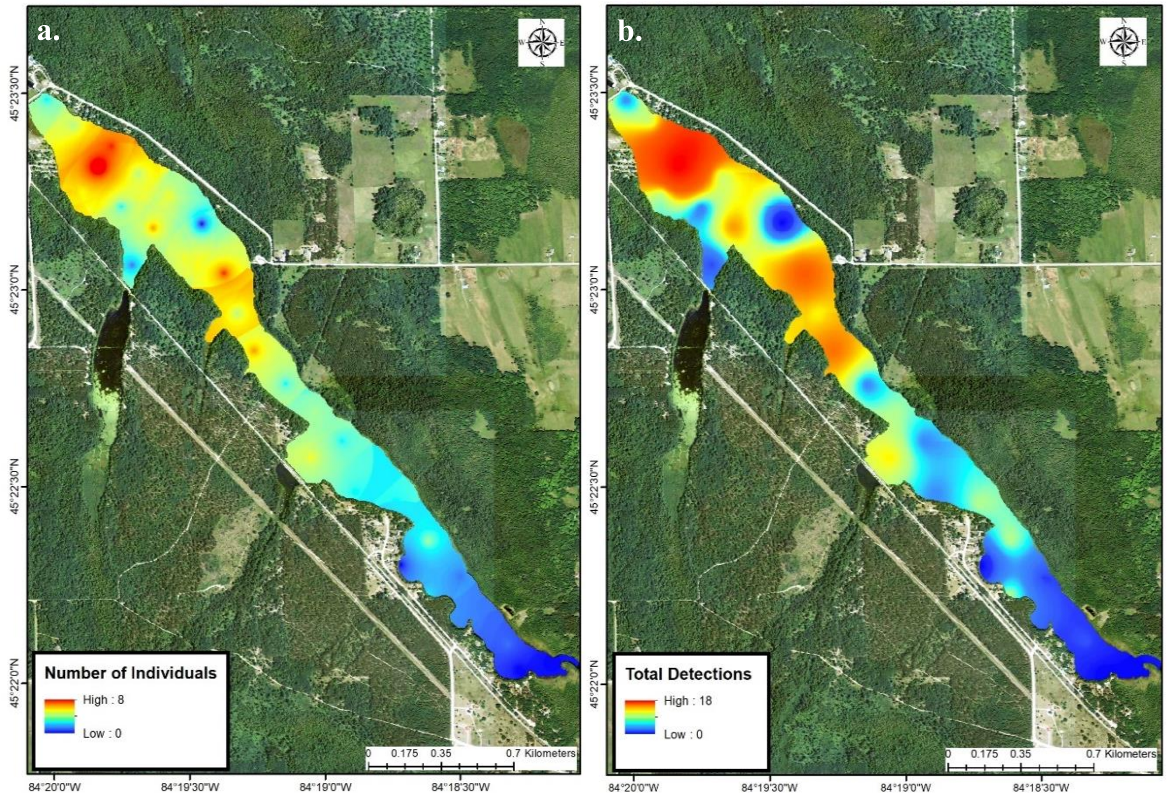

Figure 3.4: Interpolated map showing where the highest number of unique lake sturgeon were detected across Kleber Reservoir (a.). Interpolated map showing where the most lake sturgeon detections were located across Kleber Reservoir (b.). Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program.

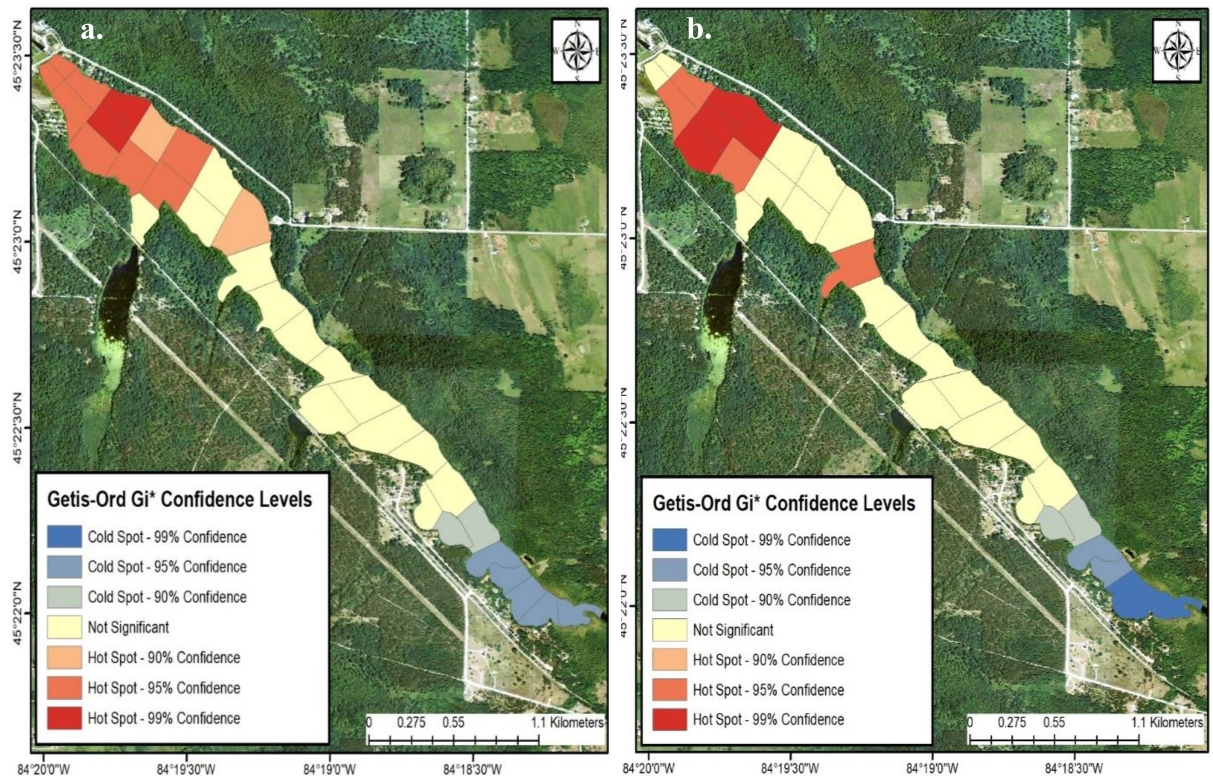

Figure 3.5: Getis-Ord GI* hot spot analysis probability map for the number of unique lake sturgeon detected in each zone (a.). Getis-Ord GI* hot spot analysis probability map for the total number of lake sturgeon detections in each zone (b.). A cold spot indicates a statistically significant cluster 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.

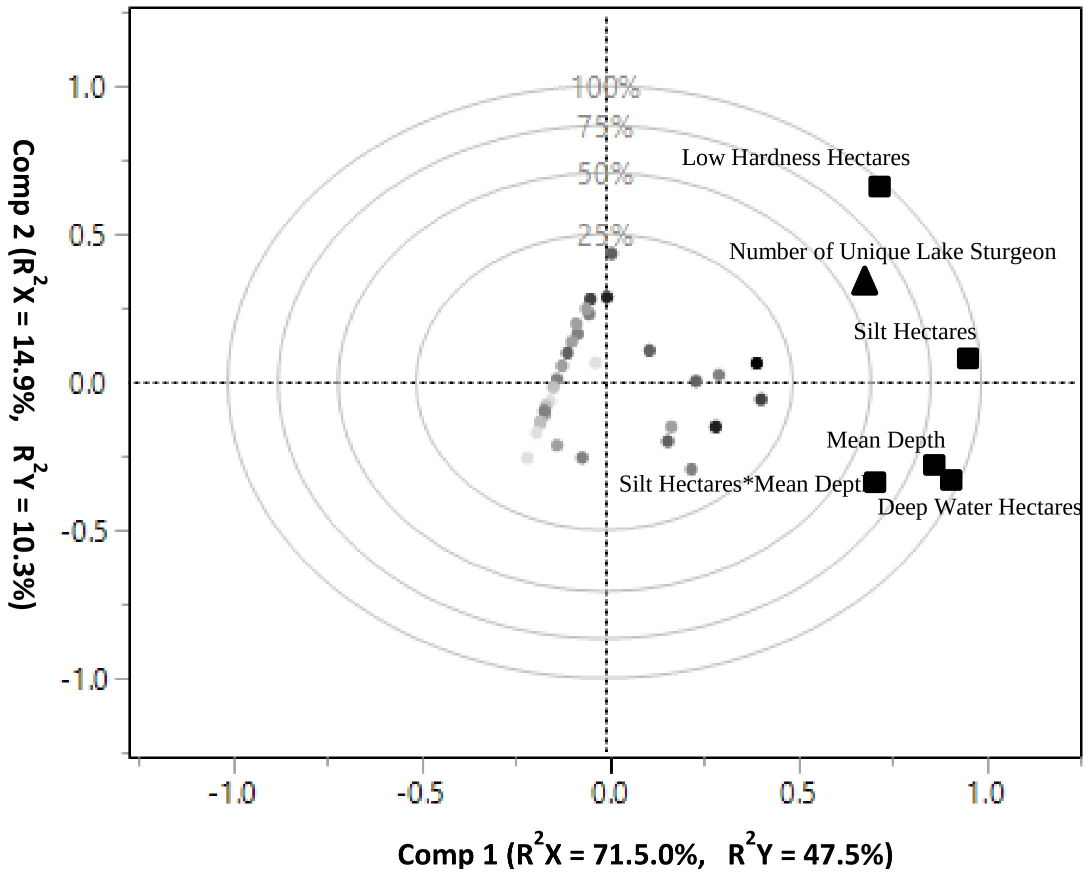

Figure 3.6: Correlation loading plot for the projection to latent structures regression (PLSR) analysis examining habitat associations with the number of unique lake sturgeon detected in each census zone. The small colored circles represent the scores for the different census zones, and the shading level 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, 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.

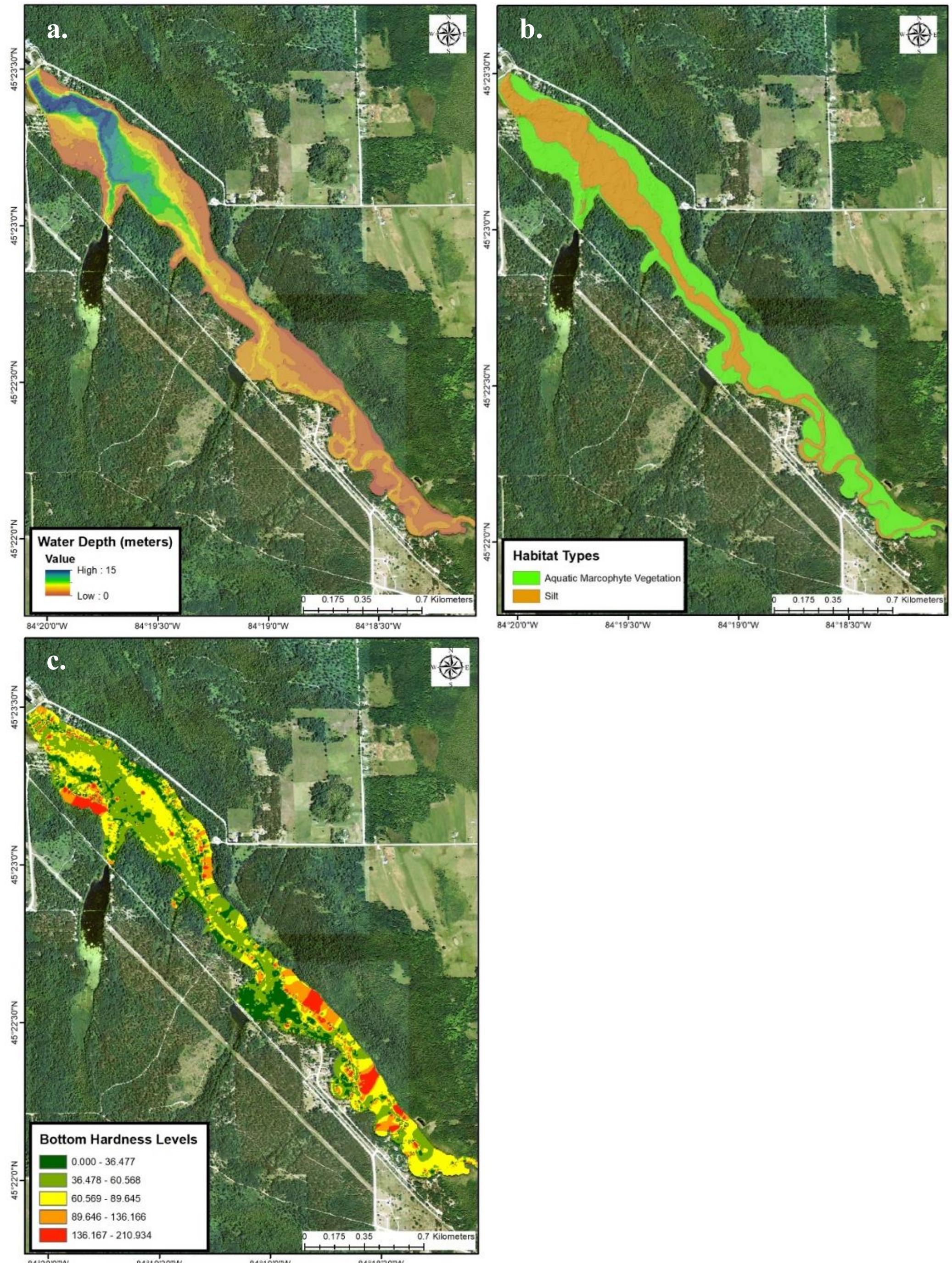

Figure 3.7: Interpolated bathymetry map of Kleber Reservoir (a). Substrate habitat map of Kleber Reservoir based on side-scan sonar imaging (b.). Interpolated bottom hardness map of Kleber Reservoir (c.). Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program.

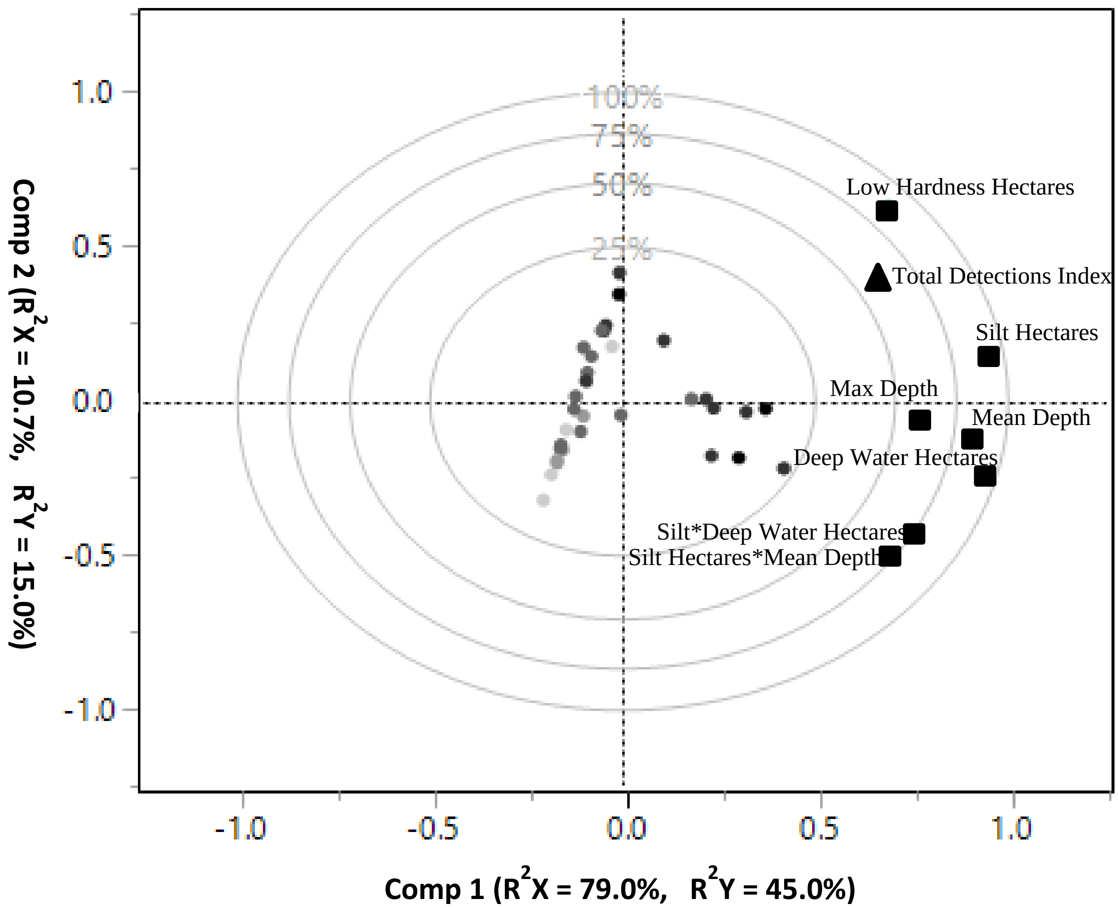

Figure 3.8: Correlation loading plot for the projection to latent structures regression (PLSR) analysis examining habitat associations with the total number of lake sturgeon detections in each zone. The small colored circles represent the scores for the different census zones, and the shading level represents 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.

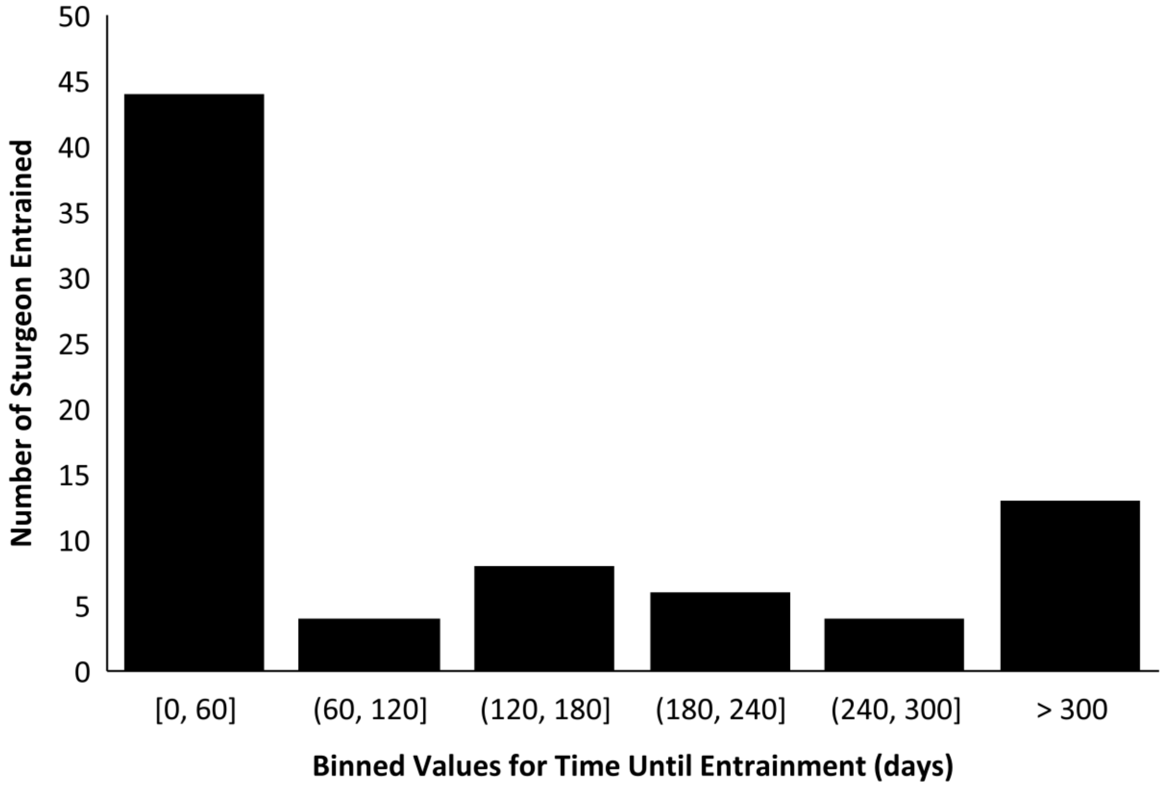

Figure 3.9: Histogram showing time until entrainment (binned into 6 categories) for 79 juvenile lake sturgeon that were entrained below Kleber Dam based on radio frequency identification (RFID) detections data.

Chapter 4:
Juvenile Lake Sturgeon Route-Specific Passage Survival and Behavior at Two Hydroelectric Dams

Abstract

Reconnecting lake sturgeon (*Acipenser fulvescens*) populations and rivers through the design and use of passage systems at hydroelectric dams is seen as a vital step toward recovery of the species. However, downstream passage behavior and survival of juvenile lake sturgeon at hydroelectric dams is poorly understood. We used stream-wide RFID antennas and the juvenile salmonid acoustic telemetry system to monitor downstream passage behavior and route-specific survival through two hydroelectric dams on the Black River in northern Michigan. A total of 62 age-2, 114 age-1, and 792 age-0 lake sturgeon were tagged and stocked above Tower Dam, while a total of 60 age-2, 118 age-1, and 817 age-0 lake sturgeon were tagged and stocked above Kleber Dam. Our observations showed that juvenile lake sturgeon usually made between 1 – 4 approaches into the forebays of both dams and usually stayed within a forebay for several hours before departing. Detections were primarily clustered in a broad area over the deepest part of the forebay downslope of the spillway at Kleber Dam, while at Tower Dam detections were clustered in the deeper part of the forebay immediately adjacent to the spillway and penstocks. Habitat use at both dams was higher in areas with more silt habitat and less aquatic vegetation and in areas that had greater mean depth and greater max depth characteristics. At Kleber Dam the survival rates for passage through the vertical-shaft Kaplan turbine systems were estimated at 70.9% (SE = 0.093) for age-0 and 44.9% (SE = 0.138) for age-

1 and age-2 lake sturgeon. At Tower Dam survival through the leffel type-z vertical-shaft turbine systems was estimated at 86.9% (SE = 0.135) for age-0 and 59.9% (SE = 0.182) for age-1 and age-2 lake sturgeon. Passage survival through the Tower Dam Spillway was estimated at 100% (SE = 0.132) for age-0 and 100% (SE = 0.188) for age-1 and age-2 lake sturgeon. Impingement mortality at Tower Dam differed by age and was 0.4% for age-0, 13.3% for age-1, and 21.8% for age-2 lake sturgeon, while impingement mortality at Kleber Dam was not observed. Our results show that spillways are capable of passing lake sturgeon with very limited mortality. Turbine design, bar-rack spacing, and fish length and age at passage are key factors in determining levels of mortality at hydro-projects and in forecasting potential recruitment benefits from lake sturgeon passage improvements and hatchery supplementation.

Introduction

Fish passage engineering has emerged as a possible tool to help reintroduce fish species above dams and to reconnect fragmented populations disconnected by dams (Boothroyd et al., 2018; Coscarelli et al., 2011; Jager et al., 2016; Koenigs et al., 2018). The spatial extent of the effects of dams on river systems is immense with at least 2,139 dams in Michigan and Wisconsin alone that obstruct the movements of migratory fish species, which limits gene flow and access to spawning and rearing habitats necessary for sustained recruitment (USACE, 2023). Thus, passage research and solutions are needed to help address wide spread habitat fragmentation and barriers to movement in river systems.

Most studies and information on fish passage is focused on surface oriented species like salmonids (Cooke et al., 2020; Jager et al., 2016). Limited information is available on route specific passage survival, behavior, and entrainment characteristics of benthic oriented species like lake sturgeon (*Acipenser fulvescens*), especially at smaller run-of-the-river hydroelectric dams that are common across the Great Lakes (Bruch et al., 2016; FERC, 2017; Jager, 2006; Kynard, 1998; Kynard and Horgan, 2001; McDougall et al., 2014a, 2013; Parsley et al., 2007). In addition, no studies have compared passage survival characteristics for benthic species between Kaplan and Leffel turbine systems that are common in the Great Lakes region (Bruch et al., 2016). Different turbine systems may inflict differing levels of mortality and necessitate the need for specialized downstream passage systems for benthic juveniles to ensure recruitment benefits of passing adults above dams are realized (Jager et al., 2016; Pracheil et al., 2016).

Lake sturgeon is a benthic oriented adfluvial, potamodromous species that undertakes spring migrations into rivers to reproduce. Juvenile lake sturgeon rear within their natal river system for a variable amount of time before out-migrating downstream into lakes, reservoirs, or larger rivers to feed and grow (Peterson et al., 2007). The lake sturgeon's migratory life history often brings it into conflict with civil infrastructure and human resource needs across the species' range. Consequently, in most states and provinces the lake sturgeon is now considered to be threatened and is of regulatory and conservation concern (Bruch et al., 2016; Latta, 2005; Peterson et al., 2007).

