Muskellunge (*Esox masquinongy*) movement patterns and habitat use in the St. Louis River Estuary and southwestern Lake Superior

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Abstract

The St. Louis River Estuary is a designated Area of Concern by the Environmental Protection Agency due to severe environmental degradation. Uncertain is the spatial ecology of muskellunge (*Esox masquinongy*), an indicator species, in relation to both degraded and restored habitats. I collaborated with the Minnesota and Wisconsin Department of Natural Resources to collect genetic samples and use passive acoustic telemetry to track 60 Muskellunge in the St. Louis River Estuary and southwestern Lake Superior for 15 months. Genetic analysis revealed that the river is utilized by two genetic strains (Wisconsin and Minnesota) that were previously stocked to restore a nearly extirpated population. According to ANOVA, Muskellunge tended to move upstream in the spring, downstream and into Lake Superior throughout summer, and to the middle river during fall and winter. Males and females spent significantly more time in the upper and lower rivers, respectively. Movements were influenced by strain in that hybrids and WI strain spent more time in the upper and middle river, and the MN strain spent more time in Lake Superior. A Random Forest model indicated that Lake Superior use was related to strain (the MN strain made up 80% of individuals using Lake Superior), but not sex or body length. Lastly, a Negative Binomial Hurdle model determined that Muskellunge were detected in restored sites more often than in non-restored, poor quality sites. A better understanding of Muskellunge ecology in the St. Louis River Estuary will guide future management and restoration efforts of Muskellunge in the St. Louis River Estuary and other areas of the Great Lakes.

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Introduction

The Great Lakes of North America are one of the largest freshwater ecosystems in the world, containing 84% and 21% of the continent's and world's surface freshwater, respectively (United States Environmental Protection Agency 2016). The Great Lakes directly affect the lives of ~35 million Americans and Canadians living in the Great Lakes basin (Austin et al. 2007), drive the regional economy, and are home to thousands of plant and animal species, especially fishes (NOAA 2017).

Great Lakes fishes play important ecological roles as predators and ecosystem engineers (McClenachan et al. 2015) and generate ecosystem services that have economic and social benefits (Brooks et al. 2007, McClenachan et al. 2015). Recreational and commercial fishing in the Great Lakes is worth billions of dollars a year to the regional economy (Hudson and Ziegler 2014). Freshwater fishes also provide food security and cultural services through religious, inspirational, and aesthetic experiences. For example, Great Lakes Lake Sturgeon (*Acipenser fulvescens*) and Lake Whitefish (*Coregonus clupeaformis*) are icons of regional identity (Lynch et al. 2015, 2016).

Freshwater ecosystems face numerous threats. Anthropogenic disturbances, such as invasive species and industrial, agricultural and urban sprawl (Brooks et al. 2007) are resulting in overexploitation, habitat loss, water quality degradation, and deteriorating aquatic flora and fauna biodiversity (Dudgeon et al. 2006, Geist and Hawkins 2016). Currently, freshwater habitats are facing the largest declines of biodiversity compared to any other ecosystem (Dudgeon et al. 2006). In fact, anthropogenic alterations threaten 65% of all inland aquatic habitat and associated biodiversity in a moderate to severe fashion (Vörösmarty et al. 2010). The loss of biodiversity, often seen in freshwater fishes (Strayer and Dudgeon 2010), diminishes ecosystem productivity and alters ecosystem function (Dudgeon et al. 2006, Lynch et al. 2016).

Decades of environmental degradation in the Great Lakes have led to restrictions on drinking water, fish and wildlife consumption, and beach use (NOAA 2016). It has also resulted in the loss of fish and wildlife populations and habitat. Roughly 50% of coastal wetlands have been destroyed in the Great Lakes (BlueAccounting 2018). Additionally, poor water quality caused by industrial pollution crashed Lake Sturgeon, Yellow Perch (*Perca flavescens*), and large-bodied invertebrate populations throughout the Great Lakes in the mid-1900s (Hudson and Ziegler 2014). Furthermore, introduced invasive mussels in the late 1980s to early 1990s contributed to the collapse of native Lake Whitefish fisheries, diporeia populations, and benthic invertebrate communities (Nalepa et al. 2005, Herbst et al. 2013). Each of these disturbances altered water clarity, reduced lake-wide productivity, and shifted ecosystems.