The rapid development of hydroelectric infrastructure in the late 1800's and early 1900's is one of the major factors that contributed to the historical decline of lake sturgeon populations (Auer and Dempsey, 2013; Peterson et al., 2007). The species was also decimated by overfishing. A valuable commercial fishery developed for lake sturgeon flesh and caviar around 1850, and by the early 1900's many populations began to decline because of over exploitation (Auer and Dempsey, 2013; Peterson et al., 2007). In Lake Michigan the commercial lake sturgeon fishery was closed in 1929 and currently lake sturgeon are estimated to be at only 1% of their historical abundance (Haxton et al., 2014; Tody, 1974). The lethal combination of overfishing, a decline in water quality, habitat loss, and habitat fragmentation is thought to have brought about rapid declines in abundance and extirpation of many lake sturgeon populations (Brousseau, 1987; Harkness and Dymond, 1961; Hay-Chmielewski and Whelan, 1997).

The loss and fragmentation of important riverine habitats by dams is one of the major factors limiting the restoration of lake sturgeon in the Great Lakes (Bruch et al., 2016; Coscarelli et al., 2011; Peterson et al., 2007). Where hydroelectric dams were built they obstructed the migratory movements of lake sturgeon, leading to the loss of spawning and rearing habitat and fragmentation of river systems that once supported the species (Dean et al., 2023; Ferguson and Duckworth, 1997; Harkness and Dymond, 1961). In particular, dams were built in areas with the greatest hydraulic head that contained natural rapids, and dams flooded this important spawning habitat and converted it from lotic into lentic habitat (Aadland, 2015; Bruch et al., 2016; Zhong and Power, 1996). Dams can also delay migration movements and cause increased energy expenditure as fish search for passage routes (Holbrook et al., 2011; Nyqvist et al., 2017b; Piper et al., 2013).

Downstream passage through turbine systems and spillways can also cause physical trauma and barotrauma, which can lead to direct mortality and delayed mortality through sublethal effects (Brown et al., 2013; Ferguson et al., 2006; Kynard and Horgan, 2001; Pracheil et al., 2016; Schilt, 2007). Protective bar rack structures meant to protect fish and prevent passage through turbine systems can also inadvertently impinge fish and cause mortality (Barnthouse, 2013; Rytwinski et al., 2017). Furthermore, passage through reservoir systems can subject fish to increased levels of predation due to disorientation in the tailrace, sublethal effects of passage, and changes in habitat caused by dams (Ferguson et al., 2006; Rieman et al., 1991; Ruggerone, 1986). The net result of these impacts is that population recruitment and carrying capacity of river system is often significantly reduced (Cooper et al., 2017; Haxton et al., 2015; Huang and Wang, 2018; Pess et al., 2008).

Identifying sources and levels of mortality in hydroelectric reservoir systems is vital to lake sturgeon recovery efforts. Juvenile lake sturgeon are a demographic group of keen interest because they migrate downstream following emergence from spawning substrate and will often encounter hydroelectric infrastructure and man-made reservoir habitat. In addition, this demographic group is highly susceptible to predation (Waraniak et al., 2019, 2018), and many populations suffer from a lack of natural juvenile recruitment (Coscarelli et al., 2011; Peterson et al., 2007; Pollock et al., 2015). Hydroelectric dams without fish passage systems offer migrating juvenile lake sturgeon two passage routes: over spillways and through turbine systems. A thorough understanding of the mortality characteristics for spillways and different turbine systems that are common in the Great Lakes is necessary to evaluate the potential recruitment benefits of fish passage engineering efforts and reintroduction programs (Coscarelli et al., 2011; Jager et al., 2016; McDougall et al., 2014a). Furthermore, it is important to understand the behavior of juvenile lake sturgeon when they interact with hydroelectric infrastructure because this information can guide fish passage engineering efforts and improve passage survival and efficiency (Goodwin et al., 2014; Pracheil et al., 2016).

To fill these knowledge gaps and to aid sturgeon passage and recovery initiatives we designed a project to simulate passage of adult lake sturgeon and spawning above hydroelectric dams in order to evaluate the fate and survival of juveniles as they migrate downstream to assess the recruitment benefits of fish passage improvements. Specifically, this project aimed to evaluate route-specific passage survival and behavior of age-0, age-1, and age-2 lake sturgeon at two hydroelectric dams with different turbine systems located along the Black River in northern Michigan, USA. Our specific objectives were to (1) quantify survival estimates for passage through Kaplan turbine systems, (2) quantify survival estimates for passage through Leffel turbine systems (similar to a Francis turbine system), (3) quantify survival estimates for passage over spillways, (4) quantify delayed mortality resulting from passage, (5) quantify initial survival across the reservoirs, (6) quantify survival in the free flowing part of the Black River below the dams, and (7) document and compare movement behavior and habitat occupancy of lake sturgeon in the immediate forebays of both dams.

Methodology

Study Area:

This study was conducted in the upper Black River located in Cheboygan County in the northern peninsula of Michigan, USA (Figure 4.1). The upper Black River is the largest tributary of Black Lake (~ 4000 ha), and it comprises the only 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 17.6 km upstream from the river mouth. The dam was built in 1949 with an average head of 13.4 meters, and it forms a reservoir with 370 hectare-meters of storage capacity. Kleber Dam has two vertical shaft Kaplan turbines, a generating capacity of 1200 kw, a bottom withdrawal spillway, and 7.6 cm vertical debris bar-rack spacing. 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 an average head of 6.1 meters, and it forms a small reservoir with 76 hectare-meters of storage capacity. The dam has two vertical shaft Leffel type-z turbine systems, a generating capacity of 560 kw, a bottom withdrawal spillway, and 2.5 cm vertical debris bar-rack spacing.

Hatchery Production:

All lake sturgeon were reared at the Black River Sturgeon Rearing Facility between April and September in 2014, 2015, and 2016. Some lake sturgeon were produced artificially through the collection of eggs and milt from spawning adult lake sturgeon in the Black River. Adult lake sturgeon within this system are marked with PIT-tags and floy-tags, which allowed us to keep track of family crosses (Crossman et al., 2011). Other lake sturgeon were naturally produced and collected with drift nets during the spring drift season in the lower part of the Black River below the spawning grounds. Naturally produced lake sturgeon larvae that were caught were then transported back to the hatchery for rearing to the appropriate age. To produce the older age-1 and age-2 lake sturgeon some individuals were seasonally transported over to the Wolf Lake State Fish Hatchery (Mattawan, MI) and over-wintered each year until they were returned to the Black River and released.

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-0, age-1, and age-2 lake sturgeon. The dimensions of the transmitters used for age-1 and age-2 lake sturgeon were 5 x 7 x 13 mm and weighed 0.6 grams. These acoustic transmitters were programmed to have a 10 second transmission rate, with an estimated life expectancy of 180 days. The dimensions of the transmitters used for age-0 lake sturgeon were 3.7 x 5.5 x 11.1 mm and weighed 0.32 grams. These acoustic transmitters were programmed to have a 15 second transmission rate, with an estimated life expectancy of 100 days. In addition, a 23 x 3.65 mm half-duplex PIT-tag (Oregon RFID, Portland, Oregon) was implanted into each lake sturgeon. The transmitters and PIT-tags were surgically implanted by performing a standard laparotomy (Hegna et al., 2019). Before surgery, all sturgeon were anesthetized for approximately 5 minutes in an anesthetic bath with 125 mg/L of tricaine methanesulfonate (MS222). Once a sturgeon became fully sedated, weight (g) and total length (mm) measurements were taken. Age-0 lake sturgeon had a mean weight of 33 g (SD = 9.97) and a total length of 205 mm (SD = 21.70). Age-1 lake sturgeon had a mean weight of 135 g (SD = 31.74) and a total length of 348 mm (SD = 40.12). Age-2 lake sturgeon had a mean weight of 479 g (SD = 88.43) and a total length of 486 mm (SD = 35.38). The sturgeon was then placed ventral side-up on the operating table and an oxygenated maintenance dose of 100 mg/L of MS222 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. An 8-15 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 1-2 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 (Hegna et al., 2019). All age-1 and age-2 lake sturgeon were held for at least 4 weeks of post-operative observation and all age-0 lake sturgeon were held for at least 10 days of post-operative observation to ensure proper healing.

In total, 140 age-0, 110 age-1, and 110 age-2 lake sturgeon were surgically implanted with acoustic and PIT transmitters. Additionally, a total of 1,664 age-0, 167 age-1, and 37 age-2 lake sturgeon were implanted with only PIT-tags. All lake sturgeon were produced and reared at the Black River Sturgeon Rearing Facility between April and September. The age-1 and age-2 juvenile lake sturgeon produced were over-wintered at the Michigan Department of Natural Resources 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#: 03/14-041-00).

Experimental Release of Lake Sturgeon:

Juvenile lake sturgeon were released in 2014, 2015, and 2016. Age-1 and age-2 lake sturgeon were released in groups of 10-12 individuals, while age-0 lake sturgeon were released in groups of approximately 50 individuals. Smaller release groups were used to avoid possible negative effects associated with high stocking densities, which could alter behavior or elevate predation risk. A total of 790 age-0, 114 age-1, and 61 age-2 lake sturgeon were released upstream of Tower Reservoir (Figure 4.1). A total of 813 age-0, 118 age-1, and 61 age-2 lake sturgeon were released upstream of Kleber Reservoir. A total of 201 age-0, 45 age-1, and 25 age-2 lake sturgeon were released below Kleber Dam to serve as "control release groups" that were not exposed to turbine passage. Age-0 lake sturgeon were released in late September of each year, while age-1 and age-2 lake sturgeon were released between July and September of each year. Age-1 and age-2 lake sturgeon were released earlier to enable active tracking in the reservoirs for a separate study. Age-0 lake sturgeon were released later in the season in order to allow them to attain adequate size for surgery and transmitter implantation.

Passage, Fine-Scale Movement, and Impingement Monitoring:

To monitor movements and entrainment we used PIT-tag monitoring technology and acoustic telemetry. 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 (Figure 4.1). Six vertically oriented antennas were installed at the Kleber Dam powerhouse to monitor outflow from the two turbine units (Figure 4.2**)**. One stream-wide antenna was installed approximately 300 meters downstream of the Kleber Dam powerhouse. Two battery powered stream-wide RFID antennas connected to solar panels were operated between April and August at the downstream most section of the river used by adult lake sturgeon for spawning at a section termed section-7 (Figure 4.1). Lastly, three stream-wide RFID antennas were installed at the highway F-05 bridge crossing located 0.85 miles upstream from the river mouth where the Black River empties into Black Lake (Figure 4.1). We also installed several RFID PIT-tag detection antennas below Tower Dam. This included two antennas below the powerhouse, two antennas below the spillway, and one large stream-wide antenna approximately 500 meters downstream.

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 commercial electrical grid power to run the antennas, except for the two seasonal antennas at section-7, which were powered by batteries connected to two 200 watt solar panels (Zamp Solar, Bend, Oregon). Half-duplex RFID antenna systems constantly switch their electromagnetic fields on and off in order 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. For this study, data collected by RFID PIT-tag monitoring started in May 2015 and continued through May 2017. The RFID antennas were regularly monitored and tested to ensure proper operation. In general, the RFID antennas had a vertical read range of 12 – 30 inches.

Hydrophones were used to detect and position the acoustic transmitters. Specifically, JSATS compatible WHS4250 hydrophone data-loggers (Lotek Inc., Newmarket, Ontario) were used. Hydrophones were deployed in arrays in front of both Tower and Kleber Dams (Figure 4.3). A total of six hydrophones were placed in an array in front of Kleber Dam and a total of five hydrophones were placed in an array in front of Tower Dam. One hydrophone was also placed in the middle of Kleber Reservoir at the location where the reservoir begins to greatly increase in width. Forebay bathymetry, tag detection tests, and computer modeling with the

UMAP acoustic positioning software (Lotek Inc., Newmarket, Ontario) were used to assess and determine the best configurations for the hydrophone arrays and detection extent. UMAP uses timed difference of arrival computational methods to compute geospatial positions of lake sturgeon tagged with acoustic transmitters. Accuracy tests were conducted for each hydrophone array for each project year by measuring the difference between calculated and known positions of transmitters. The hydrophone array in the Kleber Forebay was found to have an average accuracy of 2.18 meters (SD = 3.145) in 2015 and 1.81 meters (SD = 1.417) in 2016. The hydrophone array in the Tower Forebay was found to have an average accuracy of 4.33 meters (SD = 2.875) in 2015 and 1.85 meters (SD = 1.836) in 2016. For an acoustic transmitter detection to be validated, the transmitter had to be detected at least twice in a 40 second time period. Computed tracks of geospatial positions were then used to help assign passage routes through the dams in addition to PIT-tag detections. Computed geospatial positions were also used to quantify behavioral characteristics such as forebay residency duration and the number of approaches that lake sturgeon made into the forebays. In the analyses, a sturgeon is considered to have departed the forebay if it left the hydrophone array study area by traveling either upstream or downstream out of the area to the point that it is no longer detected for a prolonged period of time (i.e., defined as 6 hours). Impingement mortality was manually assessed in 2015 by regularly checking the bar rack structures at both dams for sturgeon during cleaning.

Statistical Analyses:

Detections of juvenile lake sturgeon from PIT-tag interrogation antennas and from acoustic telemetry hydrophone receivers were used to evaluate survival through the various parts of the hydroelectric reservoirs and downstream river system. Using the User Specified Estimating Routine (USER) software program, a maximum likelihood based Cormack-Jolly-Seber model was used to estimate detection probabilities at the monitoring sites and to derive survival estimates. USER is a software program developed by the U.S. Department of Energy and is commonly used to analyze survival data at hydroelectric projects (Lady and Skalski, 2009; Skalski et al., 2011). Powell's direction set was used as the numerical method for deriving survival estimates. Comparisons between survival estimates for different age-groups, passage routes, and dams were made using log-likelihood ratio tests. However, in many cases small sample sizes prevented formal testing with log-likelihood ratio tests.

Spatial data on the total number of lake sturgeon detections, number of unique individuals, and proportional use was analyzed spatially by dividing the forebays of Kleber and Tower Dams into six meter grid-cells. The total number of detections and the number of unique individuals detected was then summarized for each grid-cell in the forebay. A proportional use index was developed because of the inherit bias of using non-normalized raw detections data where individuals with more detections would have a greater effect on spatial analyses. The proportional use index is described by the equation $\sum_{i_c}^{I_c} \frac{D_{ic}}{D_i}$ where for each unique sturgeon (**i**) that was detected within the specified grid cell number (**c**), the number of detections (**D**) of that sturgeon within the specified grid-cell ($\mathbf{D_{ic}}$) was divided by the total number of detections of that sturgeon within the entire study area ($\mathbf{D_i}$). This computation was repeated for each unique sturgeon that was detected within the specified grid-cell where $\mathbf{i_c}$ is the *ith* sturgeon detected in the specified grid cell and where $\mathbf{I_c}$ is the total number of unique individual sturgeon detected in the specified grid cell. These individual computations for each sturgeon were then summed together to generate a composite "proportional use" score value for the specified grid-cell. This computational procedure was then repeated for each grid cell within the forebay. Global Moran's I was used to evaluate spatial autocorrelation characteristics of the proportional use data and data on the number of unique individuals detected. The Getis-Ord local hotspot analysis was used to evaluate the specific geographical locations in the forebays where spatial clustering was statistically significant. The kernel density function was used to evaluate the spatial distribution of the non-normalized total detections data. All mapping and spatial analyses were performed using ArcGIS Desktop 10.5.1 software (ESRI, Redlands, California).

Restricted maximum likelihood (REML) based mixed effects models were used to evaluate differences in residency times and inter-approach times between lake sturgeon age groups and reservoirs. In all relevant analyses fixed factors included age, reservoir, and project year, while individuals were treated as a random factor. Because of small sample sizes, data on ages were combined into two categories that included age-0 lake sturgeon in one group and the older age-1 and age-2 lake sturgeon in another group. The Tukey HSD post-hoc test was used to evaluate differences between groups when significant differences were found. To evaluate differences in count data on the number of approaches made into the two different reservoir forebays the Kruskal-Wallis test was utilized with the Chi-square approximation. Fixed factors included age, reservoir, and project year. The Steel-Dwass post-hoc test was used to evaluate differences between groups when significant differences were found. Differences in the probability of making more than one approach into a forebay was evaluated through using odds ratios tests. Odds ratio (OR) tests were performed with MedCalc statistical software version number 20.027 (MedCalc Software, Ostend, Belgium; https://www.medcalc.org). All other statistical analyses were conducted with the JMP Pro version 15 statistics software package (SAS Institute, Cary, NC, USA).

Results

Survival in the Lower Black River (below Kleber Dam to the river mouth):

During the study period between 2015 and 2017 a total of 210 age-0, 52 age-1, and 25 age-2 lake sturgeon were detected moving downstream near the mouth of the Black River at the F-05 bridge PIT-tag antenna detection site. Survival from below Kleber Dam to the F-05 bridge site in the Black River was estimated for groups of "control" lake sturgeon that were released below Kleber Dam (i.e., these release groups were not exposed to turbine passage). For these control releases we found that the age-0 lake sturgeon had a significantly lower survival rate compared to the older age-1 and age-2 lake sturgeon (LLV: -5.17, $p = 0.028$; Table 1). Age-0 lake sturgeon had an 88.1% (SE = 0.067) survival rate, while age-1 and age-2 lake sturgeon had a 100% (SE = 0.107) survival rate. Survival estimates to the F-05 bridge site for lake sturgeon that were known to have passed through the Kleber Dam powerhouse were significantly lower compared to the control lake sturgeon (LLV: -9.78, $p = 0.028$), with age-0 lake sturgeon having a 76.3% (SE = 0.085) survival rate and age-1 and age-2 lake sturgeon having an 81.7% (SE = 0.158) survival rate (Table 1).

Initial Survival Across Kleber Reservoir:

Survival estimates were made for initial movements from below Tower Dam to the forebay of Kleber Dam based on acoustic transmitter detections. Survival estimates based on PIT-tag detection data were 100% (SE = 0.035) for age-0 lake sturgeon and 100% (SE = 0.067) for age-1 and age-2 lake sturgeon. Survival estimates based on acoustic telemetry data were similar with age-0 lake sturgeon having a 100% (SE = 0.146) survival rate and age-1 and age-2 lake sturgeon having a 98.1% (SE = 0.137) survival rate (Table 1).

Kleber Dam Forebay Behavior:

Behavior of lake sturgeon in the forebay of Kleber Dam varied considerably. A total of 50 age-0, 20 age-1, and 21 age-2 lake sturgeon were detected within the forebay by acoustic receivers between 2015 and 2017. Most acoustic tag detections occurred in the deep channel downslope of where the spillway and penstock intakes are located as indicated by kernel density estimates (Figure 4.4). Global Moran's I analysis indicated that data on the number of individual lake sturgeon detected was highly clustered spatially (Moran's I = 0.863, Z = 31.20, $p < 0.001$; Figure 4.5). Getis-Ord hotspot analysis indicated that detections of the number of individuals were primarily clustered in a broad area over the deepest part of the forebay downslope of the spillway (Figure 4.6). Detections of unique individuals were greater in areas with more silt habitat and less aquatic vegetation (r_s= 0.78, $p < 0.001$) and in areas that had greater mean depth (r_s= 0.63, $p < 0.001$) and greater max depth (r_s = 0.62, $p < 0.001$) characteristics (Figure 4.7).

Similarly, Global Moran's I analysis indicated that the normalized lake sturgeon detections data based on the proportional use index was clustered spatially (Moran's I = 0.55, Z = 20.36, $p < 0.001$; Figure 4.8). Getis-Ord hotspot analysis indicated that the proportional use data were primarily clustered in the area immediately downslope of the spillway and in one smaller area immediately in front of the spillway (Figure 4.9). Habitat use based on the proportional use index was greater in areas with more silt habitat and less aquatic vegetation (r_s= 0.72, $p < 0.001$) and in areas that had greater mean depth (r_s= 0.54, $p < 0.001$) and greater max depth (r_s = 0.53, $p < 0.001$) characteristics (Figure 4.7).

Age-0 lake sturgeon made on average 3.18 different approaches into the Kleber Dam forebay (SD = 6.78, Median = 1, Range: 1 – 39) between 2015 and 2017. On average age-0 lake sturgeon resided within the forebay area for 17.43 hours (SD = 48.42, Median = 3.73, Range: 0.03 – 365) before departing. The average inter-approach time (i.e., time in-between approaches into the forebay) for the age-0 lake sturgeon was 38.81 hours (SD = 101.12, Median = 16.70, Range: 6 – 873).

Age-1 and age-2 lake sturgeon made on average 1.80 different approaches into the Kleber Dam forebay (SD = 1.14, Median = 1, Range: 1 – 5) between 2015 and 2017. On average the age-1 and age-2 lake sturgeon resided within the forebay area for 5.75 hours (SD = 10.92, Median = 1.25, Range: 0.03 – 74) before departing. The average inter-approach time for the age-1 and age-2 lake sturgeon was 184.23 hours (SD = 423.92, Median = 24.04, Range: 6 – 2290). There was no significant difference in the number of approaches made into the forebay between the age-0 and the older age-1 and age-2 lake sturgeon (Chi-square: 0.64, DF: 1, p = 0.423). Lake sturgeon appeared to make more approaches into the forebay in 2015 compared to 2016 (Chi-square: 18.50, DF: 1, p = 0.423). Also, there was no difference between the two age categories with respect to the proportion of lake sturgeon that made more than one approach into the forebay during the study time period (Z = 1.19, p = 0.232). The amount of time spent in the forebay was also similar between the age-0 and the older age-1 and age-2 lake sturgeon (F-Ratio: 2.20, DF: 1, p = 0.141), with no difference found between project years (F-Ratio: 2.91, DF: 1, p = 0.092). Lake sturgeon spent less time within the forebay during their first approach compared to subsequent approaches (F-Ratio: 6.30, DF: 1, p = 0.0127). No difference in inter-approach times was observed between the age groups (F-Ratio: 0.46, DF: 1, p = 0.503) or between project years (F-Ratio: 3.14, DF: 1, p = 0.086).

Passage Survival at Kleber Dam:

Survival estimates were calculated for the passage route through the Kleber Dam powerhouse and its vertical shaft Kaplan turbine system based on acoustic transmitter and PIT-tag detections. A total of 176 age-0, 25 age-1, and 8 age-2 lake sturgeon were detected between 2015 and 2017 passing through the powerhouse, and 96% of these passage events occurred at night. Immediate passage survival estimates were 81.8% (SE = 0.108) for age-0 lake sturgeon and 54.9% (SE = 0.127) for age-1 and age-2 lake sturgeon. The comprehensive survival estimates (i.e., includes delayed mortality) for the powerhouse were 70.9% (SE = 0.094) for age-0 lake sturgeon and 44.9% (SE = 0.138) for age-1 and age-2 lake sturgeon (Table 1). Thus, the delayed mortality rate, which encompasses the time period after passage until the lake sturgeon reached the mouth of the Black River, was 10.9% for age-0 lake sturgeon and 10% for age-1 and age-2 lake sturgeon. Impingement mortality on the debris bar-rack structure at Kleber Dam was not observed.

Tower Dam Forebay Behavior:

Behavior in the forebay of Tower Dam was highly variable. A total of 35 age-0, 11 age-1, and 20 age-2 lake sturgeon were detected within the forebay by acoustic receivers between 2015 and 2017. Most acoustic tag detections occurred in the deeper part of the channel in the immediate vicinity of the powerhouse and spillway as indicated by kernel density estimates (Figure 4.10). Global Moran's I analysis indicated that data on the number of individual lake sturgeon detected was highly clustered spatially (Moran's I = 0.832, Z = 30.33, $p < 0.001$; Figure 4.11). Getis-Ord local hotspot analysis indicated that detections of the number of individuals were primarily clustered over a broad deep portion of the forebay (Figure 4.12). Detections of unique individuals were greater in areas with more silt habitat and less aquatic vegetation (r_s= 0.66, $p < 0.001$) and in areas that had greater mean depth (r_s= 0.73, $p < 0.001$) and greater max depth (r_s = 0.75, $p < 0.001$) characteristics (Figure 4.13).

Similarly, Global Moran's I analysis indicated that the normalized lake sturgeon detections data based on the proportional use index was clustered spatially (Moran's I = 0.685, Z = 25.51, $p < 0.001$; Figure 4.14). Getis-Ord hotspot analysis indicated that the proportional use data were primarily clustered in the deeper part of the forebay immediately adjacent to the spillway and penstocks (Figure 4.15). Detections based on the proportional use index were greater in areas with more silt habitat and less aquatic vegetation (r_s= 0.65, $p < 0.001$) and in areas that had greater mean depth (r_s= 0.71, $p < 0.001$) and greater max depth (r_s = 0.74, $p < 0.001$) characteristics (Figure 4.13).

Age-0 lake sturgeon made on average 3.2 different approaches into the Tower Dam forebay (SD = 10.82, Median = 1, Range: 1 – 65) during the study period between 2015 and

2017. On average the age-0 lake sturgeon resided within the forebay area for 6.25 hours (SD = 7.50, Median = 3.32, Range: 0.03 – 38) before departing. The average inter-approach time for the age-0 lake sturgeon was 18.68 hours (SD = 13.51, Median = 13.58, Range: 6 – 79).