Ecological restoration is necessary to increase fish abundance, biodiversity, and associated ecosystem services across multiple scales (Brooks et al. 2007) and at different life stages (Mueller and Geist 2016). Habitat restoration is already occurring from estuaries on Lake Superior to Lake Ontario resulting in economic, social, and aesthetic benefits (Boston et al. 2016, Piszczek et al. 2016).

Detailed monitoring of fish abundance, movement, and habitat use is important for verifying that restoration meets the desired outcome (Lapointe et al. 2013). Monitoring is critical because fish are essential bioindicators of aquatic ecosystem health and biodiversity (Brooks et al. 2007, Pino-del-Carpio et al. 2011). Traditional fishery monitoring techniques measure population abundance or richness during a “snapshot” in time and space (e.g. gill and trap nets; Brooks et al. 2007, Rous et al. 2017). However, year-round monitoring of fishes in habitats pre- and post-restoration is needed to determine if a restoration project is effective (Brooks et al. 2007, Lapointe et al. 2013, McClenachan et al. 2015, Rous et al. 2017).

Biotelemetry, the tracking of animals with electronic tags, is one avenue to meet restoration-monitoring needs and enhance fish research. Freshwater radio and acoustic telemetry have been used to monitor the movement of aquatic organisms since the 1950s (Brooks et al. 2007, Rogers and White 2007). Telemetry can gather fine- and broad-scale data on how fish respond to environmental change over time to identify the impacts of socio-environmental change and vital habitat requirements (Crossin et al. 2017). Furthermore, acoustic telemetry improves population survival and abundance estimates when paired with mark-recapture studies and models (Pine 2003, Dudgeon et al. 2015). For instance, Holbrook et al. (2016) used acoustic telemetry to determine that traditional mark-recapture methods in the St. Mary’s River (which connects Lake Superior and Lake Huron) probably overestimated the impact of control efforts on Sea Lamprey (*Petromyzon marinus*) abundance.

Fish movement and spatial ecology research within the Great Lakes are already improving our understanding of fish reproductive biology, invasive species, and habitat use to inform restoration practices and better understand fisheries or associated life history (Landsman et al. 2011). Acoustic telemetry has been used to identify spawning and non-spawning habitat (Caswell et al. 2004, Mucha and Mackereth 2008), determine spawning migration patterns (Kelso and Gardner 2000), and inform habitat restoration (Hilts 2017, Binder et al. 2018) of numerous Great Lakes fishes. Telemetry, specifically acoustic telemetry, paired with bioindicator and economically important fish species such as Muskellunge (*Esox masquinongy*), is already making an impact in fisheries management and restoration planning and monitoring.

The Muskellunge is a large, popular freshwater game fish that is native to the Great Lakes region and south through the upper Mississippi River basin (Kerr 2011). Muskellunge are sensitive to certain environmental disturbances on spawning habitat that make them ideal bioindicators (Henson 1985, Schneider 2002). Disturbances such as habitat degradation and loss can negatively affect Muskellunge populations because of their spawning habitat requirements and tendency to display spawning site fidelity (Weller et al. 2016). Therefore, a decrease in Muskellunge abundance could indicate that ecosystem health has declined, or that a site is not yet restored. By monitoring Muskellunge abundance, habitat use and movement patterns, the progress of restoration projects can be measured and potential environmental problems can be identified before they cause permanent damage.

Muskellunge in the St. Louis River Estuary

The St. Louis River Estuary (SLRE) is a designated Great Lakes Area of Concern (AOC), an area that has experienced severe environmental degradation, and is currently undergoing extensive restoration and remediation. Muskellunge were likely extirpated from the SLRE due to overexploitation and habitat degradation in the mid-19th century

(Minnesota Department of Natural Resources, unpublished data). As a result, they were reintroduced and stocked from 1983 to 2005 to meet AOC delisting goals and expand angling opportunities (Minnesota Department of Natural Resources 2007). Two strains were stocked: a strain of Minnesota (MN) origin and another of Wisconsin (WI) origin. Additionally, Muskellunge were selected as one of three SLRE AOC indicator fish species (Muskellunge, Walleye (*Sander vitreus)* and Lake Sturgeon) to monitor the effects of restoration (Steiger et al. 2015). Only mark-recapture estimates of Muskellunge abundance have occurred on the SLRE to date, leaving their movement patterns, habitat use, and adult strain composition unknown. Ancestry is important to account for when studying and managing Muskellunge movement and habitat use where multiple strains may be present because different strains can exhibit diverse behaviors (Diana et al. 2015).

Despite the importance of Muskellunge within the SLRE AOC as a valuable bio-indicator and game species, little is known of their spatial ecology, and how it varies with genetic strain, sex and season. In this study, I investigated how many genetically distinct groups, and what proportion of these groups, made up the SLRE Muskellunge population. I then used passive acoustic telemetry to quantify Muskellunge movement patterns, compare patterns by season, sex and strain, and determine if Muskellunge were utilizing restored sites.

Methods

Study Area

The SLRE is an economically and ecologically valuable freshwater ecosystem that is located in the southwestern corner of Lake Superior in the United States (Figure

1). It drives a major tourism sector, is the nation's largest inland port, and provides aquatic habitat for a diversity of native fishes and wildlife (Harter and Axness 2013, NOAA 2016). The SLRE runs roughly 35 river kilometers along the border between Wisconsin and Minnesota, from the Fond Du Lac Dam to Lake Superior. The upper estuary is naturalized, with little development along the banks, shallow aquatic habitat throughout, and maximum depths of approximately 1-3m. The lower half of the estuary largely consists of industrial development and shipping channels (that are regularly dredged down to 9.7m depth ["St. Louis River Estuary" n.d.]) that are flanked by shallow aquatic habitat. Water flows into Lake Superior through two connecting entry canals, which influences water temperature of the lower estuary because of the cold Lake Superior waters.

The SLRE's AOC designation occurred after years of severe environmental degradation from dredging shallow aquatic habitat, filling wetlands, and discharging industrial wastes into the river. With the ultimate goal of delisting the AOC by 2025, millions of dollars in restoration efforts are already improving water quality, fish and wildlife populations, habitat quality and availability, and recreational opportunities (Steiger et al. 2015). Although almost one-third of the SLRE has been filled or dredged over the last 65 years, it continues to be a biologically rich freshwater system in the Great Lakes (Harter and Axness 2013). Common game fishes include Muskellunge, Northern pike (*Esox lucius*), Yellow perch, Walleye, Smallmouth bass (*Micropterus dolomieu*), Black crappie (*Pomoxis nigromaculatus*), and Channel catfish (*Ictalurus punctatus*) (MNDNR, unpublished data).

I used narrow sections of the river (i.e., "pinch points") to divide the study area into six sections: five within the SLRE itself and Lake Superior. Each section contained some type of previous, ongoing, or future restoration project site (Figure 1). Restoration activities include a variety of broadly grouped practices such as remediation (removal of non-native material or contaminated sediments), shoreline modification and creation (softening shoreline, recreating natural bathymetric contours), and the reestablishment of aquatic habitat (establishing emergent, submergent and riparian vegetation)(Steiger et al. 2015).

Fish Capture, Sampling, and Tagging

This study complemented the 2017 spring Muskellunge population assessment that was conducted by the MNDNR and WDNR. All Muskellunge were captured and sampled following the MNDNR Muskellunge sampling guidelines (Muskellunge Technical Committee 2017). Thirty, large-frame trap nets (1.5 x 1.8m frame, 19.05mm mesh, 30.5m lead line) were arranged throughout the SLRE in established locations and areas with known favorable spawning habitat (Figure 1). Trap nets were set during Muskellunge spring spawning from April 14th to May 11th, 2017 and checked every twenty-four hours, weather permitting.

All Muskellunge caught were transferred to a holding tank before being measured for total length to the nearest millimeter and weight to the nearest gram. Approximately 10 scales and a <2cm section of pectoral fin clip were collected for genetic and stable isotope analyses, respectively. Each fish was also marked with an internal passive integrated transponder (PIT) tag for individual identification (Muskellunge Technical Committee 2017).