Age-1 and age-2 lake sturgeon made on average 7.81 different approaches into the Tower Dam forebay (SD = 13.08, Median = 4, Range: 1 – 71) during the study period between 2015 and 2017. On average the age-1 and age-2 lake sturgeon resided within the forebay area for 40.10 hours (SD = 71.13, Median = 12.75, Range 0.05 – 470) before departing. The average inter-approach time for the age-1 and age-2 lake sturgeon was 21.96 hours (SD = 56.41, Median = 10.83, Range: 6 – 734.0).

The age-1 and age-2 lake sturgeon made significantly more approaches into the Tower Dam forebay compared with age-0 lake sturgeon (Chi-square: 18.01, DF: 1, $p < 0.001$). Age-1 and age-2 lake sturgeon were 10 times more likely to make two or more approaches into the forebay compared to age-0 lake sturgeon (OR = 10.15, 95% CI = 3.19 – 32.30, Z = 3.92, $p = 0.0001$). The number of approaches made was similar between project years (Chi-square: 0.64, DF: 1, $p = 0.424$). The older age-1 and age-2 lake sturgeon also spent more time within the forebay compared with the age-0 lake sturgeon (F-Ratio: 10.71, DF: 1, $p = 0.0018$) with no difference found between project years (F-Ratio: 1.18, DF: 1, $p = 0.278$). There was no significant difference between the amount of time spent in the forebay during the first approach compared to time spent in the forebay in subsequent approaches (F-Ratio: 1.44, DF: 1, $p = 0.232$). Both age groups of lake sturgeon had similar inter-approach times (F-Ratio: 0.50, DF: 1, $p = 0.489$), with no differences observed between project years (F-Ratio: 1.05, DF: 1, $p = 0.321$).

Passage Survival at Tower Dam:

Survival estimates were calculated for the passage route through the Tower Dam powerhouse and its vertical shaft Leffel type-z turbine system. Because Tower Dam is located above Kleber Reservoir and its hydrophone array, we were able to derive survival estimates using PIT-tag detection data and acoustic telemetry data separately. A total of 36 age-0, 11 age-1, and 6 age-2 lake sturgeon were detected between 2015 and 2017 passing through the powerhouse, and 74% of these passage events occurred at night. The comprehensive passage survival estimates based on PIT-tag detection data were 86.9% (SE = 0.135) for age-0 lake sturgeon and 59.9% (SE = 0.132) for age-1 and age-2 lake sturgeon (Table 1). The comprehensive survival estimates based on acoustic transmitter detection data were similar, with age-0 lake sturgeon having a 90.9% (SE = 0.166) survival rate and age-1 and age-2 lake sturgeon having a 58.8% (SE = 0.122) survival rate.

Survival estimates were also calculated for the passage route through the spillway at Tower Dam. A total of 41 age-0, 3 age-1, and 10 age-2 lake sturgeon were detected passing through the spillway, and 87% of these passage events occurred at night. The comprehensive passage survival estimates based on PIT-tag detection data were 100% (SE = 0.132) for age-0 lake sturgeon and 99.9% (SE = 0.188) for age-1 and age-2 lake sturgeon (Table 1). The comprehensive survival estimate based on acoustic transmitter detection data for all ages combined was similar, with a 100% (SE = 0.235) survival rate estimate.

Impingement mortality rates on the Tower Dam debris bar-rack structure were calculated based on direct visually observed mortality counts. Age-0 lake sturgeon were observed to have a low mortality rate at only 0.4%. However, mortality rates were considerably higher for the older lake sturgeon, with age-1 lake sturgeon having a 13.3% mortality rate and age-2 lake sturgeon having a 21.8% mortality rate.

Comparing Behavioral Characteristics Between the Forebays at Kleber and Tower Dams:

Behavioral differences and similarities were found between the two different reservoir forebays with regards to the number of approaches that lake sturgeon made (Chi-square: 23.93, DF: 3, $p < 0.001$). The age-0 lake sturgeon made similar numbers of approaches into both forebays in Tower and Kleber Reservoirs (Steel-Dwass, Hodges-Lehman = 0, Z = -1.64, p = 0.355). However, age-0 lake sturgeon were 2.5 times more likely to make two or more approaches into the Kleber Dam forebay compared to the Tower Dam Forebay (OR = 2.50, 95% CI = 0.87 – 7.16, Z = 1.69, p = 0.090). Conversely, the age-1 and age-2 lake sturgeon made more approaches into the Tower Dam forebay than they did at the Kleber Dam forebay (Steel-Dwass, Hodges-Lehman = 2, Z = 3.24, p = 0.006). Age-1 and age-2 lake sturgeon were 2.43 times more likely to make two or more approaches into the Tower Dam forebay compared to the Kleber Dam Forebay (OR = 2.43, 95% CI = 0.92 – 6.42, Z = 1.79, p = 0.073).

Some differences and similarities in residency times were also found between the two reservoir forebays (F-Ratio: 11.87, DF: 1, $p < 0.001$). The age-0 lake sturgeon had similar residency times in the forebays of both Kleber and Tower Dams (Tukey HSD, T-Ratio: 0.86, p = 0.828). However, the older age-1 and age-2 lake sturgeon had significantly longer residency times in the Tower Dam forebay compared to the Kleber Dam forebay (Tukey HSD, T-Ratio: -4.29, $p < 0.001$). There was no significant difference in inter-approach times between the two forebays and age groups (F-Ratio: 0.487, DF: 1, p = 0.485).

Discussion

Forebay Behavior:

Our results showed considerable variability in forebay behavior between lake sturgeon age-classes (age-0 vs. age-1 and age-2) and dam environments (Kleber Dam vs Tower Dam); however, results were consistent between sampling years. Juvenile lake sturgeon usually made between 1 – 4 approaches into the forebays of both dams and usually stayed within a forebay for several hours before departing. We observed that lake sturgeon spent less time within the forebay at Kleber Dam during their first approach into the forebay compared with subsequent approaches. This may be due to an initial outmigration pulse that was observed following stocking of sturgeon into the reservoirs. We also found that the older age-1 and age-2 lake sturgeon made significantly more approaches into and spent more time within the forebay at Tower Dam compared with age-0 lake sturgeon. Age-0 lake sturgeon were more likely to make two or more approaches into the Kleber Dam forebay compared to the Tower Dam forebay. Conversely, the age-1 and age-2 lake sturgeon made more approaches into the Tower Dam forebay than they did at the Kleber Dam forebay. The older age-1 and age-2 lake sturgeon also had longer residency times within the Tower Dam forebay compared to the Kleber Dam forebay.

The differences we observed in behavior between age groups and between dams is likely due to physical differences between the two dams and reservoirs. Tower Reservoir is considerably smaller and shallower than Kleber Reservoir and this less favorable habitat may have been a factor that promoted age-0 lake sturgeon to leave Tower Reservoir more quickly than Kleber Reservoir. In addition, the bar-rack spacing is narrower at Tower Dam than at Kleber Dam, which likely prevented the larger age-1 and age-2 lake sturgeon from quickly leaving Tower Reservoir. In addition, the entrance into the Tower Dam forebay is restricted by an old railroad crossing that creates a very narrow entrance and exit. These two factors may account for the greater number of approaches into and longer residency times at the Tower Dam forebay that the older age-1 and age-2 lake sturgeon had, as these sturgeon would have been largely confined within this smaller reservoir system. The absence of observed behavioral differences between the age groups at Kleber Dam is likely because the larger bar-rack spacing at Kleber Dam was considerably less size selective compared with Tower Dam.

Few studies have evaluated fine-scale behavior of juvenile lake sturgeon in the forebays of hydroelectric dams for comparison. McDougall et al. (2014) tracked the movements of five adult lake sturgeon that made 17 recorded movements, three subadult lake sturgeon that made 20 recorded movements, and one juvenile lake sturgeon that made three recorded movements into the forebay of the Slave Falls Generating Station in Manitoba. The authors observed that lake sturgeon resided within the forebay for shorter periods of time compared with our results. They found that the average residency time within the forebay was 0.45 hours, with no differences observed between size-classes. The researchers also noted similar to our observations that some lake sturgeon would stay within the forebay for days at a time, while many others only made brief visits into the forebay before departing. Research examining movements of white sturgeon (*Acipenser transmontanus*) through fish ladders has similarly shown variable residency times ranging from one minute to six months (Parsley et al., 2007).

Spatial Analysis and Habitat Use:

The acoustic transmitter detections and habitat use patterns that we observed in the forebays of both dams showed distinct spatial clustering. In the Tower Dam forebay lake sturgeon used areas of deeper water located immediately adjacent to the dam, while in the Kleber Dam forebay lake sturgeon did not use areas as much that were immediately next to the dam. This difference in spatial habitat characteristics used may be explained by the fact that there is a steep slope that lake sturgeon must climb in the Kleber Dam forebay before they can actually enter the area in the immediate vicinity of the spillway and powerhouse. No such steep slope exists in the Tower Dam forebay. Other studies have comparably found that bathymetric features such as river narrows and areas that rapidly decrease in depth can restrict movements of lake sturgeon (McDougall et al., 2014a, 2013). We also found that juvenile lake sturgeon habitat use was greater in areas with more silt habitat and less aquatic vegetation and in areas that had higher mean depth and max depth characteristics. Past research has also similarly shown that lake sturgeon tend to use deeper areas with silt and sand substrates and avoid aquatic vegetation (Gerig et al., 2011; Hegna et al., 2020; Holtgren and Auer, 2004; Kempinger, 1996; Trested et al., 2011). Forebay characteristics like bathymetry, substrate, and aquatic vegetation may be key factors that can influence forebay movements, residency time, entrainment susceptibility, and the success of fish passage engineering efforts. The apparent aversion that lake sturgeon have for aquatic vegetation could be used to help guide juveniles toward safer passage routes at hydroelectric dams. The fact that juvenile lake sturgeon of all ages spent a considerable amount of time using habitat in front of the dams, may be promising for the design of passage systems that can engage juvenile lake sturgeon to pass through safer routes, such as spillways or juvenile bypass systems.

Passage Survival Estimates:

The different river reaches, passage routes, and turbine designs that we examined were characterized by different juvenile lake sturgeon survival characteristics. The vast majority of passage events at the dams occurred at night. Past research has similarly noted the propensity for nocturnal behavior by juvenile lake sturgeon, which is likely a predator avoidance strategy (Benson et al., 2005; Caroffino et al., 2009; Holtgren and Auer, 2004). Survival rates in the free flowing part of the Black River below Kleber Dam were higher for age-1 and age-2 lake sturgeon (~100%) than for age-0 lake sturgeon (~88%). We also observed that initial survival across Kleber Reservoir was at or near 100% regardless of age group. No similar studies with survival estimates exist on juvenile lake sturgeon. For comparison, Karppinen et al. (2021) evaluated passage mortality rates of Atlantic salmon smolts across four different dams on the Mustionjoki River in Finland and found that mortality rates ranged between 0%–50% in the forebays, 4%–64% in the power stations, and 2–30%/km for downstream river migration after passage of a dam.

Turbine mortality rates differed by age group and turbine design. We found that older age-1 and age-2 lake sturgeon at Kleber Dam suffered from higher passage mortality rates (~55%) at the Kaplan turbine system than age-0 lake sturgeon (~30%). Similarly, older age-1 and age-2 lake sturgeon at Tower Dam suffered from higher passage mortality rates (~40%) at the Leffel turbine system than age-0 lake sturgeon (~10-15%). The differences between the age groups is attributable to the fact that older lake sturgeon are larger in size and have a higher blade strike probability during turbine passage (Pracheil et al., 2016). Many of the older age-1 and age-2 lake sturgeon likely were prevented or deterred from entering the turbines by the protective bar-rack structures at both dams. However, the integrity of the bar rack structures, especially at the bottom was not able to be verified. In addition, juvenile lake sturgeon may have been impinged on the bar-rack structures and killed before actually passing through a turbine system. We also observed that passage survival of age-0 lake sturgeon was considerably higher at the Leffel turbine system (~85-90%) compared with the Kaplan turbine system (~70%). River systems that have similar Leffel turbine systems on them would likely have higher net juvenile recruitment rates compared with river systems with similar Kaplan turbine systems and may require less fish passage engineering efforts to achieve acceptable project survival rates.

To our knowledge the unpublished study by Phipps et al. (2016) is the only other field study that has evaluated hydro-turbine passage survival rates of juvenile lake sturgeon (Bruch et al., 2016). In the study HI-Z balloon tags were used and lake sturgeon were artificially injected directly into Leffel turbines. Similar to our results the study found that passage survival rates through the Leffel turbine system at Shawano Paper Mill Dam were high at approximately 92.7% and 90.6% for fingerling and yearling lake sturgeon, respectively. During the study, only one juvenile was recaptured with visible injuries that consisted of a damaged gill, hemorrhaged left eye, and hemorrhaged brain. Similarly, in a laboratory study researchers found that juvenile white sturgeon had a >0.99 probability of survival when passing through an axial-flow hydrokinetic turbine, with only one injury reported (Amaral et al., 2015). The observed high survival and low injury rate experienced by age-0 juvenile sturgeon may be due to their small size, cartilaginous body structure, protective scutes, and the low head level of the dams that were evaluated (Phipps et al., 2016).

We observed that passage survival at the Tower Dam spillway was at or near 100% for all age groups, which indicates that small spillways are able to safely pass juvenile lake sturgeon. McDougall et al. 2014 used acoustic telemetry to monitor downstream passage of four adult size (878–1,287 mm FL) and seven subadult size (554–706 mm) lake sturgeon at the Slave Falls Generating Station on the Winnipeg River, Manitoba. Similar to our results the authors found that downstream passage survival was high at approximately 91%. Seven of the 11 (64%) downstream-passage events in the study were determined to have occurred through the bottom-draw regulating sluices, but the remainder could not be assigned a passage route. The researchers also tagged a total of 12 juvenile lake sturgeon (426–501 mm FL) with transmitters, but unlike our results, downstream passage of juveniles was not observed during the study, perhaps due to small sample size and differences in reservoir habitat suitability. Our results indicated that spillway passage is associated with high survival. Consequently, spillway operations may be able to be modified to take advantage of the nocturnal behavior and seasonal outmigration patterns of juvenile lake sturgeon in order to increase passage survival at hydro-projects.

Delayed Mortality:

Delayed mortality from passage through the Kaplan turbine system accounted for approximately 10% of the total mortality rate, regardless of age group. To our knowledge no studies have estimated delayed passage mortality characteristics for juvenile sturgeon.

However, delayed passage mortality has been examined in other species and is thought to be an important factor that can affect population recruitment (Budy et al., 2002; Harrison et al., 2019). In a study on the Columbia River at McNary Dam Ferguson et al. (2006) found that 46% - 70% of total passage mortality for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) was a result of delayed mortality. We also found that those lake sturgeon that successfully passed through the powerhouse at Kleber Dam had lower downstream survival rates in the Black River compared with lake sturgeon that did not have to pass through the dam. This finding would appear to suggest that sublethal effects of turbine passage may have influenced downstream survival. A study on American eels (*Anguilla rostrata*) similarly found that eels that had passed an upstream dam on the Penobscot River experienced a higher mortality rate at a second downstream dam compared with eels that had not yet passed a dam, indicating that sublethal effects affected downstream survival (Mensinger et al., 2021).

Impingement Mortality:

The results of our study indicated considerable impingement mortality on the debris bar-rack structure at Tower Dam. Impingement mortality was at least approximately 13% for age-1 lake sturgeon and 22% for age-2 lake sturgeon. However, impingement mortality was inconsequential for the smaller age-0 lake sturgeon (~0.4%). No impingement mortality was documented at the Kleber Dam debris bar-rack structure. The smaller 2.5 cm vertical bar-rack spacing at Tower Dam and possible hydraulic flow differences may have contributed to the higher observed mortality compared with Kleber Dam, which has 7.6 cm vertical bar-rack spacing.

No other studies have documented impingement mortality characteristics of lake sturgeon. However, similar to our results studies on juvenile pallid (*Scaphirhynchus albus*) and shortnose sturgeon (*Acipenser brevirostrum*) have shown that juveniles are vulnerable to impingement at moderate flow velocities (Kynard et al., 2006; Kynard and Horgan, 2001). Specifically, 7.7–12.5% of shortnose sturgeon were impinged at 2 ft/sec and 33.3–40.0% were impinged at 3 ft/sec in an artificial flume bypass experiment (Kynard et al., 2006). In another laboratory study, researchers found that 52% of juvenile green sturgeon (*Acipenser medirostris*) were entrained after passing three times within 1.5 meters of a water-diversion pipe because of poor avoidance behavior (Mussen et al., 2014). Past research has shown that lake sturgeon are poor swimmers compared to salmonids (Peake et al., 1997). Specifically, the geometry of the lake sturgeon tail generates 18% less thrust compared to trout over sustained and prolonged swimming speeds, and the body of a sturgeon generates approximately 3.5 times more drag compared with trout (Webb, 1986). This makes lake sturgeon uniquely vulnerable to impingement as observed in our study and provides engineering challenges. Our results clearly indicate that bar-rack spacing and structure design has the potential to greatly impact impingement mortality and the net recruitment of juveniles (Rytwinski et al., 2017). Flow rates around bar-rack structures must be a major consideration in the evaluation and design of lake sturgeon passage systems.

Management Implications:

Our results indicate that turbine passage and bar rack impingement can inflict a substantive amount of mortality that increases with fish size. Therefore, the development and implementation of downstream passage systems for juvenile lake sturgeon is warranted to improve recruitment benefits from passing adults above dams. Considerable attention should be given to assessing flow rate dynamics around bar-rack structures to avoid the high levels of impingement mortality that this study observed. Leffel turbine systems were associated with higher survival compared with Kaplan turbine systems. Consequently, river systems with only Leffel turbine systems may require less fish passage engineering efforts to achieve acceptable project survival rates that allow for successful recruitment. Our study found that spillway passage is associated with high survival. As a result, downstream fish passage efforts should focus on promoting juvenile lake sturgeon to pass through spillways in absence of other engineered bypass routes. Research should focus on evaluating the utility of various deterrents (e.g., sound, bubbles, electricity, habitat) and engineered structures (e.g., angled louvers) in directing juveniles toward spillways and away from powerhouses. The apparent aversion that lake sturgeon have for aquatic vegetation could be used to help guide juveniles toward safer passage routes at dams. Spillway operations may also be able to be modified to take advantage of the nocturnal behavior and seasonal outmigration patterns of juvenile lake sturgeon in order to increase passage survival at hydro-projects.

Acknowledgments

This study was funded by the Great Lakes Fishery Trust (project No. 2012–1302). Additional funding was also provided by the Mich igan Department of Natural Resources through the State Wildlife Grant Program. We also thank the hatchery staff at the Black River Sturgeon Rearing Facility, including John Bauman, Nathan Barton, Douglas Larson, Shaley

Valentine, Zachary Witzel, Andrew Lockwood, Stefan Tucker, Jason Lyons, Rebecca Colby, Garret Johnson, Dillon Ross, Ryan Walquist, Adam Chaston, and Jenna Ruzich, for their valuable assistance with the project and with the production and management of the juvenile lake sturgeon.

Tables

Table 4.1: Comparison of juvenile lake sturgeon pit-tag based passage survival estimates by reach/location and by age group. Control fish are those that did not pass through a dam, while passage fish are those that passed through the Kleber Powerhouse.

Reach/Location	Survival Estimates (SE)	
	Age-0	**Age-1 & Age-2**
Kleber Dam Powerhouse	70.9% (SE = 0.094)	44.9% (SE = 0.138)
Tower Dam Powerhouse	86.9% (SE = 0.135)	59.9% (SE = 0.132)
Tower Dam Spillway	100% (SE = 0.132)	99.9% (SE = 0.188)
Below Kleber Dam to River Mouth (control fish)	88.1% (SE = 0.067)	100% (SE = 0.107)
Below Kleber Dam to River Mouth (passage fish)	76.3% (SE = 0.085)	81.7% (SE = 0.158)
Initial movement across Kleber Reservoir	100% (SE = 0.035)	100% (SE = 0.067)

Figures

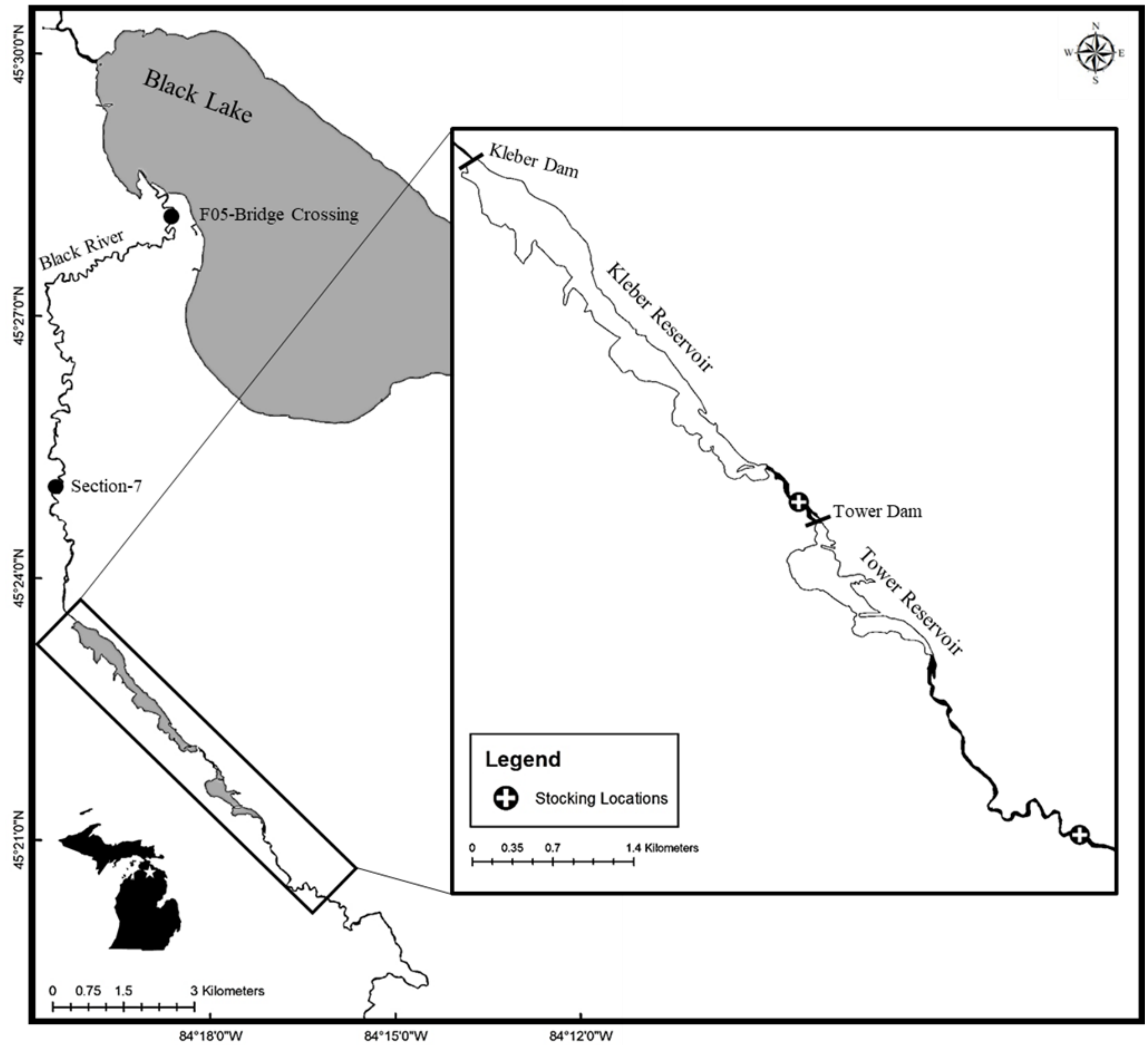

Figure 4.1: Map of Black Lake and the upper Black River system located in Cheboygan County, Michigan. The inset map highlights Kleber Dam, Kleber Reservoir, Tower Dam, and Tower Reservoir, along with the lake sturgeon stocking locations used for the research project. RFID antennas were located at the F05-bridge crossing, section-7, Kleber Dam, and Tower Dam.

a.

b.