Sixty mature Muskellunge were chosen to tag with the goal of equal numbers of both sexes and a representative sample of adult Muskellunge lengths. Adult Muskellunge are defined as at least 30 inches, or 762 mm, in length (Muskellunge Technical Committee 2017). The target mean length for males and females in the sample was based on sex-specific mean lengths from all previous Muskellunge assessments on the SLRE (1997 to 2014). Muskellunge larger than 1219mm were also chosen because they are considered as “trophy” sized individuals that are targeted by anglers. Muskellunge were tagged with coded acoustic transmitters (VEMCO, V16-4H, 16mm dia. x 68mm, 24g mass in air). Each tag had an output frequency of 69kHz, an estimated tag life of 5 years, and was powered by a lithium battery (158dB output power). Tags emitted short pulses at random, with a nominal delay of 60 seconds for 8 months during spring, summer and fall. The transmitters then shifted their ping rate to every 90 seconds during the 4 winter months to maximize tag lifespan. Muskellunge are also believed to exhibit reduced movement during this time of year (Miller and Menzel 1986, Pankhurst et al. 2016, Younk et al. 1996).

Muskellunge receiving acoustic tags were handled so as to reduce stress. Before surgery, all instruments and transmitters were sterilized with Nolvasan S (0.78% dilution in water) and Muskellunge were individually transferred to a separate tub and anaesthetized with 15mg/L of Aqui-S 20E (10% Eugenol). Fish remained in the holding tank until equilibrium was lost (Diana et al. 2015). Muskellunge were then transferred to a water-filled, sponge cradle and held upside down with their gills submerged. The fish's eyes were covered with a handler's wet hand for protection and to reduce stress. Transmitters were surgically implanted into the coelomic cavity through a 2-3cm incision. The incision was closed with 2-4 non-absorbable sutures (polyamide pseudo monofilament, 3/8 cutting needle) and surgeries lasted an average of 3.5 minutes (maximum 5 minutes). All tagged fish were marked with an external, individually numbered spaghetti tag (Floy manufacturing, Seattle, Washington) that was positioned laterally at the base of the dorsal fin. Muskellunge were monitored post-surgery in a holding tank, and released when they regained equilibrium. All fish were released approximately 400m to 1000m from their capture trap net to avoid immediate recapture (Jeramy Pinkerton and Dan Wilfond, MNDNR, personal communication).

Electric Fish Handling Gloves (Smith Root, pulsed DC) were also used to assure sedation and immobilization of Muskellunge for the duration of the surgery. The Electric Fish Handling Gloves transmitted a low amperage and low voltage electric current that ranged between 0.016 and 0.0063 amps and was independently controlled. The fish was immobilized when both electric gloves touched opposite ends of the fish, completing the electric circuit. Muskellunge recovered within a few minutes, if not immediately, when released from the gloves.

The pairing of chemical anesthesia and electroanesthesia has been successfully used to surgically implant transmitters in fish (Landsman et al. 2015), as well as using electroanesthesia alone (Wilson et al. 2017). Electroanesthesia has successfully sedated and immobilized a variety of species such as Muskellunge (Pankhurst et al. 2016), Lake

Trout (*Salvelinus namaycush*) (Faust et al. 2017) and Striped Bass (*Morone saxatilis*) (Jennings and Looney 1998). Studies show that electroanesthesia provides rapid induction and recovery times (Faust et al. 2017) in addition to the same, if not lower, stress levels in fish when compared to chemical anesthetics (Sattari et al. 2009, Ward et al. 2017b).

Genetic Laboratory Analysis

DNA for genetic analysis was extracted from scale or tissue samples by boiling in a chelating resin and amplified by polymerase chain reaction (PCR) using methods described by Miller et al. (2009). Thirteen microsatellite loci from Sloss et al. (2008) were used to genotype and determine the ancestry of all Muskellunge sampled in the population assessment, including the 60 acoustically tagged individuals (all loci reported in Sloss et al. [2008] except EmaA5). These loci effectively distinguished multiple Muskellunge strains across Minnesota populations, including the SLRE (Miller et al. 2012).

Passive Acoustic Telemetry Array

Tagged Muskellunge were tracked via an array of 40 acoustic receivers (VEMCO, 69kHz) that were deployed in March and April 2017 in the SLRE and western Lake Superior (Figure 1) (Table A1). Working with agency biologists, we deployed two types of acoustic receivers: the VR2W (32 receivers) and VR2Tx (8 receivers). Both receivers had the same capabilities, but the VR2Tx also recorded descriptive data (e.g. temperature, tilt and noise values) and could communicate information through a transponder while still deployed. Each receiver was positioned vertically, with the hydrophone ~0.5m above the river or lake floor. Acoustic receivers were moored to a rebar spike that was secured within a 30 to 40kg concrete anchor. These anchors were then attached to a smaller, 14kg anchor by galvanized wire rope to aid receiver retrieval.