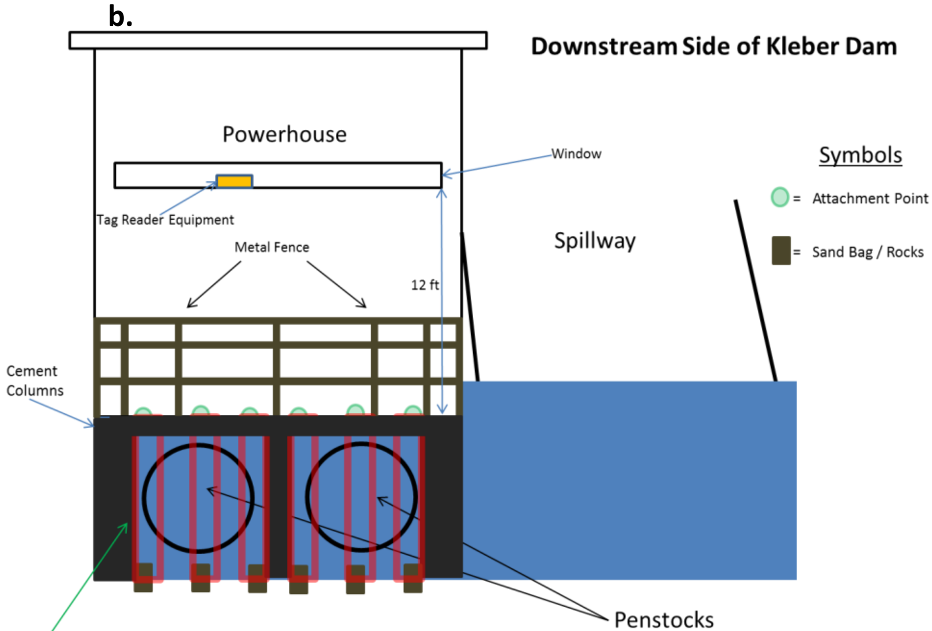

Figure 4.2: Photograph of the downstream side of Kleber Dam (a.) and diagram of the RFID PIT-tag detection system constructed at the Kleber Dam powerhouse, which consisted of a series of six vertically oriented RFID antennas (b.).

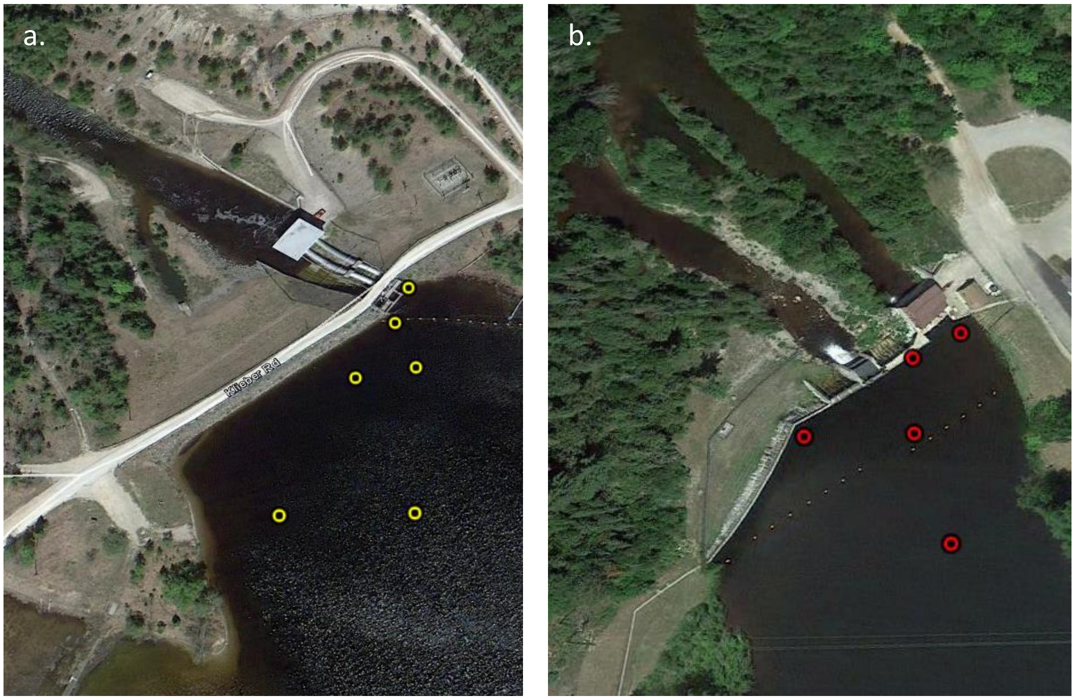

Figure 4.3: Aerial imagery of the Kleber Dam forebay showing the arrangement of the six hydrophones (yellow circles) deployed in the array (a.) and the Tower Dam forebay showing the arrangement of the five hydrophones (red circles) deployed in the array (b.). Imagery from Google Earth dated May 15, 2013.

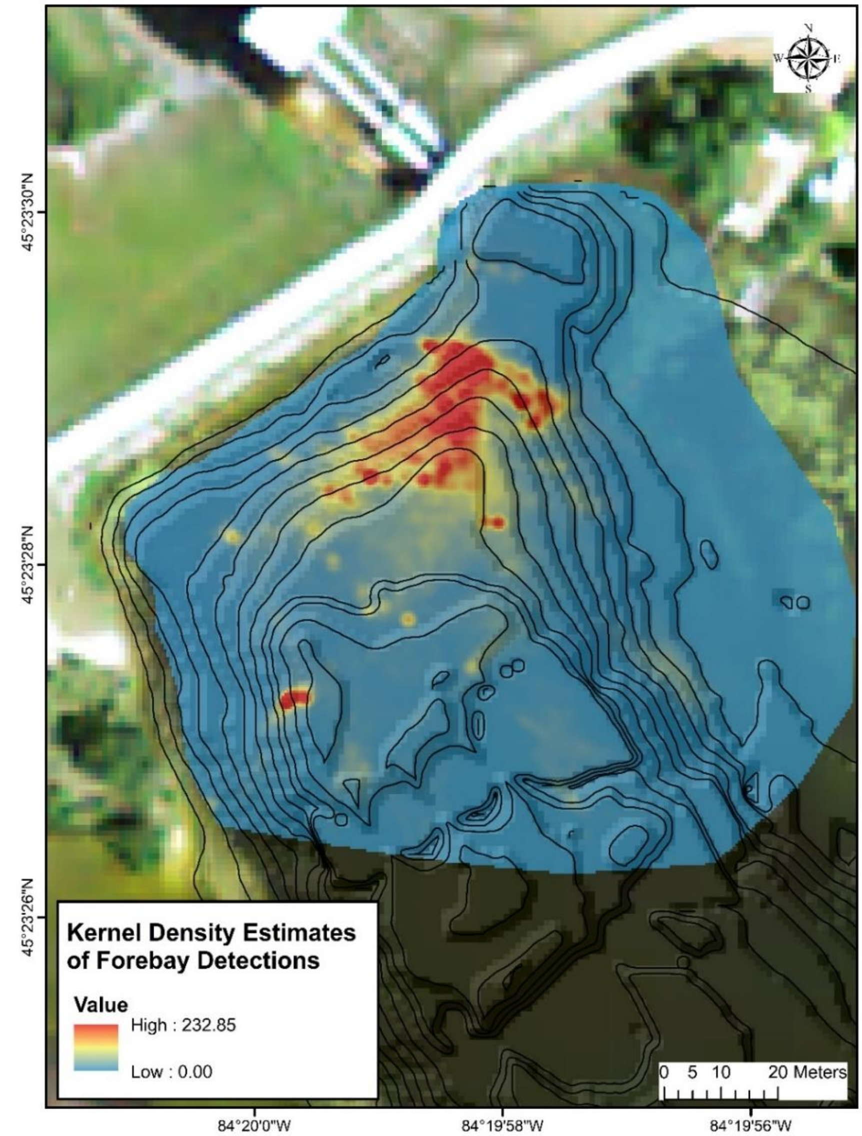

Figure 4.4: Kernel density map showing the spatial density of lake sturgeon detections across the forebay of Kleber Dam.

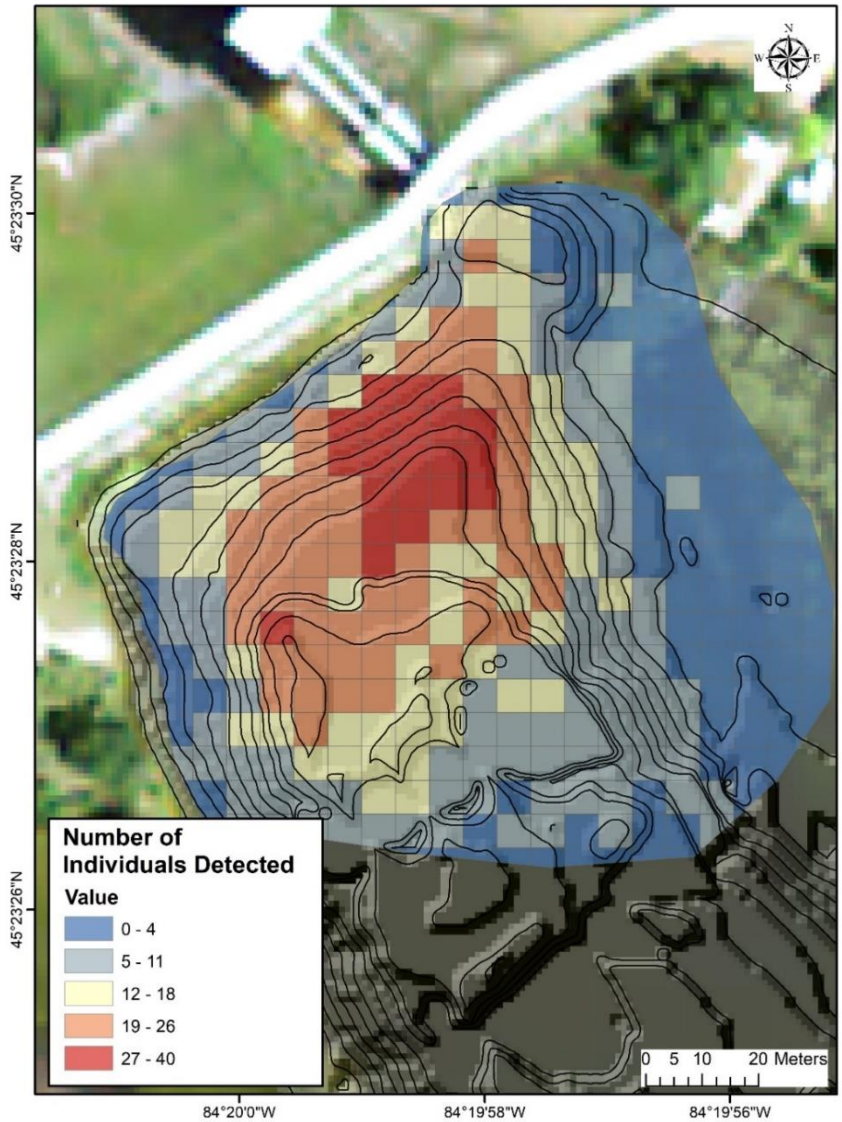

Figure 4.5: Map showing the number of unique individual lake sturgeon detected in each grid-cell within the Kleber Dam forebay.

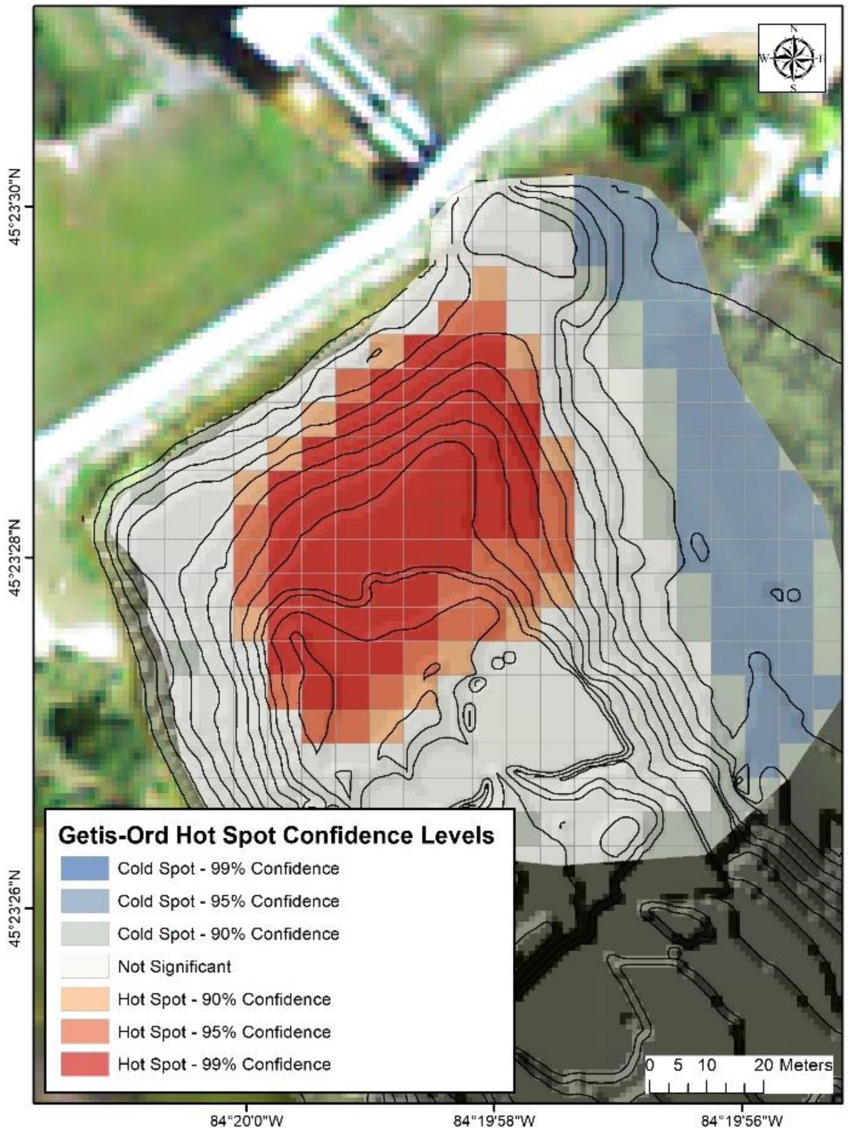

Figure 4.6: Getis-Ord hot spot analysis map of the number of unique individual lake sturgeon detected in each grid-cell within the Kleber Dam forebay.

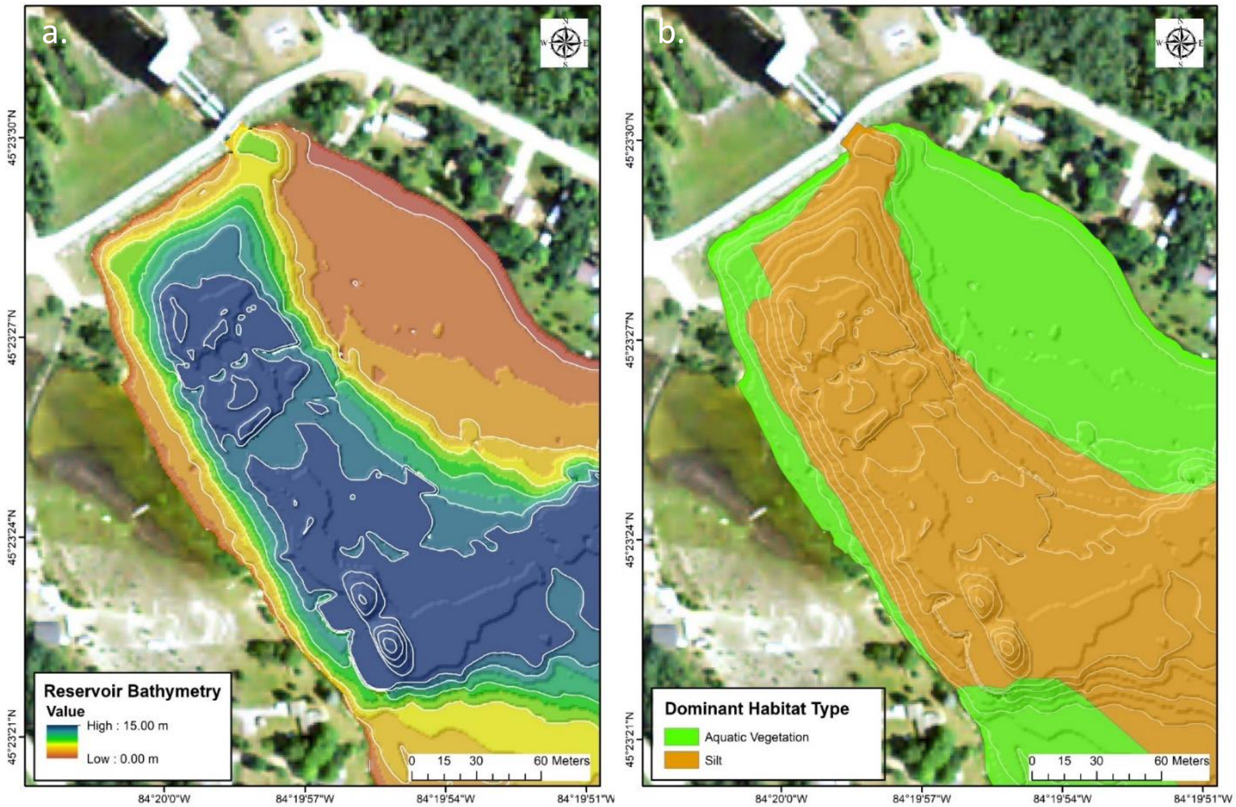

Figure 4.7: Maps showing bathymetry (a.) and habitat characteristics (b.) of the Kleber Dam forebay.

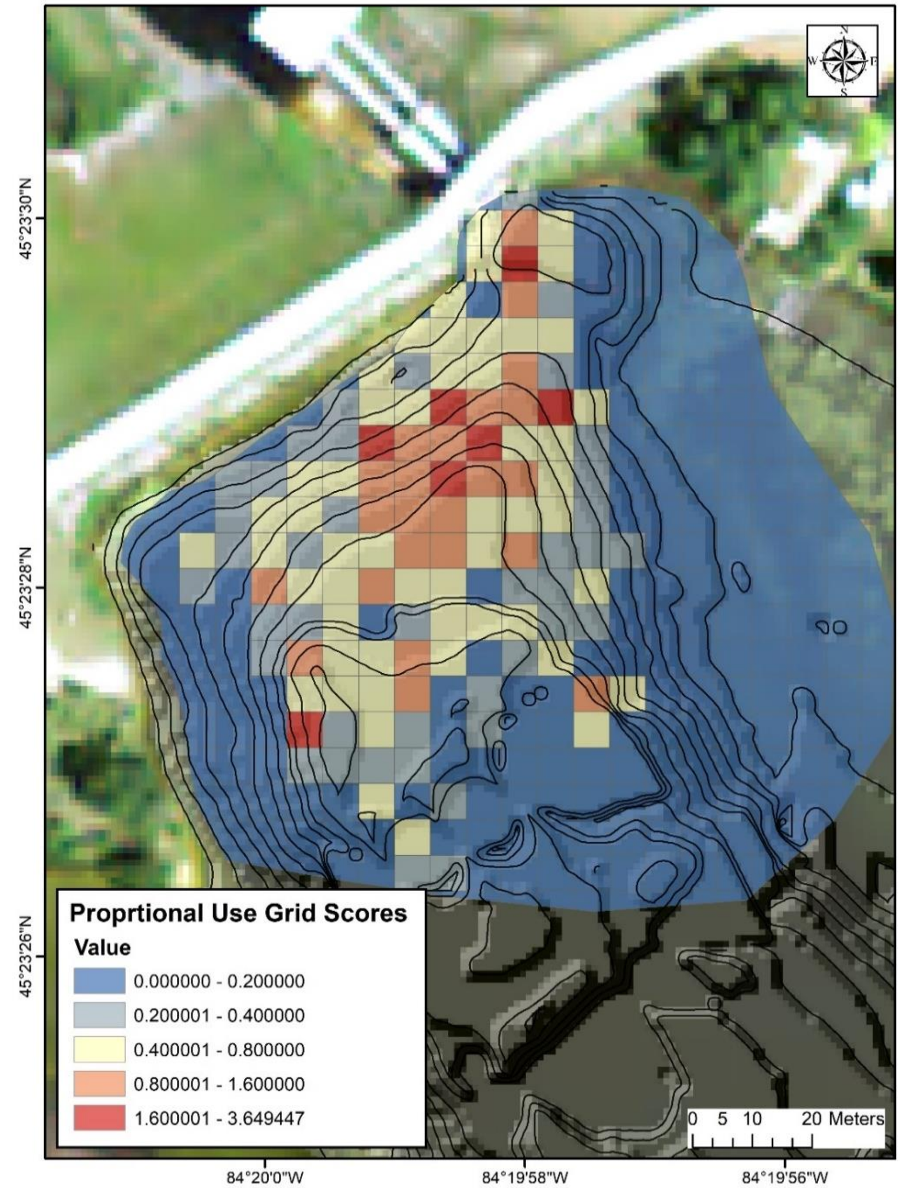

Figure 4.8: Map showing proportional use grid scores for lake sturgeon detected within the Kleber Dam forebay.

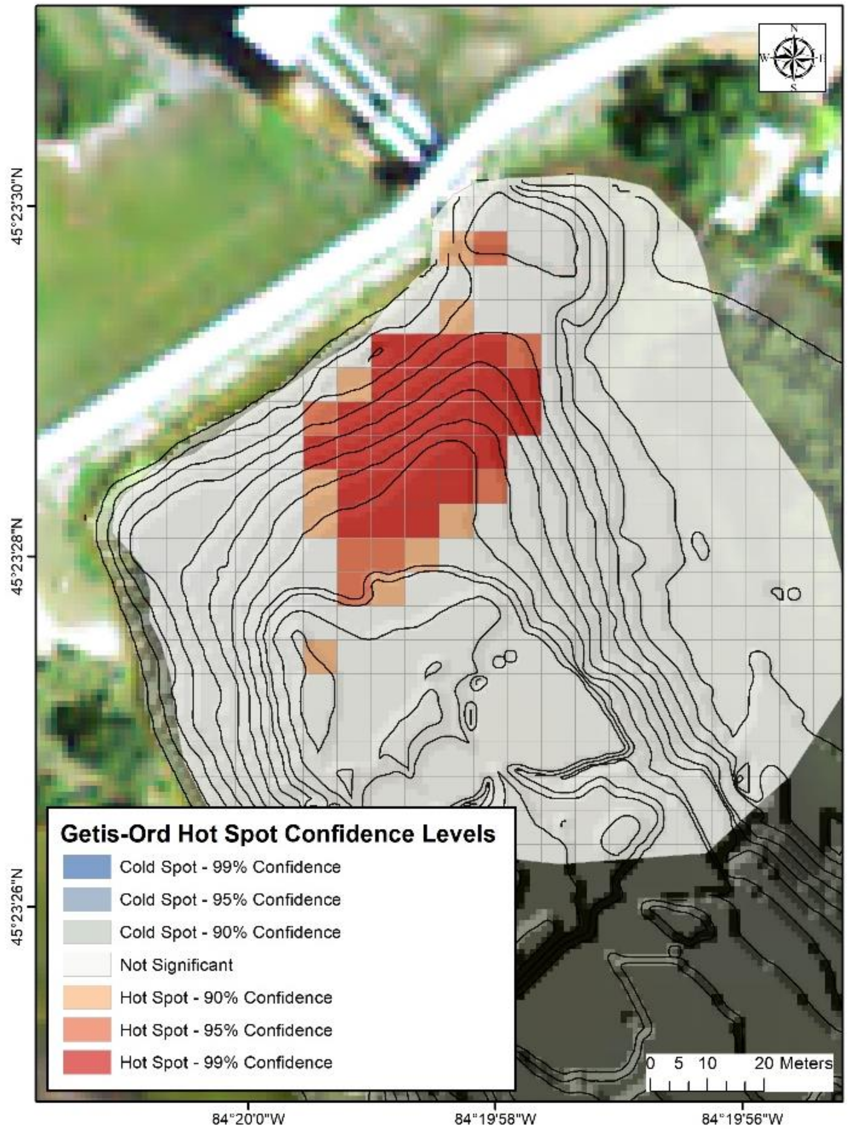

Figure 4.9: Getis-Ord hot spot analysis map of proportional use grid scores for lake sturgeon detected within the Kleber Dam forebay.

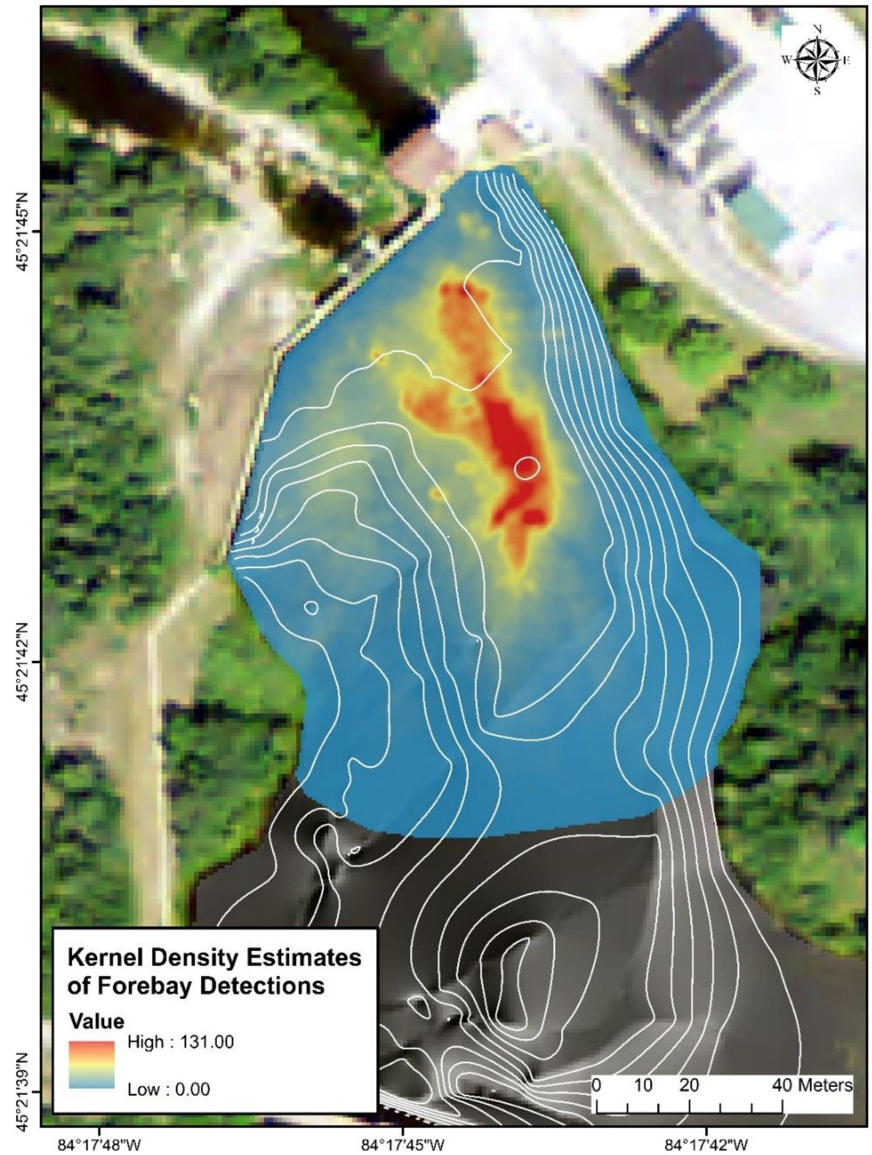

Figure 4.10: Kernel density map showing the spatial density of lake sturgeon detections across the forebay of Tower Dam.

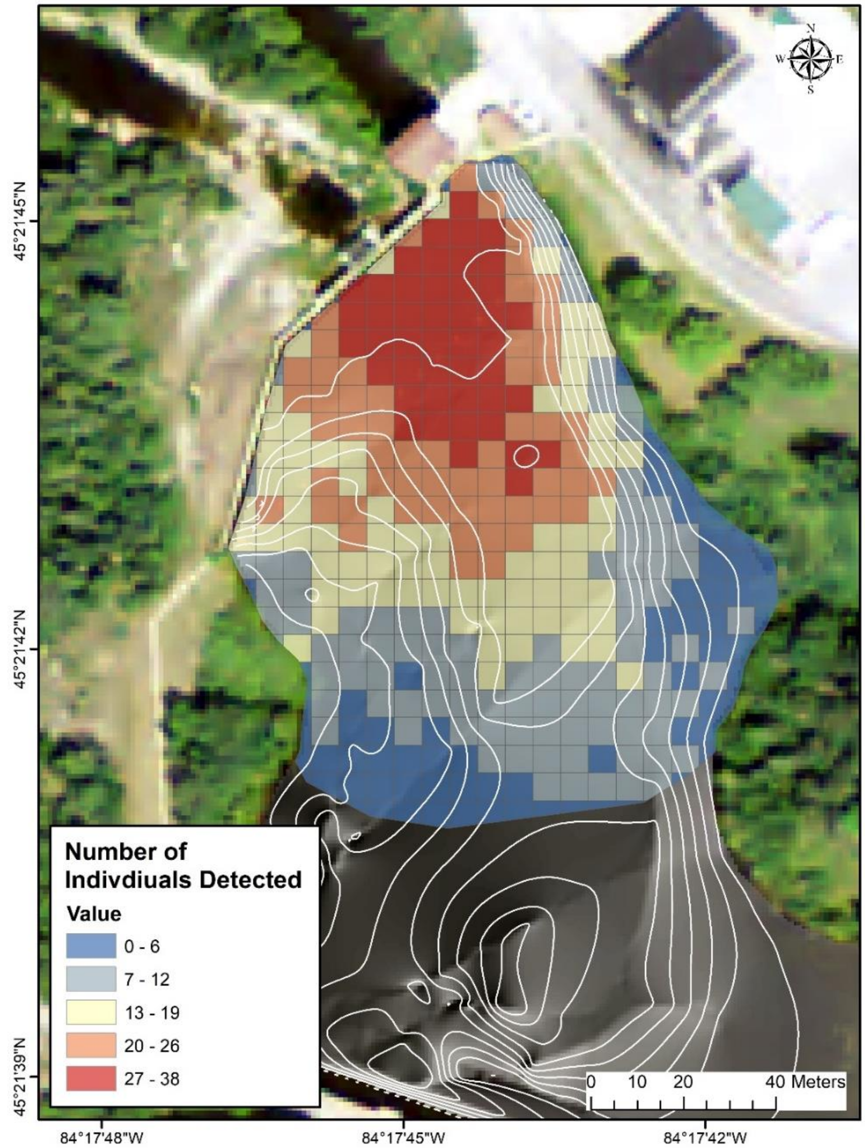

Figure 4.11: Map showing the number of unique individual lake sturgeon detected in each grid-cell within the Tower Dam forebay.

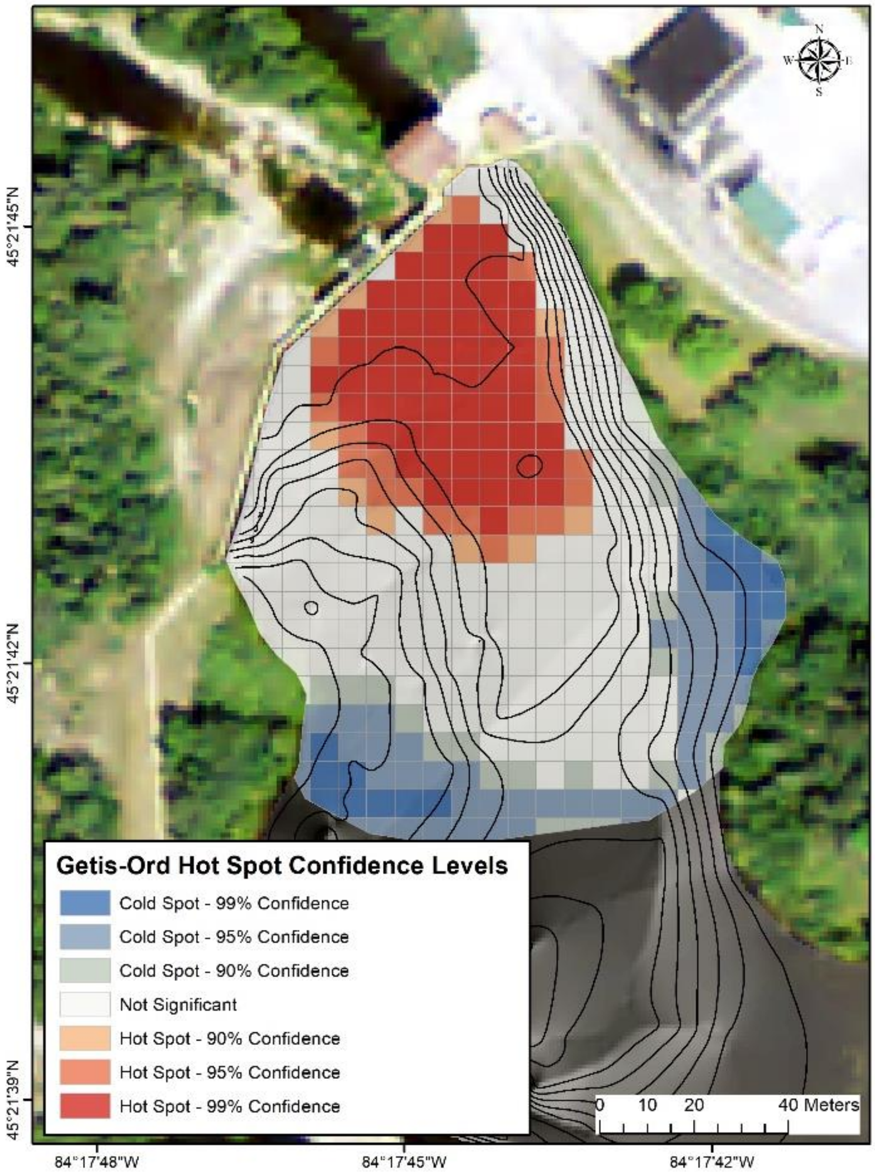

Figure 4.12: Getis-Ord hot spot analysis map of the number of unique individual lake sturgeon detected in each grid-cell within the Tower Dam forebay.

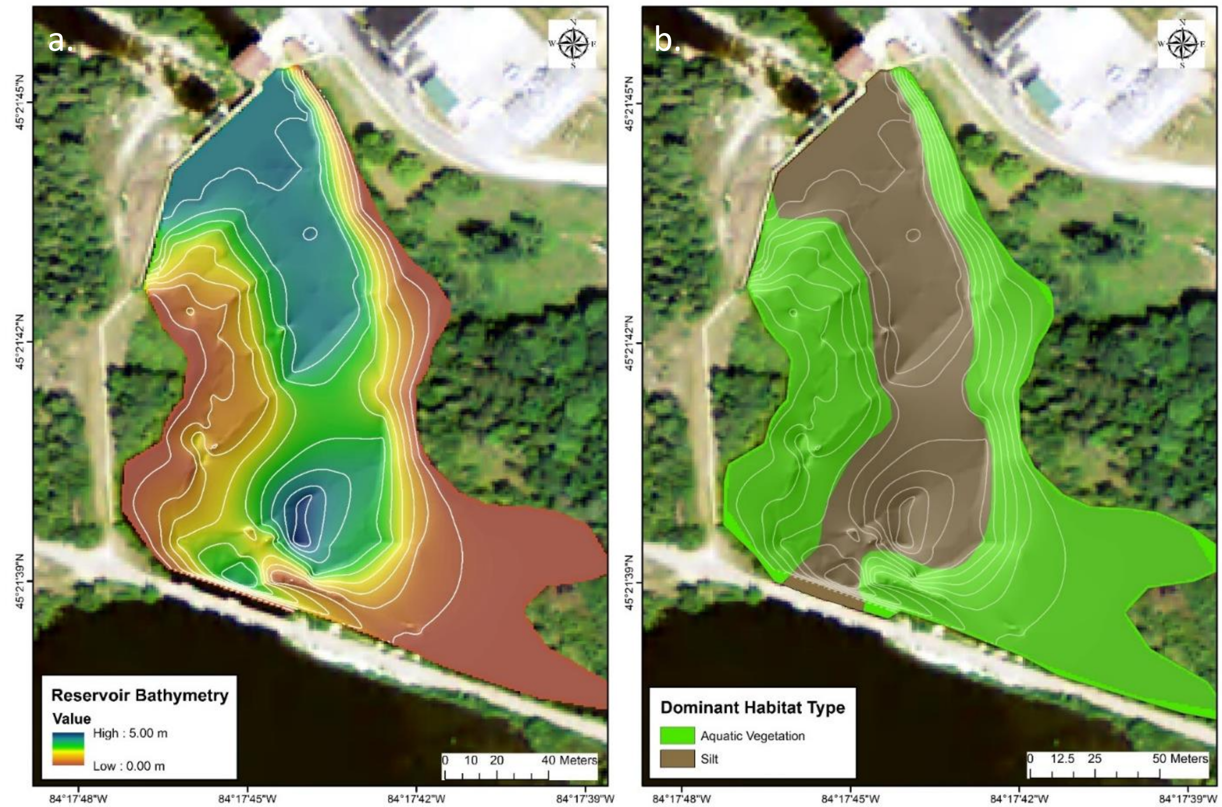

Figure 4.13: Maps showing bathymetry (a.) and habitat characteristics (b.) of the Tower Dam forebay.

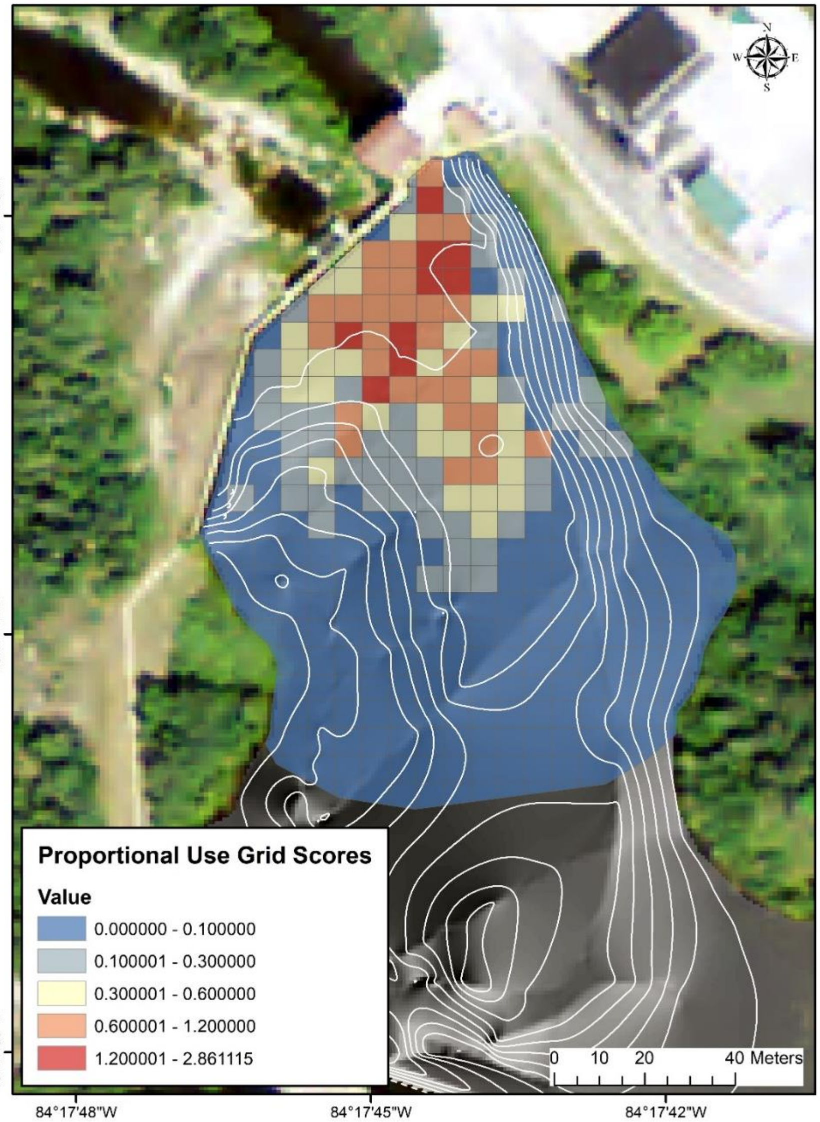

Figure 4.14: Map showing proportional use grid scores for lake sturgeon detected within the Tower Dam forebay.

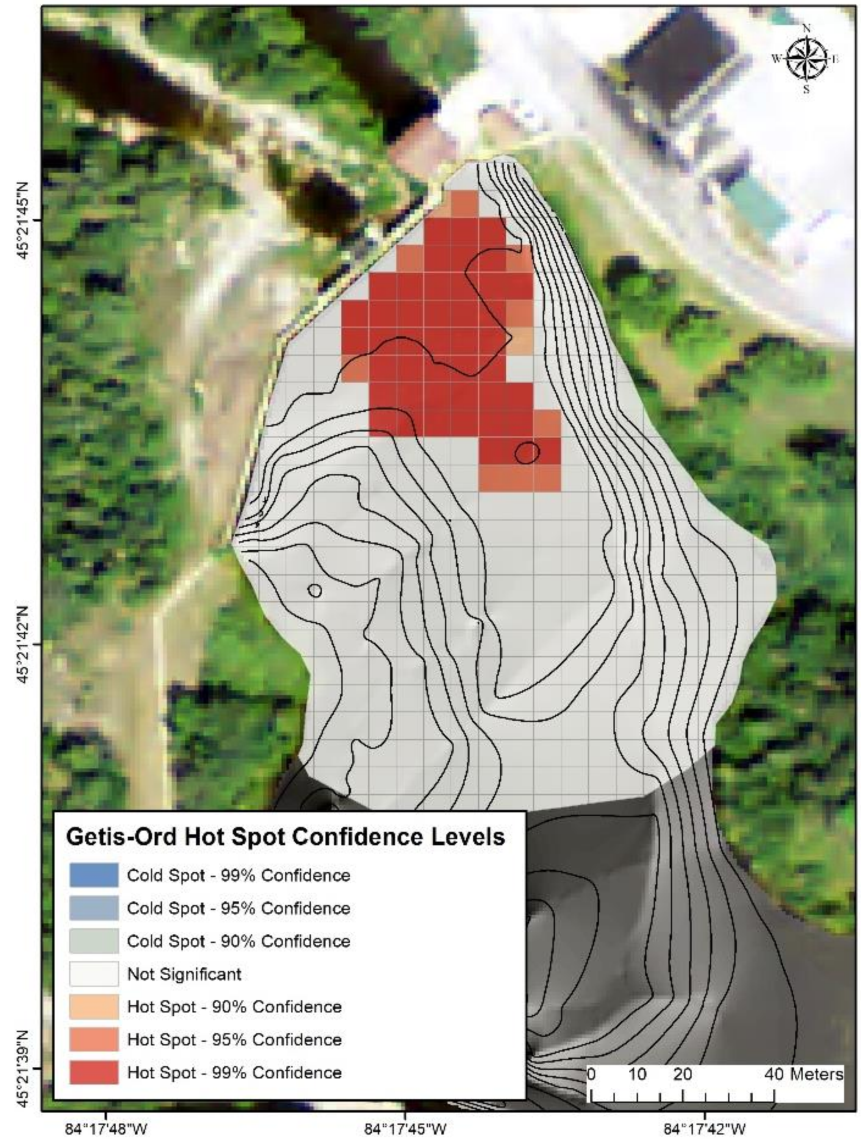

Figure 4.15: Getis-Ord hot spot analysis map of proportional use grid scores for lake sturgeon detected within the Tower Dam forebay.

Chapter 5:
Residency and Outmigration Behavior of Juvenile Lake Sturgeon Stocked Above Two Different Sized Hydroelectric Reservoirs

Abstract

The effects of spatio-temporal movements on an ecological system can be substantial and varied. The historical proliferation of hydroelectric dams across North America led to a loss in river system connectivity and alteration of habitat and flow regimes. Lake sturgeon is a species of conservation concern that inhabits many river systems that are impaired by dams, and hatchery supplementation programs and fish passage improvement efforts are increasingly being implemented to restore remnant populations. However, the recruitment benefits of passing adults above dams remains uncertain because limited information is available on the behavior and movements of juvenile lake sturgeon in hydroelectric reservoir river systems. We conducted a 4-year study to assess the behavioral response of stocking age-0, age-1, and age-2 lake sturgeon into two different sized reservoirs on the Black River in northern Michigan. The majority of observed juveniles out-migrated from the reservoir system in less than 60 days and greater than 90% of movements occurred at night. However, of the age-0 lake sturgeon observed 37% stayed in the reservoir system for more than 179 days and 11% stayed in the reservoir system for more than 499 days. Of the age-1 and age-2 lake sturgeon observed 27% stayed in the reservoir system for more than 179 days and 10% stayed in the reservoir system for more than 499 days. The age-0 lake sturgeon resided within the reservoir system and in the free flowing part of the river for longer periods of time compared with the older lake sturgeon.

We further observed that juveniles had shorter residency times in the smaller reservoir with shallower bathymetry compared with the larger reservoir. We also found that family group and production origin (hatchery produced vs. naturally produced) can have an influence on residency behavior. Outmigration numbers consistently peaked in the spring and fall months and were found to be related to temporal changes in water temperature and discharge levels. Water temperature was specifically found to have a threshold type relationship with outmigration numbers. Our results indicate that juveniles can persist within and rely upon resources in small reservoirs for extended periods of time, and that outmigration from reservoirs is influenced by seasonal changes in temperature and discharge. The bathymetry characteristics of a reservoir may also heavily influence the level of residency and entrainment in a system and this should be assessed and factored into hatchery supplementation planning. Additionally, operations at dams may be able to be modified to take advantage of outmigration behavior through the selective operation of spillways at night during peak outmigration time periods to facilitate safer passage of juvenile lake sturgeon.

Introduction

Movement is a fundamental process in ecological systems that involves an organism changing its location over space and time based on selective pressures and trade-offs in survival, growth, and reproductive value. Migratory movements can be categorized as "gametic" for reproduction, as "alimental" for resource acquisition, and "climatic" for reaching areas with better environmental conditions to improve fitness (Harden-Jones, 1968). There are many factors that can promote migratory movements. Organisms may move to take advantage of more profitable foraging areas for growth and survival (Kaeriyama and Ueda, 1998; Varpe, 2017). Movements may also be made to avoid unfavorable environmental conditions that could cause physiological stress and reduce growth and survival (McKee et al., 2022; Shaw, 2020). Finally, movements may be undertaken to find suitable habitat for reproduction to improve fitness (Varpe, 2017). These migratory movements are often associated with seasonal variations in abiotic factors such as changes in temperature and water discharge levels (Bunn and Arthington, 2002; Quinn and Adams, 1996).

The effects of spatio-temporal movements on an ecological system can be substantial and varied. Movement can redistribute energy from one area to another, such as in the case of Pacific salmonids (Naiman et al., 2002; Tonra et al., 2015). Genetic variability within a population can be increased or decreased through immigration and emigration movements (Hughes et al., 2008; Jager et al., 2001). Both emigration and immigration movements can also impact population growth and long-term population viability (Jager et al., 2001). Movement also shapes the geographic distribution of a population within a landscape, which can impact interspecific and intraspecific interactions (Shaw, 2020). Lastly, movement can directly influence the spread of pathogens through time and space (Altizer et al., 2011).

Over the past 150 years the connectivity of our riverine systems in North America has been dramatically altered by the development of dams for hydroelectric power, water storage, and flood control (Cooper et al., 2017; Wang et al., 2011a). Across the United States there are approximately 91,807 dams that fragment river systems and 49% of these are less than 25 ft in height (USACE, 2023). These dams create barriers that migratory fish must encounter and negotiate over the course of their life history, which can delay migration movements and cause increased energy expenditure as fish search for passage routes (Holbrook et al., 2011; Nyqvist et al., 2017a; Piper et al., 2013). Downstream passage through turbine systems and spillways can also cause physical trauma and barotrauma, which can lead to direct mortality and delayed mortality through sub-lethal effects (Brown et al., 2013; Ferguson et al., 2006; Kynard and Horgan, 2001; Pracheil et al., 2016). Moreover dams can alter macroinvertebrate and plankton communities, disrupt sediment and nutrient transport, and affect water chemistry and temperature characteristics (Van Looy et al., 2014; Ward and Stanford, 1983).

Dams have the effect of converting free flowing lotic habitat into vast areas of lentic habitat with completely different environmental and habitat characteristics. Fish that prefer lotic habitat are inevitably replaced by species that can inhabit lentic habitat and deep water (Aadland, 2015). The operation of hydropeaking dams on rivers can also cause greater short-term flow variability for the generation of electricity. Dams also decrease the magnitude of seasonal flow through their action of regulating flood pulses. As a result, hydrologic regulation through dams can disrupt important cues for migratory movements (Baras and Lucas, 2001; Dean et al., 2023).

Lake sturgeon (*Acipenser fulvescens*) is a potamodromous, fluvial-dependent species of regulatory and conservation concern that is considered threatened in most states and provinces (Bruch et al., 2016; Latta, 2005; Peterson et al., 2007). The historical decline of lake sturgeon populations in the Great Lakes primarily resulted from significant levels of overfishing in the 1800’s and early 1900’s, which was subsequently compounded by the development of hydroelectric infrastructure (Harkness and Dymond, 1961; Hay-Chmielewski and Whelan, 1997). Although most lake sturgeon fisheries were closed in the early 1900’s, populations have not recovered and are estimated to be at only 1% of their historical abundance (Haxton et al., 2014; Tody, 1974). While the fishing pressure has largely been eliminated, the historical alterations that disconnected adult spawning and juvenile rearing habitats in riverine systems through the construction of dams remain ever-present across the vast majority of river systems in the Great Lakes. Dams are widely believed to be one of the major factors currently limiting lake sturgeon restoration (Coscarelli et al., 2011; Ferguson and Duckworth, 1997; Peterson et al., 2007).

Hatchery supplementation programs and improvements to fish passage at dams have increasingly been proposed or implemented to restore lake sturgeon populations (Baker and Scribner, 2017; Boothroyd et al., 2018; Bruch et al., 2016; Coscarelli et al., 2011; Ganus et al., 2018; Isermann et al., 2022; McDougall et al., 2020). However, reintroduction through adult passage and stocking presupposes that juveniles are able to survive in reservoirs and successfully pass through hydroelectric dams. These assumptions need to be empirically evaluated to guide restoration activities. While information is available on the movement and habitat use characteristics of juvenile lake sturgeon throughout the species range (Benson et al., 2005; Boase et al., 2014; Holtgren and Auer, 2004; Smith and King, 2005; Trested et al., 2011), minimal data is available on behavior of young juveniles in reservoirs (Ganus et al., 2018; Hrenchuk et al., 2017; McDougall et al., 2014a, 2014b, 2013), and even less information is known about the post-stocking behavior of young juveniles in small reservoirs in the Great Lakes (Bruch et al., 2016).