We distributed acoustic receivers unevenly throughout the SLRE, with a priority on AOC-restored sites or potential restoration sites. We deployed two to three receivers in each of the six river pinch points so that we could identify transitions between river sections (Figure 1). The majority of receivers used at pinch points were VR2Tx because of their additional capabilities. All receivers were deployed at depths ranging from 1m to 20m, and in a mixture of habitats such as SAV, floating leaf vegetation (FLV), and bare substrate.

Receivers were retrieved, downloaded, fitted with new batteries, and redeployed in the same location in fall 2017 and 2018. However, eleven receivers in depths generally <1.8m were retrieved in late September 2017 for the winter to prevent ice damage or loss, and then redeployed in April 2018. In mid-June 2017, two receivers (serial number (SN) 103398 and 103403) stopped gathering data due to battery and equipment failure, respectively. A new receiver was deployed in early September 2017 to replace the faulty equipment (SN 103403) and new batteries were placed in the other receiver (SN 103398) (Table A1).

Acoustic receiver data were uploaded to the Great Lakes Acoustic Telemetry Observation System (GLATOS) database of tag detections (project code: SLRMU). GLATOS supports collaborative acoustic telemetry research in the Great Lakes by making all transmitter and acoustic receiver data available to individual project researchers (GLATOS n.d.).

Range Testing

Receiver detection range and variability are important to understand because they are influenced by tag power, line of sight, and natural and manufactured environmental noise (Huveneers et al. 2016, VEMCO 2017a). For instance, detection range may be lower in areas with turbid water, variable bottom topographically, fast current, or wave turbulence (VEMCO 2017a). Therefore, receiver detection range should be accounted for in analyses when using raw detection data and considered when interpreting all results. Detection ranges are based on probabilities rather than fixed distances because conditions that affect detections can differ by location and time (VEMCO 2017a). Detection range is commonly defined as the maximum distance from a receiver that some proportion of tag transmissions can be detected (Kessel et al. 2014).

Twelve range tests were conducted throughout the SLRE in the summer of 2016 and 2017 and analyzed with VEMCO Range Test software (Version 1.10.29.0, https://vemco.com/vemco-range-test-software/) (Table B1). Two methods were used to assess detection range. Short-term detection range tests were conducted using a fixed testing transmitter, or “sentinel tag” (VEMCO, V16 fixed), at set distances from a receiver (Bertelsen and Hornbeck 2009, Payne et al. 2010). These tests were conducted from an anchored boat with the sentinel tag placed at different distance intervals from seven receivers for 10-minute periods. The second, more comprehensive method involved a single, fixed sentinel tag combined with receivers set at regular distance intervals (Bertelsen and Hornbeck 2009, Topping and Szedlmayer 2011). Minnesota DNR researchers conducted five 5-day detection range tests before the study began.

Data Analysis

Genetic analysis to determine ancestry

I used a Bayesian clustering method in the software program STRUCTURE (Pritchard et. al, 2000; version 2.3.4) to determine the number of genetically distinct sources (K) that contributed to the Muskellunge population in the SLRE, and the proportion of each individual's ancestry that originated from these sources. Archived genetic data from Minnesota and Wisconsin Muskellunge strains were included to associate distinct sources with known stocked strains. STRUCTURE analysis evaluated ten iterations at K=1-5 using a burn-in period of 50,000 followed by 200,000 Markov Chain Monte Carlo repetitions. The model assumed default options with possible admixture, correlated allele frequencies, and no prior population information. The best-supported K was determined by likelihood values and the post-hoc delta K method (Evanno et al. 2005) within STRUCTURE Harvester (Earl and vonHoldt 2012).

Estimated proportions of ancestry attributed to distinct strains were used to classify individuals categorically into likely ancestral groups, either pure strain or hybrid crosses between strains. Ancestry composition thresholds for classifying individuals were chosen based on ten STRUCTURE replications of simulated genotypes generated from the archived genetic data from source strains (Table C1). A chi-squared test was used to determine if there was a significant difference in proportion of strain groups between tagged and untagged individuals.