Identifying juvenile lake sturgeon residency and outmigration characteristics in reservoirs is vital for determining connectivity between reservoir systems, average age and size at outmigration, suitability of reservoir habitat, the potential recruitment benefits from passing adult lake sturgeon above dams, and the recruitment benefits of hatchery stocking programs (Coscarelli et al., 2011). In particular, trap and transport of adult lake sturgeon above dams is increasingly being viewed as a restoration method, but limited information is available on what would happen to juveniles that are produced above reservoirs and the amount of recruitment benefits that might be expected (Boothroyd et al., 2018; Bruch et al., 2016; Koenigs et al., 2018). Also, knowledge of outmigration patterns would provide guidance to hydroelectric operations to allow for more efficient and safer passage of out-migrating juveniles (Cooke et al., 2020; Jager et al., 2016). Furthermore, data on age-classes most likely to out-migrate from reservoirs is needed to inform the design of size-class specific downstream passage systems for lake sturgeon (Jager et al., 2016; Kynard et al., 2006; Kynard and Horgan, 2001). Reservoirs also contain different types and compositions of habitats, and there is little long-term monitoring information available on how long juvenile lake sturgeon may use habitat within different sized reservoirs (Coscarelli et al., 2011; Ganus et al., 2018; McDougall et al., 2017, 2014a).

To meet these information needs and aid sturgeon passage and recovery initiatives we designed this project to evaluate the long-term residency and out-migration movement characteristics of age-0, age-1, and age-2 lake sturgeon stocked into two different sized reservoirs on the Black River in northern Michigan. The purpose of this project was to simulate the passage of adults above dams, which would result in spawning and reproduction above reservoirs, in order to assess the fate of juveniles that are produced and the benefits of reintroduction efforts on recruitment. Our specific objectives were to (1) quantify residency characteristics by age in two different sized reservoir systems, (2) determine residency characteristics in the free flowing part of the Black River, (3) investigate the influence of family group and production origin on outmigration behavior, (4) evaluate the effects of multiple dams on outmigration behavior and, and (5) evaluate outmigration patterns and timing in association with environmental and hydroelectric operations data.

Methodology

Study Area:

This study was conducted in the upper Black River located in Cheboygan County in the northern lower peninsula of Michigan (Figure 5.1). The upper Black River is the largest tributary of Black Lake, and it comprises the sole spawning area 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 17.6 km upstream from the river mouth. The dam was built in 1949 with an average head of 13.4 meters, and it forms a reservoir with 370 hectares 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 adult spawning and juvenile rearing. Tower Dam is located 5 km upstream of Kleber Dam. Tower Dam was built in 1917, has an average head of 6.1 meters, and it forms a small reservoir with 76 hectares 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.

Hatchery Production:

All lake sturgeon were reared at the Black River Sturgeon Rearing Facility between April and September in 2014, 2015, and 2016. Some lake sturgeon were produced artificially (i.e., hatchery produced) through the collection of eggs and milt from spawning adult lake sturgeon in the Black River. Adult lake sturgeon within this system are marked with PIT-tags and floy-tags, which allowed us to keep track of family crosses (Crossman et al., 2011). Other lake sturgeon were naturally produced and collected with drift nets during the spring drift season in the lower part of the Black River below the spawning grounds. Naturally produced lake sturgeon larvae that were caught were then transported back to the hatchery for rearing to the appropriate age. These two different larvae production origins are referred to as hatchery produced and naturally produced hereafter. To produce the older age-1 and age-2 lake sturgeon some individuals were seasonally transported over to the Wolf Lake State Fish Hatchery (Mattawan, MI) and over-wintered each year until they were returned to the Black River and released.

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-0, age-1, and age-2 lake sturgeon. The dimensions of the transmitters used for age-1 and age-2 lake sturgeon were 5 x 7 x 13 mm, and they weighed 0.6 grams in air. These acoustic transmitters were programmed to have a 10 second transmission rate, with an estimated life expectancy of 180 days. The dimensions of the transmitters used for age-0 lake sturgeon were 3.7 x 5.5 x 11.1

mm, and they weighed 0.32 grams in air. These acoustic transmitters were programmed to have a 15 second transmission rate, with an estimated life expectancy of 100 days. In addition, a 23 x 3.65 mm half-duplex PIT-tag (Oregon RFID, Portland, Oregon) was implanted into each lake sturgeon. The transmitters and PIT-tags were surgically implanted by performing a standard laparotomy (Hegna et al., 2018). Before surgery, all sturgeon were anesthetized for approximately 5 minutes in an anesthetic bath with 125 mg/L of tricaine methanesulfonate (MS222). 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/L of MS222 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 8-15 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 1-2 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 age-1 and age-2 lake sturgeon were held for at least 4 weeks of post-operative observation and all age-0 lake sturgeon were held for at least 10 days of post-operative observation to ensure proper healing.

In total 140 age-0, 110 age-1, and 110 age-2 lake sturgeon were surgically implanted with acoustic and PIT transmitters. Additionally, a total of 1,664 age-0, 167 age-1, and 37 age-2 lake sturgeon were implanted with only PIT-tags. All lake sturgeon were produced and reared at the Black River Sturgeon Rearing Facility between April and September. The age-1 and age-2 juvenile lake sturgeon produced were 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#: 03/14-041-00).

Experimental Release of Lake Sturgeon:

Juvenile lake sturgeon were released in 2014, 2015, and 2016. Age-1 and age-2 lake sturgeon were released in small groups of 10-12 individuals, while age-0 lake sturgeon were released in groups of approximately 50 individuals. Smaller release groups were used to avoid possible negative effects associated with high stocking densities, which could alter behavior or elevate predation risk. A total of 790 age-0, 114 age-1, and 61 age-2 lake sturgeon were released upstream of Tower Reservoir (Figure 5.1). A total of 813 age-0, 118 age-1, and 61 age-2 lake sturgeon were released upstream of Kleber Reservoir. A total of 201 age-0, 45 age-1, and 25 age-2 lake sturgeon were released below Kleber Dam to serve as "control fish" for a separate survival study. Age-0 lake sturgeon were released in September of each year, while age-1 and age-2 lake sturgeon were released between July and September of each year. Age-1 and age-2 lake sturgeon were released earlier to enable active tracking in the reservoirs for a separate study. Age-0 lake sturgeon were released later in the season in order to allow them to attain adequate size for surgery and transmitter implantation.

Movement and Entrainment Monitoring:

To monitor movements and entrainment we used PIT-tag monitoring technology. 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 (Figure 5.1). 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 approximately 300 meters 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 (Figure 5.1). Lastly, three stream-wide RFID antennas were installed at the F05-bridge crossing located 0.85 miles upstream from the river mouth where the Black River empties into Black Lake (Figure 5.1). We also installed several RFID PIT-tag detection antennas below Tower Dam (Figure 5.1). This included two antennas below the powerhouse, two antennas below the spillway, and one large stream-wide antenna approximately 500 meters downstream.

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 batteries connected to two 200 watt solar panels (Zamp Solar, Bend, Oregon). Half-duplex RFID antenna systems constantly switch their electromagnetic fields on and off in order 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 September 2014 and continued through September 2018.

Environmental and Operations Data Collection:

Several types of environmental and operations data were collected during the multiyear project. Operations data from Kleber and Tower Dams including discharge and spillway gate level information was collected through electronic instrumentation on an hourly basis by the company operating the hydroelectric dams. Temperature data was collected on an hourly basis through the placement of HOBO temperature loggers (Onset Computer Corp., Bourne, MA).

Statistical Analysis:

Residency was defined as the duration of occupancy of a defined geographic area. The starting time point was either the stocking date or the first detection date of entry into the geographic area. The ending time point was the first downstream detection date outside of the geographic area. The geographic areas evaluated for residency included Tower Reservoir, Kleber Reservoir, the reservoir system as a whole, and lastly the lower Black River from below Kleber Dam to the river mouth at the F05 bridge crossing. Reservoir system residency was defined as beginning at the stocking date into either Tower or Kleber Reservoirs and ending at the first downstream detection date below Kleber Dam.

The observed lake sturgeon residency data was highly variable with outliers and was nonparametric in distribution. Consequently, the non-parametric Kruskal-Wallis test was used to evaluate differences in residency times between age-groups, family groups, stocking locations, and geographic regions of the river system. Post-hoc testing was accomplished with pairwise Wilcoxon tests. The likelihood of residency based on counts of lake sturgeon comparing age-groups, reservoirs, and time periods were made by calculating statistical odds ratios. The likelihood of movements occurring during the daytime or night was also made by calculating statistical odds ratios.

Over the multiyear time period of the project there were occasional time periods when temperature, discharge, and spillway data lapsed due to system outages. Missing temperature data was imputed by using temperature data from a nearby stream gauge on the Ausable River (USGS Site#: 04136000). Missing discharge and spillway gate level data was imputed by averaging values of the same time period from other years the data was recorded.

To assess the temporal relationships between monthly average temperature, discharge, and spillway gate level with the number of out-migrating lake sturgeon the pre-whitened cross-correlation function was used to evaluate which temporal lags of the input variables had the strongest association with the response variable (i.e., monthly outmigration numbers). Granger causality tests were then used to assess potential relationships. Formal modeling was then pursued for those variables that had an observed Granger causal relationship with the response variable. Monthly average discharge and spillway gate level were formally evaluated through the use autoregressive integrated moving average (ARIMA) time series regression models. Optimal model structure was determined through comparison of Akaike Information Criterion (AIC) values and review of autocorrelation and partial autocorrelation diagnostic data.

Temperature was observed to exhibit a threshold type relationship with the response variable. Because of this threshold relationship, traditional time series diagnostics and ARIMA modeling were not able to be constructively used to evaluate this dataset. As a result, a threshold time series regression was used to evaluate the relationship between temperature and outmigration numbers. Optimal model structure, including the number of structural thresholds, was identified by using AIC values and review of autocorrelation and partial autocorrelation diagnostic data. For all analyses, no route-specific passage analyses were performed to differentiate spillway and powerhouse passage events.

The non-parametric Kruskal-Wallis tests and associated post-hoc tests were completed with JMP Pro version 16 statistics software package (SAS Institute, Cary, NC). Time series cross-correlations and Granger causality tests were completed with IBM SPSS Statistics version 29 software (IBM Corp., Armonk, NY). ARIMA time series regression modeling was completed with Statgraphics Centurion version 19 (Statistical Graphics Corporation, Warrenton, VA). The threshold time series regression analysis was completed with Stata statistical software version 18 (StataCorp., College Station, TX).

Results

Reservoir Residency Characteristics:

Overall, 46% of both the age-0 and the older age-1 and age-2 lake sturgeon that were originally stocked into Kleber Reservoir were detected out-migrating downstream during the course of the study. Similarly, 41% of the age-0 and 49% of the age-1 and age-2 lake sturgeon that were originally stocked into Tower Reservoir were detected out-migrating from the reservoirs during the study.

Residency times varied widely for the lake sturgeon that were observed (i.e., detected after stocking). Most lake sturgeon only resided for a short period of time within the reservoir system, with 47% of age-0 and 62% of age-1 and age-2 lake sturgeon out-migrating within 60 days after stocking (Figure 5.2). Age-0 lake sturgeon resided within the reservoir system on average for 177 days (SD = 251.02, Mdn = 68, Range: 0.47 – 1323.48) based on observations from 561 individuals, while the age-1 and age-2 lake sturgeon resided within the reservoir system on average for 162 days (SD = 295.77, Mdn = 9, Range: 0.43 – 1493) based on observations from 112 individuals. The age-0 lake sturgeon resided within the reservoir system for longer amounts of time compared with the age-1 and age-2 lake sturgeon (X^2 = 17.95, DF = 1, p < 0.001). Age-0 lake sturgeon that were stocked into Tower Reservoir resided marginally longer within the reservoir system compared with age-0 lake sturgeon that were stocked into Kleber Reservoir (Z = 1.78, p = 0.074). Similarly, age-1 and age-2 lake sturgeon that were stocked into Tower Reservoir resided longer within the reservoir system compared with age-1 and age-2 lake sturgeon that were stocked into Kleber Reservoir (Z = 2.53, p = 0.011). Also, differences in residency times were observed among different family groups (X^2 = 98.21, DF = 29, p < 0.001). In particular, hatchery produced lake sturgeon resided longer within the reservoir system compared with naturally produced lake sturgeon (X^2 = 9.19, DF = 1, p = 0.002). Of the age-0 lake sturgeon observed 37% stayed in the reservoir system for more than 179 days and 11% stayed in the reservoir system for more than 499 days. Of the age-1 and age-2 lake sturgeon observed 27% stayed in the reservoir system for more than 179 days and 10% stayed in the reservoir system for more than 499 days. Age-0 lake sturgeon were 1.62 times more likely (95% CI = 1.03 – 2.55, Z = 2.10, p = 0.036) to stay in the reservoir system for more than 179 days compared with the older age-1 and age-2 lake sturgeon.

In Kleber Reservoir most observed lake sturgeon only resided within the reservoir for a short period of time, with 50% of age-0 and 68% of the older age-1 and age-2 lake sturgeon out-migrating within 60 days (Figure 5.3). Age-0 lake sturgeon resided within Kleber Reservoir on average for 165 days (SD = 248.85, Mdn = 61, Range: 0.61 – 1322.54) based on observations from 378 individuals, while the age-1 and age-2 lake sturgeon resided within Kleber Reservoir on average for 159 days (SD = 307.92, Mdn = 5, Range: 0.43 – 1461.73) based on observations from 82 individuals. In total 39% of the age-0 (n = 316) and 41% of the age-1 and age-2 (n = 74) lake sturgeon that were originally stocked into Kleber Reservoir were detected out-migrating from the reservoir below Kleber Dam. The age-0 lake sturgeon resided within Kleber Reservoir for longer amounts of time compared with the age-1 and age-2 lake sturgeon ($X^2 = 12.51$, DF = 1, $p < 0.001$). Age-0 lake sturgeon that were originally stocked into Kleber Reservoir resided longer within the reservoir compared with age-0 lake sturgeon that were originally stocked into Tower Reservoir ($Z = -2.98$, $p = 0.003$). No differences in residency times were observed between initial stocking locations for the older age-1 and age-2 lake sturgeon ($Z = 1.19$, $p = 0.232$). Also, differences in residency times were observed among different family groups ($X^2 = 51.13$, DF = 20, $p < 0.001$). In particular, hatchery produced lake sturgeon resided longer within the reservoir system compared with naturally produced lake sturgeon ($X^2 = 7.03$, DF = 1, $p = 0.008$). Of the age-0 lake sturgeon observed 34% stayed in Kleber Reservoir for more than 179 days and 10% stayed in the reservoir for more than 499 days. Of the age-1 and age-2 lake sturgeon observed 24% stayed in Kleber Reservoir for more than 179 days and 11% stayed in the reservoir for more than 499 days. Age-0 lake sturgeon were 1.58 times more likely (95% CI = 0.92 – 2.74, $Z = 1.65$, $p = 0.098$) to stay in the reservoir for more than 179 days compared with the older age-1 and age-2 lake sturgeon.

In Tower Reservoir most observed lake sturgeon only resided within the reservoir for a short period of time, with 65% of age-0 and 54% of the older age-1 and age-2 lake sturgeon out-migrating within 60 days (Figure 5.4). Age-0 lake sturgeon resided within the reservoir on average for 80 days (SD = 157.88, Mdn = 10, Range: 0.37 – 982.10) based on observations from 143 individuals, while the age-1 and age-2 lake sturgeon resided within the reservoir on average for 69 days (SD = 145.97, Mdn = 16, Range: 0.78 – 927.11) based on observations from 55 individuals. In total 41% of the age-0 (n = 325) and 49% of the age-1 and age-2 (n = 85) lake sturgeon that were originally stocked into Tower Reservoir were detected out-migrating from the reservoir below Tower Dam. No differences in residency times were observed between the different age groups ($X^2 = 1.03$, DF = 1, $p = 0.310$). In addition, no differences in residency times were found among family groups ($X^2 = 8.00$, DF = 8, $p = 0.434$). Naturally produced lake sturgeon were not detected to allow for comparison. Of the age-0 lake sturgeon observed 16% stayed in Tower Reservoir for more than 179 days and 9% stayed in the reservoir for more than 299 days. Of the age-1 and age-2 lake sturgeon observed 9% stayed in Tower Reservoir for more than 179 days and 5% stayed in the reservoir more than 299 days. The odds of lake sturgeon staying in Tower Reservoir were similar between the age groups ($p > 0.200$).

Comparing Reservoirs and Behavior:

Residency characteristics differed significantly between Kleber and Tower Reservoirs ($X^2 = 31.64$, DF = 3, $p < 0.001$). Residency times for age-0 lake sturgeon were considerably longer in Kleber Reservoir than in Tower Reservoir ($t = 3.60$, $p < 0.001$). Similarly, residency times for age-1 and age-2 lake sturgeon were longer in Kleber Reservoir than in Tower Reservoir ($t = 2.18$, $p = 0.029$). Age-0 lake sturgeon in Kleber Reservoir were 2.67 times more likely (95% CI =

1.62 – 4.38, Z = 3.90, $p < 0.001$) to stay within the reservoir for more than 179 days before out-migrating compared to age-0 lake sturgeon in Tower Reservoir. Age-0 lake sturgeon in Kleber Reservoir were also 2.19 times more likely (95% CI = 1.17 – 4.11, Z = 2.45, p = 0.014) to stay within the reservoir for more than 299 days compared with age-0 lake sturgeon in Tower Reservoir. Age-1 and age-2 lake sturgeon in Kleber Reservoir were 3.23 times more likely (95% CI = 1.13 – 9.20, Z = 2.19, p = 0.029) to stay within the reservoir for more than 179 days before out-migrating compared to age-1 and age-2 lake sturgeon in Tower Reservoir. Age-1 and age-2 lake sturgeon in Kleber Reservoir were also 3.57 times more likely (95% CI = 0.97 – 13.07, Z = 1.92, p = 0.055) to stay within the reservoir for more than 299 days compared with age-1 and age-2 lake sturgeon in Tower Reservoir.

Lower River Residency Characteristics:

In the Black River system below Kleber Dam residency times within the river were shorter compared to residency times in the reservoirs ($p < 0.001$). In the Black River age-0 lake sturgeon resided within the system on average for 50 days (SD = 89.15, Mdn = 12, Range: 0.001 – 390.26) based on observations from 191 individuals, while the older age-1+ lake sturgeon resided within the river on average for 18 days (SD = 25.78, Mdn = 3, Range: 0.001 – 81.65) based on observations from 75 individuals (Figure 5.5). The age-0 lake sturgeon resided within the Black River for longer amounts of time compared with the older age-1+ lake sturgeon (X^2 = 8.65, DF = 1, p = 0.003). No differences in river residency times were observed between lake sturgeon that were originally stocked into Kleber Reservoir compared with Tower Reservoir for age-0 lake sturgeon (Z = -0.84, p = 0.399) and the older age-1+ lake sturgeon (Z = -0.95, p =

0.341). However, those lake sturgeon that were stocked directly into the Black River below Kleber Dam had longer residency times compared with those lake sturgeon that volitionally out-migrated from the reservoirs for age-0 lake sturgeon ($Z = -5.87$, $p < 0.001$) and the older age-1+ lake sturgeon ($Z = -2.78$, $p = 0.005$). Differences in residency times were found among family groups ($X^2 = 18.33$, DF = 10, $p = 0.050$). However, no differences in residency times were observed between hatchery produced and naturally produced lake sturgeon ($X^2 = 0.01$, DF = 1, $p = 0.940$). Of the age-0 lake sturgeon observed 19% stayed in the river for more than 59 days, 16% stayed in the river for more than 89 days, and 11% stayed in the river for more than 179 days. Of the older age-1+ lake sturgeon observed 15% stayed in the river for more than 59 days and 0% stayed in the river for more than 89 days. Similar numbers of both age groups stayed in the river for more than 59 days ($Z = 0.80$, $p = 0.422$). However, age-0 lake sturgeon were 28.70 times more likely (95% CI = 1.73 – 475.59, $Z = 2.34$, $p = 0.019$) to stay in the river for more than 89 days and 19.04 times more likely (95% CI = 1.14 – 318.48, $Z = 2.05$, $p = 0.040$) to stay in the river for more than 179 days compared with the older age-1+ lake sturgeon.

Outmigration Seasonality and Timing:

The movement of juvenile lake sturgeon out of the reservoir system had clear seasonal trends (Figure 5.6). Standard meteorological start and end dates were used to define the temporal scope of each season. Of the age-0 lake sturgeon observed, 61.7% out-migrated into the Black River below Kleber Dam in the fall, 9.6% in the winter, 26.3% in the spring, and 2.1% in the summer. Age-0 lake sturgeon were 74.0 times more likely (95% CI = 40.7 – 134.4, $Z = 14.13$, $p < 0.001$) and 15.2 times more likely (95% CI = 10.9 – 21.1, $Z = 16.25$, $p < 0.001$) to out-migrate in the fall than in the summer or winter respectively. Age-0 lake sturgeon were also 4.5 times more likely (95% CI = 3.5 – 5.8, Z = 11.66, p < 0.001) to out-migrate during the fall than in the spring.

Of the age-1 and age-2 lake sturgeon observed, 36.6% out-migrated into the Black River below Kleber Dam in the fall, 8.9% in the winter, 16.1% in the spring, and 38.4% in the summer. Age-1 and age-2 lake sturgeon were 5.9 times more likely (95% CI = 2.8 – 12.5, Z = 4.60, p < 0.001) and 3.0 times more likely (95% CI = 1.6 – 5.7, Z = 3.41, p < 0.001) to out-migrate in the fall than in the winter or spring respectively. The likelihood of outmigration was similar between fall and summer for age-1 and age-2 lake sturgeon (Z = 0.28, p = 0.782). Age-0 lake sturgeon were 1.9 times more likely (95% CI = 1.1 – 3.2, Z = 2.27, p = 0.023) to out-migrate in the spring and 2.8 times more likely (95% CI = 1.8 – 4.2, Z = 4.79, p < 0.001) to out-migrate in the fall compared with the older age-1 and age-2 lake sturgeon. In contrast, the older age-1 and age-2 lake sturgeon were 26.6 times more likely (95% CI = 14.4 – 56.8, Z = 9.56, p < 0.001) to out-migrate during the summer compared with age-0 lake sturgeon. The outmigration movements were overwhelmingly nocturnal and similar between the age-groups with 93.6% of the age-0 and 95.5% of the age-1 and age-2 lake sturgeon outmigration movements occurring at night (Z = 0.83, p = 0.404).

Environmental and Operations Data Associated with Outmigration:

Monthly average temperature had a distinct threshold relationship with the number of lake sturgeon out-migrating from the hydroelectric reservoir system into the Black River below Kleber Dam (Figure 5.6). Temperature was most strongly cross-correlated with outmigration numbers over time at lag 0 ($r = 0.17$, SE = 0.164) and lag -1 ($r = 0.28$, SE = 0.167). However, the threshold nature of the relationship confounds the true extent of the relationship and typical time series evaluation tools such as cross-correlation and Granger causality tests were inadequate for assessing this type of relationship. Consequently, the effects of temperature were modeled through using threshold time series regression. Comparison of AIC values indicated that one structural threshold at 11.40 °C was best for optimum model performance. The analysis indicated that as water temperature increased the number of out-migrating lake sturgeon increased over time up to a threshold level of approximately 11.40 °C (Region 1: $\beta = 4.23$, $z = 6.22$, $p < 0.001$). As water temperature increased past this threshold level, the number of out-migrating lake sturgeon decreased (Region 2: $\beta = -1.72$, $z = -2.76$, $p = 0.006$). The threshold model explained 51.54% (RMSE = 11.214) of the variance between outmigration numbers and temperature over time.

The observed water temperature relationship is directly linked to annual seasonal temperature fluctuations. Seasonal time periods where water temperature is changing substantially were associated with the highest levels of outmigration (Figure 5.6). Outmigration numbers generally increased in the spring as the water temperature warmed. Outmigration numbers decreased into and over the summer months as the water temperature continued to increase above the identified threshold level. Outmigration numbers then subsequently increased in the fall when the water temperature began to decrease below the threshold level.

There are two routes by which water and out-migrating lake sturgeon can leave the reservoir system. Water may be discharged directly through the powerhouse system via the turbine systems or water may be discharged through the spillway via the tainter gate system. Monthly average discharge from Kleber Dam was related to the number of juvenile lake sturgeon observed out-migrating from the reservoir system (Figure 5.6). Discharge was most strongly cross-correlated with outmigration numbers at lag 0 ($r = 0.34$, SE = 0.164) and lag -1 ($r = 0.49$, SE = 0.167). Discharge was found to have a Granger causal relationship with outmigration numbers ($F = 2.60$, $p = 0.037$). Similarly, monthly average spillway gate position was found to be related to outmigration numbers. Spillway gate position was most strongly cross-correlated with outmigration numbers at lag 0 ($r = 0.30$, SE = 0.164) and lag -1 ($r = 0.59$, SE = 0.167). Spillway gate position was also found to have a Granger causal relationship with outmigration numbers ($F = 2.93$, $p = 0.022$). Average discharge and spillway gate position were most strongly cross-correlated together at lag 0 ($r = 0.34$, SE = 0.164) and lag -1 ($r = 0.57$, SE = 0.167).

ARIMA time series regression modeling was used to fully evaluate the time series relationship between outmigration numbers and average discharge and spillway gate level. The best performing model for discharge was an ARIMA model of the form (1,0,0)x(1,0,1) + Average Discharge ($R^2 = 0.42$, RMSE = 12.87), which showed that discharge level was positively related with outmigration numbers over time ($t = 1.75$, $p = 0.085$). The best performing model for spillway gate level was an ARIMA model of the form (2,0,1)x((1,0,1) + Average Spillway Gate Level ($R^2 = 0.57$, RMSE = 11.45), which showed that average spillway gate level was positively related with outmigration numbers ($t = 5.91$, $p < 0.001$). In addition, the interaction between average discharge level and average spillway gate level was significant ($t = 2.64$, $p = 0.011$). Distinct peaks in powerhouse discharge levels and spillway gate levels were temporally associated with peaks in outmigration numbers of juvenile lake sturgeon (Figure 5.6).

Discussion

Reservoir Residency Characteristics:

Our study documented the residency and out-migration characteristics of stocked juvenile lake sturgeon over a period of four years between 2014 -2018 in an impounded part of the Black River located in northern Michigan. The project sought to simulate the passage of adults above dams which, would result in spawning and reproduction above reservoirs, in order to assess the fate of juveniles that are produced and the recruitment benefits of reintroduction efforts associated with improvements in lake sturgeon passage around hydroelectric dams. Overall, 46% of both the age-0 and the older age-1 and age-2 lake sturgeon that were originally stocked into Kleber Reservoir and 41% of the age-0 and 49% of the age-1 and age-2 lake sturgeon that were originally stocked into Tower Reservoir were detected out-migrating from the reservoirs during the study. The majority of the lake sturgeon stocked above the hydroelectric dams only resided within the reservoirs for a short period of time, with 50% of age-0 and 68% of the older age-1 and age-2 lake sturgeon staying less than 60 days within Kleber Reservoir. Similarly, in Tower Reservoir 65% of age-0 and 54% of the older age-1 and age-2 lake sturgeon stayed less than 60 days within the reservoir. In contrast with our observations, Barth et al. (2011) observed that juvenile lake sturgeon in a larger reservoir on the Winnipeg River made limited movements, with 90.8% of juveniles being captured within two river kilometers of their original capture locations. Similarly, McDougall et al. (2014a) observed no downstream passage events for juvenile lake sturgeon residing in the smaller Slave Falls Reservoir on the Winnipeg River, but annual downstream passage rates of 21% and 2.9% were estimated for sub-adults and adults, respectively.

However, a significant proportion of the lake sturgeon in our study did stay within the reservoir system for extended periods of time relying on the resources of the reservoirs. Specifically, 10% of age-0 and 11% of age-1 and age-2 lake sturgeon stayed within Kleber Reservoirs for more than 499 days before out-migrating. Likewise, within Tower Reservoir 9% of age-0 and 5% of age-1 and age-2 lake sturgeon stayed more than 299 days within the reservoir. The study by Ganus et al. (2018) is the only published study to our knowledge that has assessed post-stocking behavior of age-1 and age-2 juvenile lake sturgeon in a reservoir system. Their two year monitoring study showed variable residency rates, with 32% of stocked lake sturgeon in 2011 and 9% of lake sturgeon in 2012 out-migrating from Cheatham Reservoir on the Cumberland River (Ganus et al., 2018). For comparison, Cheatham Reservoir is approximately 24 times larger than Kleber Reservoir and would provide substantially more space and resources.

It is important to note that juvenile lake sturgeon are still being detected out-migrating from the reservoirs as of 2023, so juveniles may reside within reservoirs for longer periods of time than what this study was able to document (Larson pers. comm). What is apparent is that juvenile lake sturgeon are able to make use of habitats within small reservoirs and survive within them for extended periods of time. McDougall et al. (2017) found that lake sturgeon populations can successfully persist in reservoirs as small as 10 river kilometers provided there is adequate habitat to support spawning, drifting, and rearing. Beamesderfer et al. (1995)

similarly found that white sturgeon (*Acipenser transmontanus*) were able to successfully live within fragmented reservoirs on the Columbia River when suitable habitat existed, although they did find that reproductive potential per recruit, yield per recruit, and the number of recruits were lower in the impoundments than in the free flowing part of the river. A study that examined the impact of hydroelectric infrastructure on lake sturgeon abundance across Ontario also found that relative abundance, growth, and condition were significantly greater in unregulated rivers than in regulated rivers (Haxton et al., 2015). The fact that sizeable proportions of juvenile lake sturgeon remained within small reservoirs for extended periods of time has consequences for passage survival, as larger and older individuals are more susceptible to hydroelectric turbine mortality and bar-rack impingement, which may have implications for recruitment, fish passage engineering, and hydroelectric dam operations (Bruch et al., 2016; Coscarelli et al., 2011; Hegna et al., 2023; Pracheil et al., 2016).

Differences in residency characteristics were observed between the two age-groups within the reservoirs. Age-0 lake sturgeon stayed within Kleber Reservoir for longer periods of time compared with the older age-1 and age-2 lake sturgeon. In contrast, residency times were similar between the age-groups in Tower Reservoir. Information on long-term lake sturgeon reservoir residency characteristics and post-stocking behavior is generally lacking (Bruch et al., 2016; Cooke et al., 2020). A study on Slave Falls Reservoir found age-related differences in entrainment over an 18-month time period, with 0% of juveniles, 27% of subadult lake sturgeon tagged in the lower reservoir, and 8.7% of tagged adults moving downstream out of the reservoir (McDougall et al., 2013). Older and larger lake sturgeon generally require more space, more resources, and make longer movements (McDougall et al., 2013; Smith and King, 2005), which may explain why the older age-1 and age-2 lake sturgeon out-migrated from Kleber Reservoir more rapidly than the age-0 lake sturgeon. Smith and King (2005) specifically observed that juvenile lake sturgeon longer than 90 cm made greater daily movements and had larger home range sizes compared with juveniles that were shorter than 90 cm. Tower Reservoir contains less suitable habitat because it is shallower and smaller, which may explain why both age-groups responded similarly to this less favorable reservoir environment in terms of residency time.

Comparing Reservoirs and Behavior:

Multiple differences in residency characteristics were observed between Kleber and Tower Reservoirs. Age-0 lake sturgeon had longer residency times in Kleber Reservoir compared with Tower Reservoir. Also, the older age-1 and age-2 lake sturgeon had longer residency times in Kleber Reservoir compared with Tower Reservoir. Kleber Reservoir is almost five times larger than Tower Reservoir. The smaller size and shallower bathymetry of Tower Reservoir may have provided less suitable habitat conditions that had the effect of "pushing" juvenile lake sturgeon out of the reservoir more quickly in contrast with Kleber Reservoir, indicating potential sink-source habitat dynamics within the system (Dias, 1996; Diffendorfer, 1998). Indeed, age-0 lake sturgeon were 2.19 times and age-1 and age-2 lake sturgeon were 3.57 times more likely to stay more than 299 days within Kleber Reservoir compared with Tower Reservoir. Previous research has documented that juvenile lake sturgeon tend to avoid shallow water habitats with abundant aquatic vegetation, which is what characterizes much of Tower Reservoir, and prefer habitats with deep water and silt that lack aquatic vegetation

(Barth et al., 2011; Boase et al., 2014; Hegna et al., 2020; Holtgren and Auer, 2004).

The fact that the deepest water in Tower Reservoir was located immediately next to Tower Dam would have made juveniles more susceptible to incidental entrainment compared with the environment in Kleber Reservoir. McDougall et al. (2013) similarly found that reservoir bathymetry could influence entrainment susceptibility of lake sturgeon, with river narrows restricting movement and limiting entrainment susceptibility for certain geographic areas within the Slave Falls Reservoir. The bathymetry in front of Kleber Dam is quite different from Tower Dam. In order to enter the penstocks at Kleber Dam an individual would have to ascend in elevation to much shallower water depths and follow a narrower side channel into the powerhouse. The fact that Kleber Reservoir is considerably deeper, larger, and that deep water habitat is not exclusively located immediately adjacent to the dam in the reservoir may have provided much more suitable habitat and resources that promoted longer periods of residency and limited incidental entrainment of juvenile lake sturgeon. Thus, the bathymetry characteristics of a reservoir may heavily influence the level of residency and entrainment in a system, and these characteristics should be evaluated thoroughly when planning hatchery supplementation or fish passage improvements for lake sturgeon.

Lower River Residency Characteristics:

In the free flowing part of the Black River below Kleber Dam differences in residency characteristics were observed. On average age-0 lake sturgeon resided within the river for 50 days and the older age-1+ lake sturgeon resided within the river for 18 days. The age-0 lake sturgeon had longer residency times compared with the older age-1+ lake sturgeon in the lower river. All of the observed age-1+ lake sturgeon out-migrated from the lower river system within 81 days, while 11% of the age-0 lake sturgeon stayed within the river for more than 179 days, indicating the importance of riverine habitat for young juveniles.   We did not monitor the usage of the river mouth itself, but juveniles may have continued usage of that part of the river for longer periods of time after they passed our lower most PIT-tag detection antenna. In addition, this study did not assess seasonal repeat usage of the river by juveniles after initial outmigration. Similar to our results, a study on the Lower Fox River observed that stocked age-0 lake sturgeon resided within the free flowing part of the Fox River for between 6 – 41 days before out-migrating (Tucker et al., 2022). Benson et al. (2005) in their radio telemetry study similarly noted that during the fall age-0 lake sturgeon took from mere days to upwards of a month to out-migrate from the Peshtigo River into Green Bay.

Stocking Location and Effects of Multiple Dams:

Initial stocking location and the effects of passing through two dams had some effects on downstream lake sturgeon residency characteristics. Those juvenile lake sturgeon that were stocked into Tower Reservoir resided longer within the reservoir system than those lake sturgeon that were stocked into Kleber Reservoir. The longer system residency time is likely due to longer required travel distance and the multiple dams that juveniles must negotiate during their outmigration when stocked above Tower Dam. Other researchers have similarly noted the extra time and energy that must be spent by fish species in negotiating passage routes through multiple barriers and the associated lethal and sub-lethal effects of passage (Barnthouse, 2013; Eyler et al., 2016; Karppinen et al., 2021; Molina-Moctezuma et al., 2021;

Piper et al., 2013). Interestingly, age-0 lake sturgeon that were originally stocked into Kleber Reservoir had longer residency times within Kleber Reservoir compared with age-0 lake sturgeon that were originally stocked into Tower Reservoir. No such residency difference was observed for the older age-1 and age-2 lake sturgeon. The reasons for the difference in age-0 residency times are uncertain but could be caused by a couple factors. Initial passage through Tower Dam may provide a motivating factor for continued downstream outmigration. Also, the time of year at which age-0 lake sturgeon leave Tower Reservoir and enter Kleber Reservoir could subsequently contribute to shorter residency times in Kleber Reservoir because seasonal cues in temperature and discharge may already be at peak levels for motivating outmigration when the juveniles initially leave Tower Reservoir. Lastly, no differences in lower river residency times were observed between lake sturgeon that were originally stocked into Kleber Reservoir compared with Tower Reservoir, indicating that the juvenile lake sturgeon responded similarly to the free flowing riverine environment after passage regardless of the number of dams passed.

Effects of Family and Production Origin (hatchery vs naturally produced larvae):

Our data also showed that family genetic background can have an effect on residency behavior. Differences in residency times with respect to family group were observed in the reservoir system as a whole, within Kleber Reservoir, and within the lower Black River. The importance of the effects of genetic variability on life history traits such as migration timing is widely recognized (Gharrett and Smoker, 1993; Kovach et al., 2013; Quinn et al., 2000). In addition, several studies have documented the influence of genetic effects specifically on lake sturgeon behavior during early ontogeny (Dammerman et al., 2020, 2016, 2015). The different family groups responded uniformly with respect to residency in Tower Reservoir likely because this reservoir was less suitable because of its smaller size and shallower bathymetry. In addition, our results showed that hatchery produced lake sturgeon had longer residency times within the reservoir system as a whole and within Kleber Reservoir compared with naturally produced lake sturgeon. While no studies have examined differences in migration behavior between hatchery produced and naturally produced lake sturgeon, Urke et al. (2013) found that wild Atlantic salmon (*Salmo salar*) smolts had a stronger response and relationship to water temperature variations and accumulated water discharge than hatchery-reared smolts with respect to outmigration timing. Another study on Atlantic salmon found that wild adult salmon ascended the Imsa River earlier than hatchery reared salmon, and the hatchery reared salmon strayed more, stayed within the river for a shorter period of time, and a higher proportion of them returned to the ocean without spawning compared with the wild salmon (Jonsson et al., 1991). Our study results highlight the importance of accounting for family effects and genetic diversity in hatchery supplementation programs to ensure that a diversity of traits and behaviors are reintroduced into a river system to enhance adaptability of reintroduced lake sturgeon populations.

Seasonality, Timing, and Environmental Cues of Outmigration:

The outmigration of juvenile lake sturgeon was highly seasonal and was temporally related to the interrelated factors of water temperature, spillway gate operation level, and powerhouse discharge level. Based on this multi-year dataset, outmigration numbers consistently peaked in the spring and fall months during times of noted water temperature changes. Specifically, water temperature was found to have a threshold type relationship with outmigration numbers where the relationship was found to change from positive to negative past 11.4 °C in the best fit threshold time series regression model. Similar to our results, Benson et al. (2005) found that outmigration of age-0 lake sturgeon in the Peshtigo River was triggered when water temperature fell below 13.8 °C during the fall. In contrast, Caroffino et al. (2009) suggested that age-0 lake sturgeon may leave their natal river before there is a seasonal decline in water temperature based on mark-recapture abundance estimates. Our results clearly showed that downstream movements were associated with water temperature changes and that individual lake sturgeon out-migrated at varying levels across all seasons and not just during the fall time period.

Our results showed that juvenile lake sturgeon outmigration from the reservoir system occurred throughout the year with notable peaks occurring in the fall and spring. These peaks in outmigration numbers corresponded with time periods of higher discharge through the powerhouses and spillways. Discharge levels are directly related to seasonal changes in precipitation, run-off, and snow melt in a watershed. Our time series analysis indicated that concurrent monthly spillway gate level and discharge conditions and those conditions occurring one month prior were most strongly associated with predicting monthly outmigration numbers. Other researchers have anecdotally noted the tendency for juvenile lake sturgeon to out-migrate during periods of increased river discharge but quantitative analysis and fine-scale data on outmigration behavior is lacking (Benson et al., 2005; Bruch et al., 2016; Ganus et al., 2018; Tucker et al., 2022). Similar to our results, Weber and Flammang (2019) found that average

April discharge level and the number of days discharge exceeded 14 m^3/s was strongly associated with the level of walleye emigration observed from a reservoir, which ranged from 0.02 to 0.26 on an annual basis.

We observed that approximately 61.7% of age-0 and 36.6% of age-1 and age-2 lake sturgeon out-migrated during the fall. In the spring approximately 26.3% of age-0 and 16.1% of age-1 and age-2 lake sturgeon out-migrated. The observed lower number of older lake sturgeon out-migrating in the fall is likely an artifact due to that age category being stocked in the summer and because this age group had a greater propensity to out-migrate more quickly. Other researchers have similarly noted the tendency for juvenile lake sturgeon to out-migrate during the fall time period (Altenritter et al., 2013; Benson et al., 2005; Caroffino et al., 2009; Holtgren and Auer, 2004). Benson et al. (2005) indicated that young juvenile lake sturgeon likely out-migrate in the fall in order to find deeper water that is more protective from winter conditions. In contrast with our observations, Ganus et al. (2018) observed that the majority of juvenile lake sturgeon outmigration passage events occurred between January and June in a large reservoir on the Cumberland River, which could be due to differences in reservoir size, climate, and hydrologic regime. The older age-1 and age-2 lake sturgeon in our study were more likely to out-migrate during the summer months compared with age-0 lake sturgeon likely because that time period was closer to when they were released and because this age-group had a greater propensity to out-migrate more quickly after stocking.

We also observed that the vast majority of the outmigration movements (>90%) occurred during the nighttime hours, indicating that juvenile lake sturgeon migratory movements out of impounded river systems are largely nocturnal. Other researchers have similarly observed that juvenile lake sturgeon movements primarily occur at night in the Peshtigo, Moose, and Niagara River systems (Benson et al., 2005; Chiasson et al., 1997; Hughes, 2002). McDougall et al. (2014a) similarly observed that juvenile movements into the seven-bay sluiceway on Slave Falls Reservoir only occurred at night, although sample size was small (n = 3). Research suggests that juvenile lake sturgeon may be more active at night to avoid predators and because they are able to use electrosensory detection to forage in low visibility environments (Wishingrad et al., 2015; Zhang et al., 2012). Hydroelectric dam operations may be able to be modified to take advantage of the temporal behavioral characteristics that we have observed in this study. Specifically, during the peak outmigration seasons in the fall and spring bottom draw spillways may be able to be selectively operated at night to enhance passage survival for out-migrating juvenile lake sturgeon.

Management Implications:

In summary, our results indicate that the majority of juvenile lake sturgeon will out-migrate rapidly from small reservoir systems in the fall and spring after stocking and that outmigration movements are nocturnal. However, our data also showed that juvenile lake sturgeon can persist within and rely upon resources in small reservoirs for extended periods of time over multiple years. Outmigration from reservoirs was largely initiated by seasonal changes in water temperatures and discharge during the spring and fall. Therefore, through the monitoring of water temperature and discharge dynamics hydroelectric projects can identify peak outmigration time periods over which operations may be able to be modified. Specifically, operations at dams may be able to be modified to take advantage of outmigration behavior through the selective operation of spillways at night during these peak outmigration time periods to facilitate safer passage and improve recruitment of juvenile lake sturgeon. The bathymetry characteristics of a reservoir may also heavily influence the level of residency and entrainment in a system. Reservoirs that are smaller and shallower are expected to have lower long-term residency rates compared with larger reservoirs. As reservoir size and habitat quality increases the length of residency is expected to also increase. As residency time increases the greater the number of age cohorts within a reservoir, which would result in larger juveniles inhabiting the reservoir and encountering hydroelectric dam infrastructure during outmigration. Therefore, age and size related factors need to be considered based on the characteristics of the reservoir system when engineering size specific passage systems for juvenile lake sturgeon.

Acknowledgments

This study was funded by the Great Lakes Fishery Trust (project No. 2012–1302). Additional funding was also provided by the Michigan Department of Natural Resources through the State Wildlife Grant Program. We also thank the hatchery staff at the Black River Sturgeon Rearing Facility, including John Bauman, Nathan Barton, Douglas Larson, Shaley Valentine, Zachary Witzel, Andrew Lockwood, Stefan Tucker, Jason Lyons, Rebecca Colby, Garret Johnson, Dillon Ross, Ryan Walquist, Adam Chaston, and Jenna Ruzich, for their valuable assistance with the project and with the production and management of the juvenile lake sturgeon.

Figures

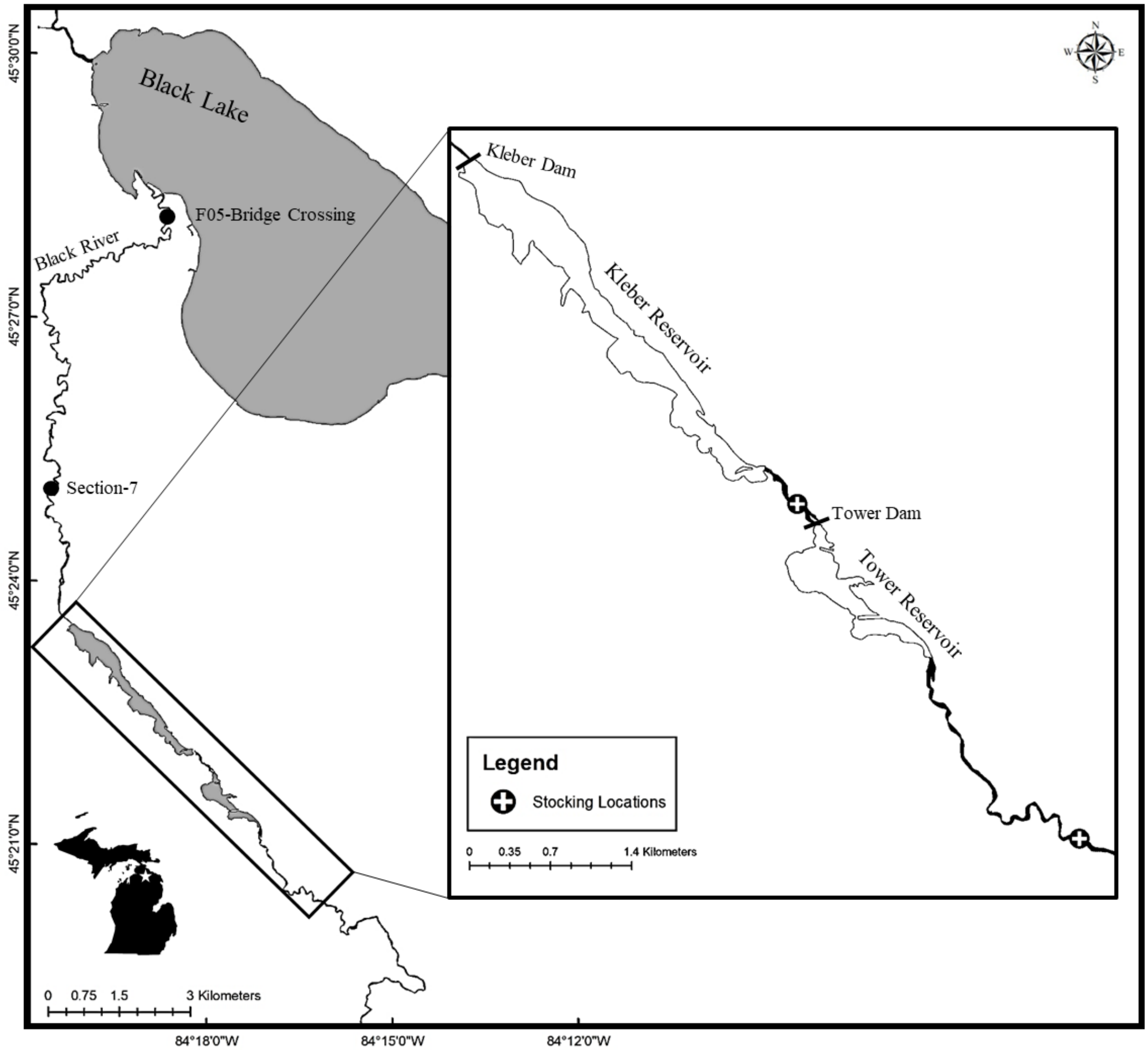

Figure 5.1: Map of Black Lake and the upper Black River system located in Cheboygan County, Michigan. The inset map highlights Kleber Dam, Kleber Reservoir, Tower Dam, and Tower Reservoir, along with the lake sturgeon stocking locations used for the research project. PIT-tag antennas were located at the F05-bridge crossing, section-7, Kleber Dam, and at Tower Dam.

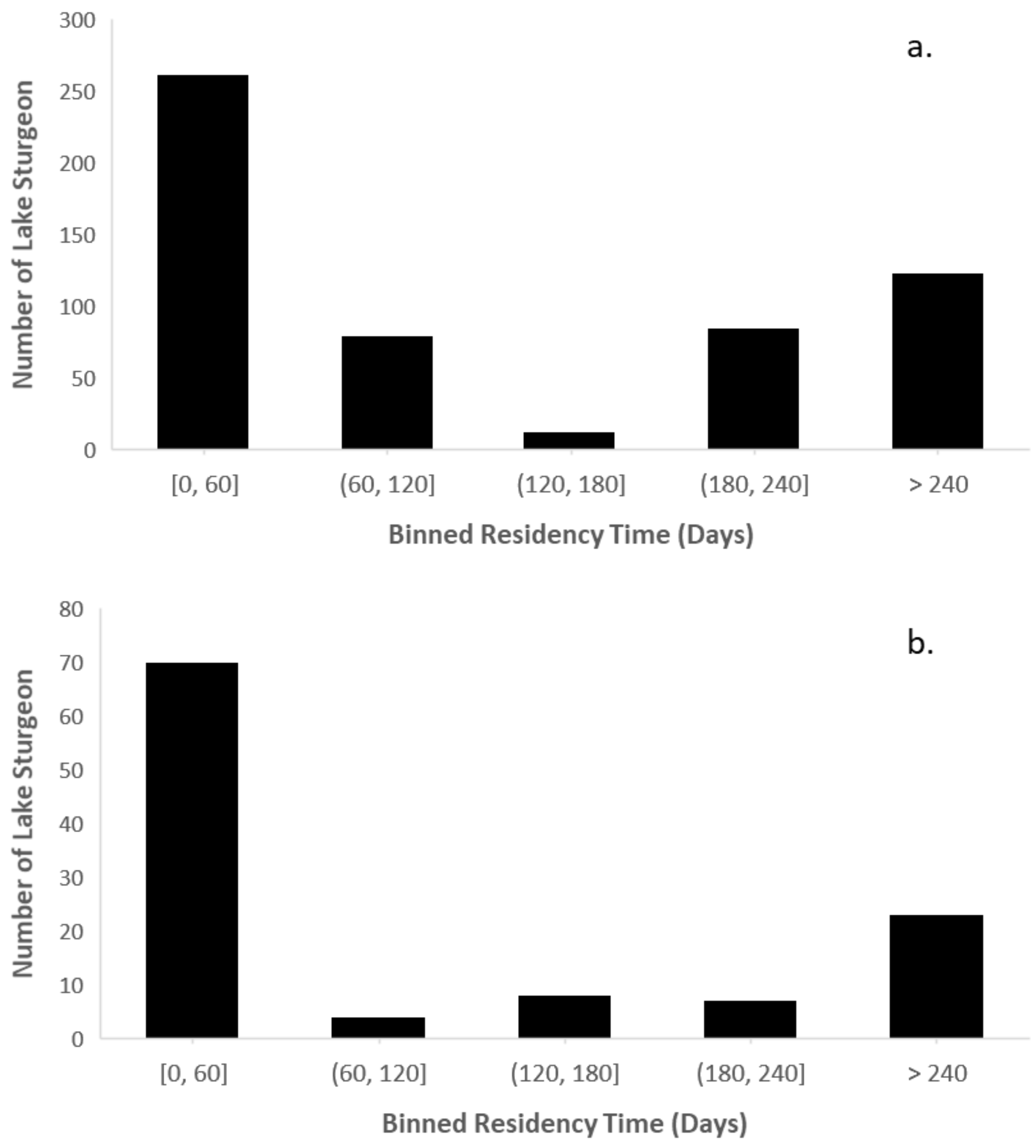

Figure 5.2: Histograms of observed residency times for age-0 (a.) and age-1 and age-2 (b.) lake sturgeon in the reservoir system.

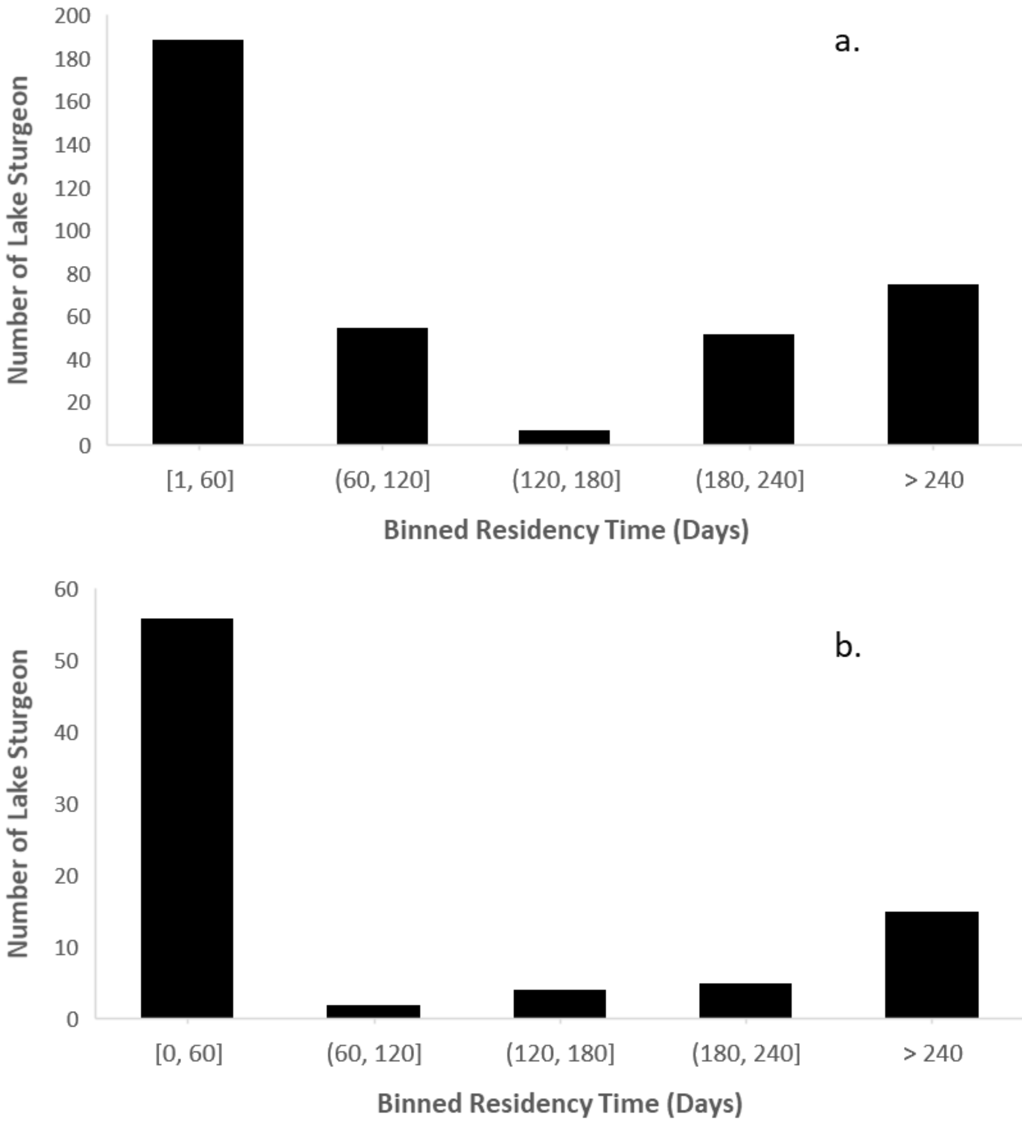

Figure 5.3: Histograms of observed residency times for age-0 (a.) and age-1 and age-2 (b.) lake sturgeon in Kleber Reservoir.

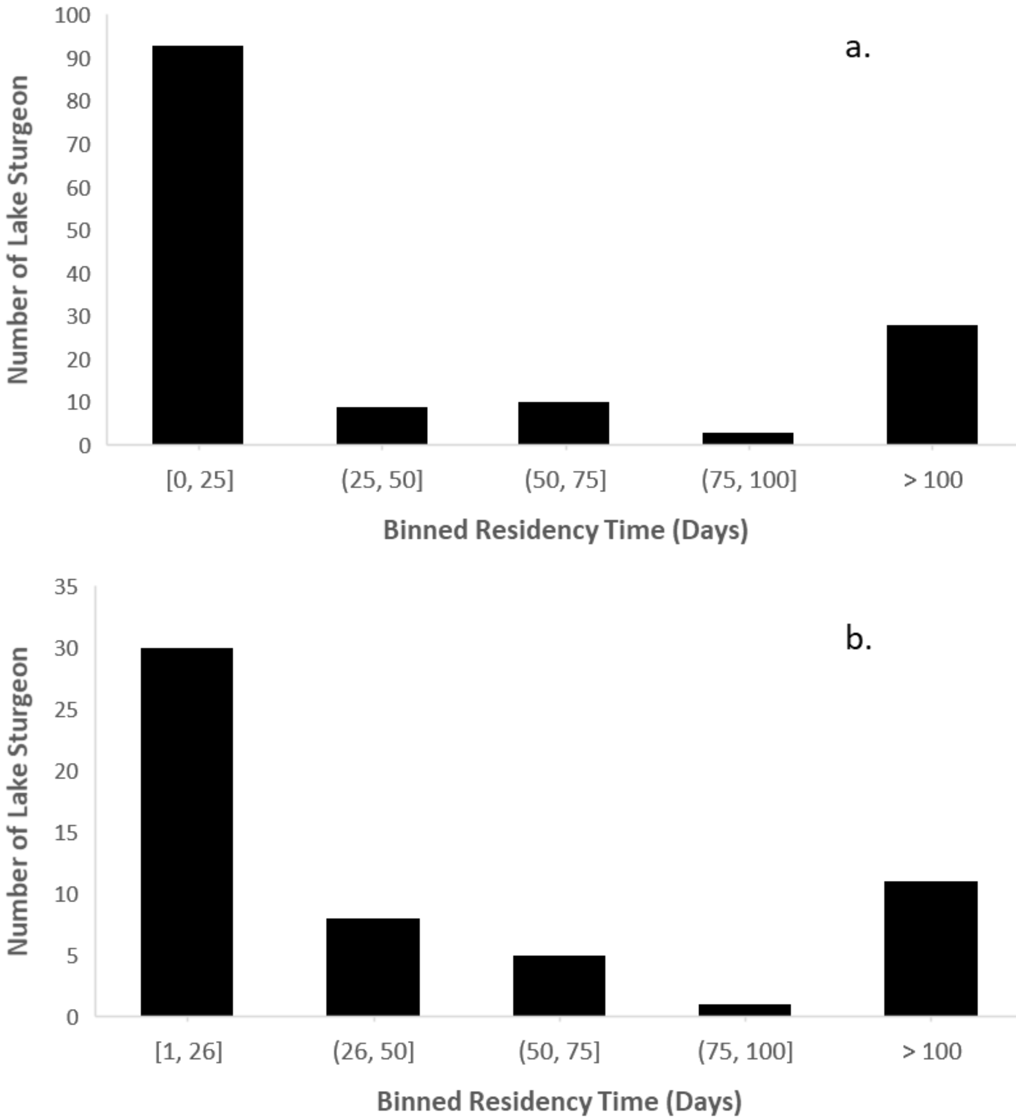

Figure 5.4: Histograms of observed residency times for age-0 (a.) and age-1 and age-2 (b.) lake sturgeon in Tower Reservoir.

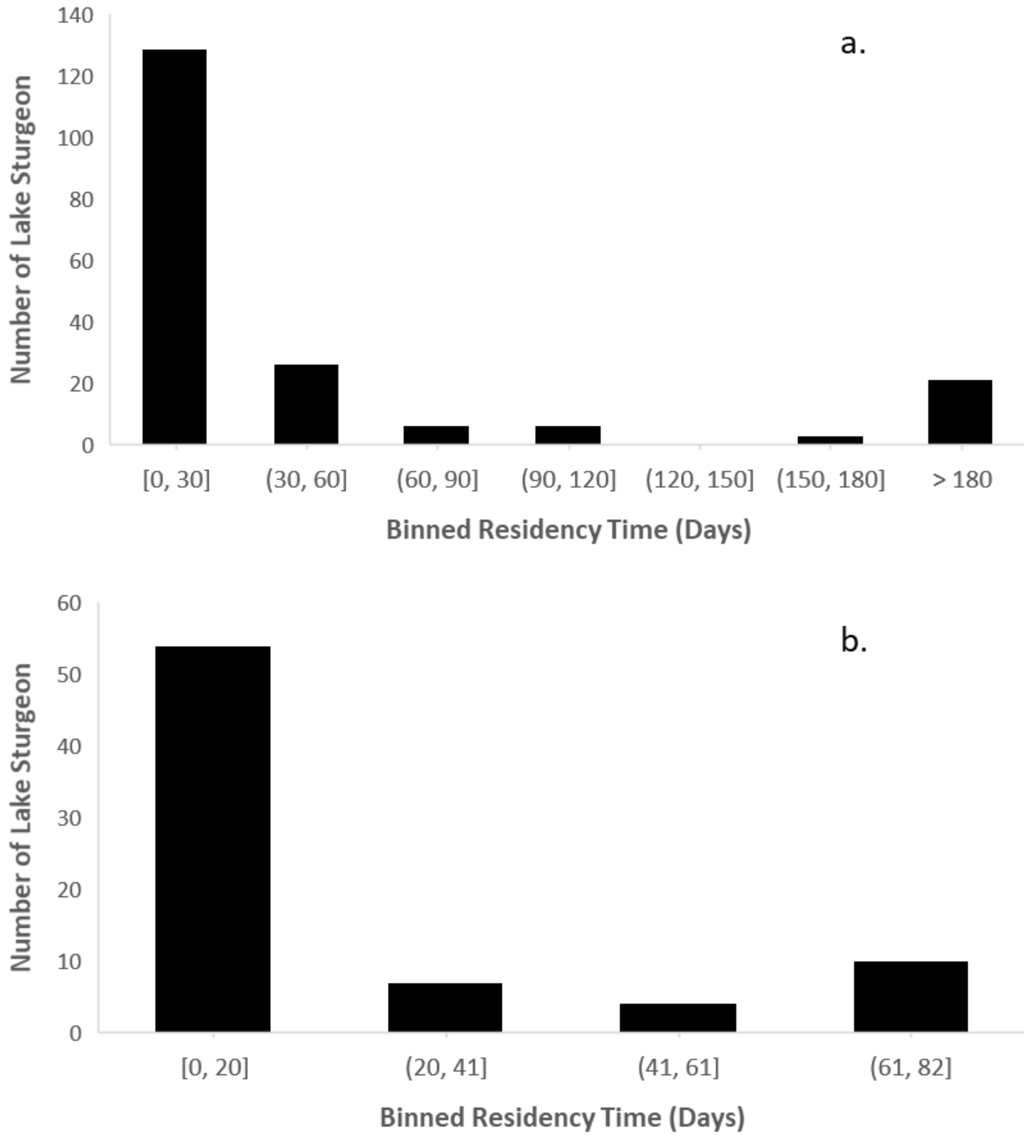

Figure 5.5: Histograms of observed residency times for age-0 (a.) and age-1+ (b.) lake sturgeon in the lower Black River below Kleber Dam.

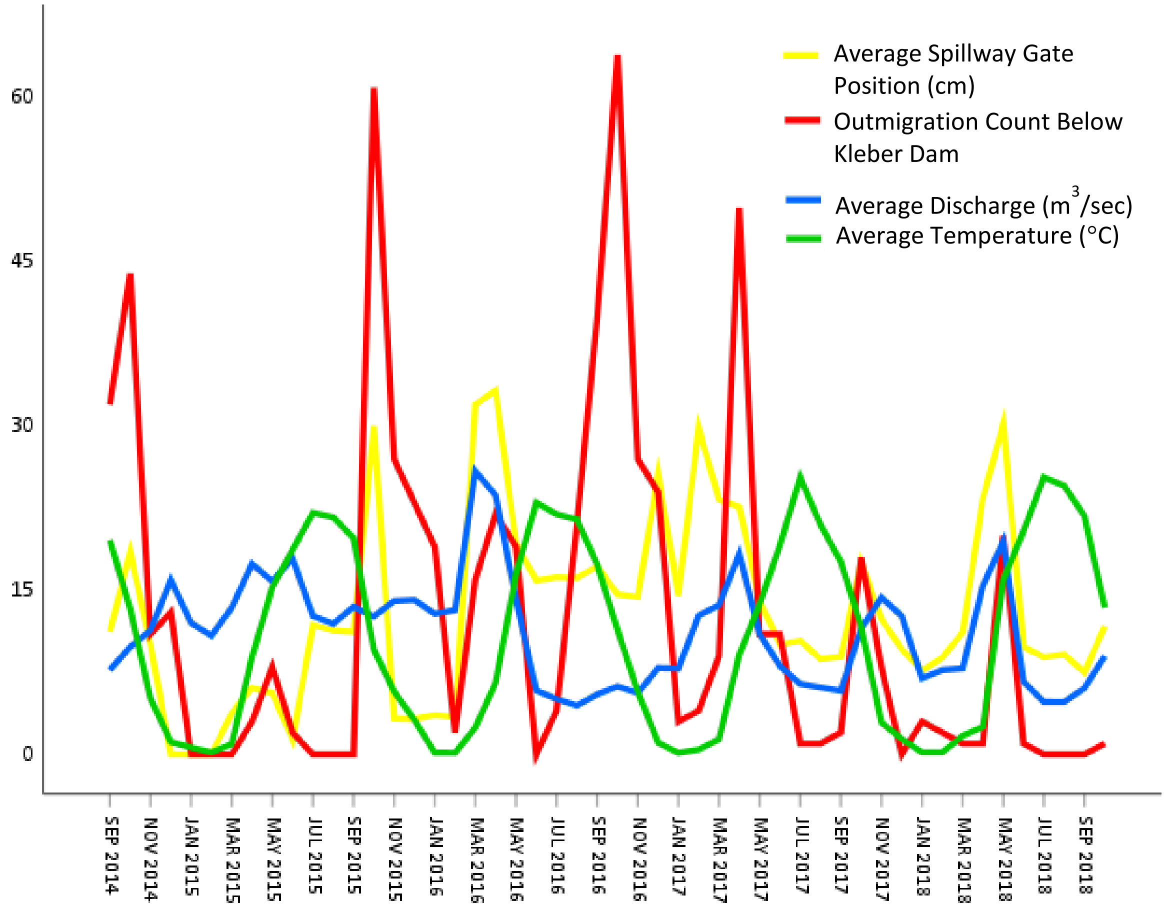

Figure 5.6: Time series graph showing out-migration counts of juvenile lake sturgeon below Kleber Dam (red line) along with average powerhouse discharge (m^3/sec; blue line), average spillway gate position (cm; yellow line), and average water temperature (°C; green line) at Kleber Dam. The spillway gate position controls how much water is discharged through the spillway. The higher the gate position the more water that is discharged through the spillway.

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APPENDIX:
CHAPTER 3 SUPPLEMENTARY MATERIALS

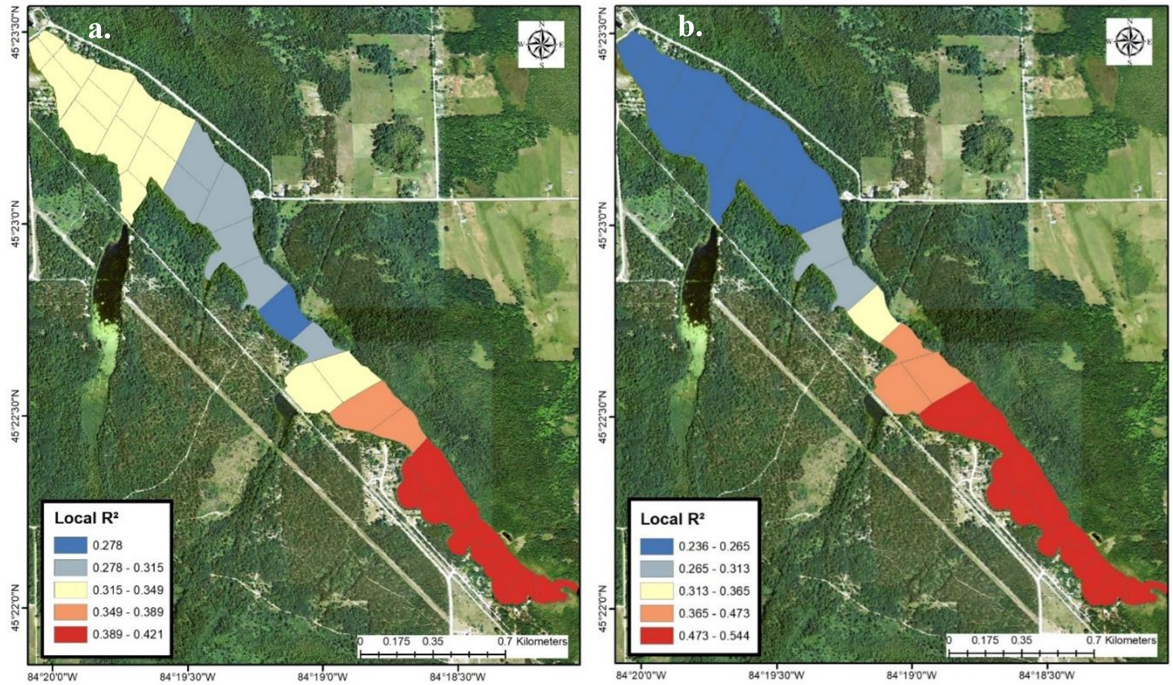

Figure S3.1: Geographically weighted regression (GWR) analysis map showing how the local R^2 relationship between the amount of silt hectares and the number of unique lake sturgeon detected in each zone varies across Kleber Reservoir (a.). GWR analysis map showing how the local R^2 relationship between the amount of low hardness hectares ($\leq$ 60 hardness units) and the number of unique lake sturgeon detected in each zone varies across Kleber Reservoir (b.). Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program.

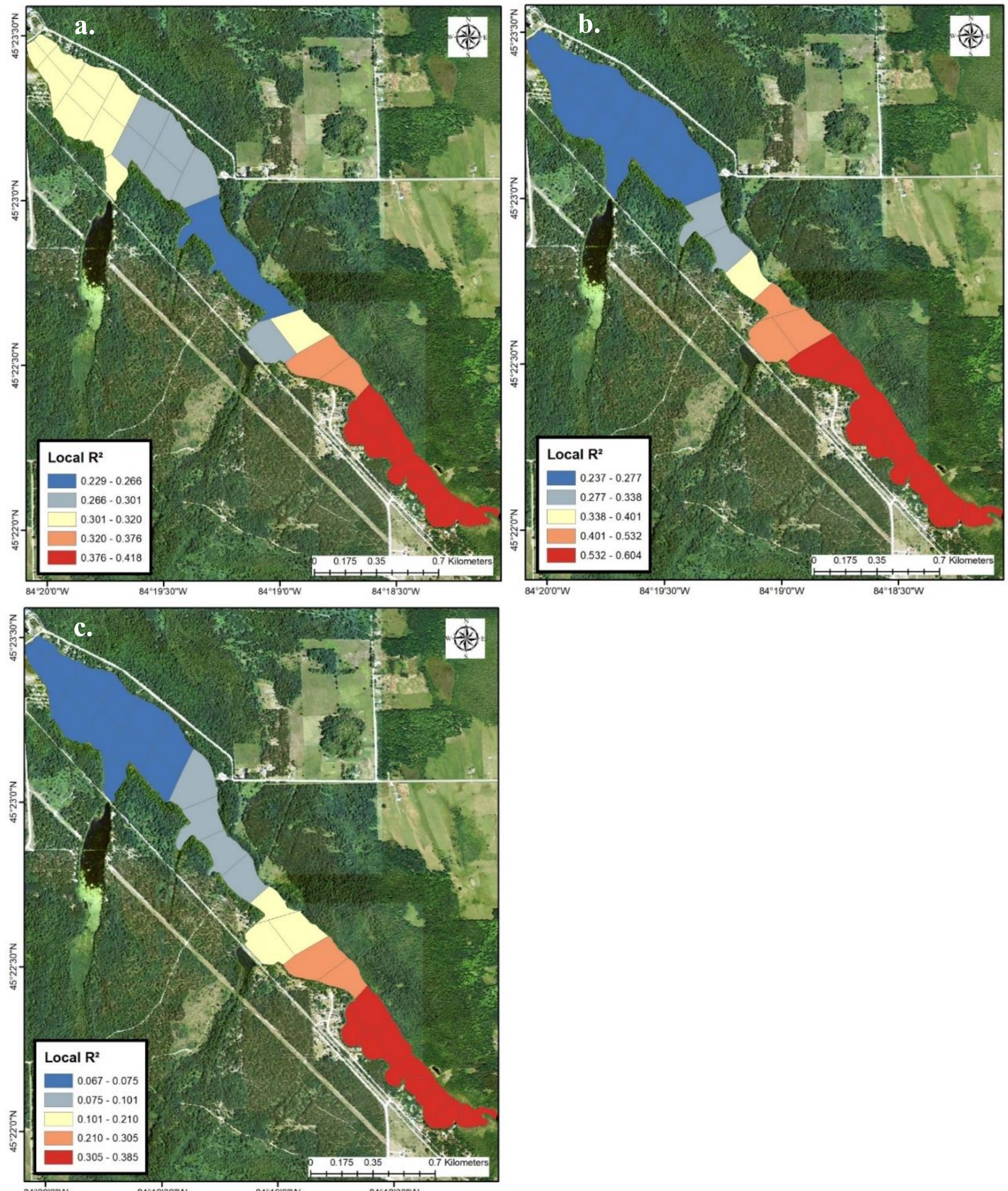

Figure S3.2: Geographically weighted regression (GWR) analysis map showing how the local R^2 relationship between the amount of silt hectares and the total number of lake sturgeon detections in each zone varies across Kleber Reservoir (a.). GWR analysis map showing how the local R^2 relationship between the amount of low hardness hectares (≤ 60 hardness units) and the total number of lake sturgeon detections in each zone varies across Kleber Reservoir (b.). GWR analysis map showing how the local R^2 relationship between max depth and the total number of lake sturgeon detections in each zone varies across Kleber Reservoir (c.). Map imagery is from the United States Department of Agriculture National Agriculture Imagery Program.