Acoustic data to assess movement and habitat use

The study period began when all Muskellunge were acoustically tagged and continued until the first day that acoustic receivers were downloaded (May 9th 2017-August 6th 2018 or 455 days). All analyses were performed using R version 1.1.423 (R Core Team 2016). I used VUE software (VEMCO version 2.3.0) and the glatos package (Holbrook et al. 2018) to identify false detections (based on the time between individual transmitter detections [Pincock 2012]) and correct for each receiver's internal time lag (VEMCO 2017b).

Population movements

I calculated the residence time of each individual within each study section of the SLRE to evaluate if sex, strain, or season affected movement patterns. Zones were assigned per individual with one hour time bins with the xts package (Ryan and Ulrich 2018) and Last Observation Carried Forward (LOCF) function in R. Pinch point receivers acted as dividers by identifying when an individual moved from one section to another. If an individual visited more than one zone within an hour, then their time was split evenly between the zones within that one-hour time bin. An initial subset of telemetry data were used to determine pinch point efficiency by dividing the number of transitions missed by the number of transitions at each pinch point. Transitions missed were identified when an individual was detected in a new section without being detected on a pinch point receiver. I used ANOVAs to evaluate the differences in residency time in each section with sex, strain (categorical), and season. A Tukey–Kramer HSD post hoc test was used to determine the difference between means when an effect was significant. Seasons were defined as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February).

Lake Superior use

I used a random forest model (Breiman 2001, Cutler et al. 2007) via the randomForest package (Liaw and Wiener 2002) to determine if Muskellunge presence in Lake Superior varied by sex, strain, or length. I determined whether a Muskellunge was using Lake Superior with the LOCF residency code. An individual was considered to have used Lake Superior if it spent at least one full one hour time bin in Lake Superior.

Habitat and restored area use

I used a Negative Binomial Hurdle model with the pscl package (Jackman 2017) to determine if habitat characteristics of each receiver site within the SLRE influenced Muskellunge occupancy or number of transmitter detections. I used this model because of its ability to successfully handle over dispersion and zero-inflation due to indistinguishable true and false zeros (Martin et al. 2005, Warton 2005). However, I was not able to account for repeated measures within the Hurdle model due to our small sample size. To determine if the repeated measures were influencing our result, we also fit Binomial and Poisson Generalized Linear Mixed Effects models containing the same variables, but with individual as the random effect. The response variable was the number of detections per individual per hectare meters (a measure of volume) within a detection radius for a given receiver. Detection radius was based on range testing. Usable area within a detection range was taken into account because some receivers were within the detection radius of shore or other structures so a full circular area was not available. For each individual, receivers were excluded from analysis if they were in river sections that individual never visited. Average depth, FLV, SAV, and restoration status (i.e., restored, proposed for restoration but not yet restored, and natural riverine habitat) were explanatory variables. Vegetation and depth data were obtained from the United States Environmental Protection Agency (Jonathon Launspach, USEPA, unpublished data). Average depth and proportion of SAV and FLV within the usable area of the detection radius of each receiver was calculated within ArcMap 10.6.1. Restoration activities consisted of broadly grouped practices ranging from soil remediation, shoreline modification and creation, and the reestablishment of aquatic habitat (Steiger et al. 2015).

Results

Sixty Muskellunge were surgically implanted with acoustic transmitters (Table D1). All recaptured individuals in 2017 and 2018 had healed incisions. The sample was composed of thirty females ($\bar{x}$ = 1123mm, 905mm-1280mm range) and twenty-eight males ($\bar{x}$ = 993mm, 791mm-1132mm range), and two individuals of unknown sex. The length distributions of the tagged sample and the total sample population were very similar (Two-sample Kolmogorov-Smirnov test, $P = 0.91$). Each individual logged 4,161 – 230,180 detections, with an average of 109,546 over ~15 months or 455 days. Every receiver within the SLRE array detected at least one tagged Muskellunge. Two of our Muskellunge were also detected by four United States Fish and Wildlife Service's (USFWS) receivers on Lake Superior's south shore (Figure 1). Receiver SN 103398 did not collect data from January 4, 2018 to September 26, 2018 due to equipment failure. No data were downloaded from receiver SN 127689 from April 27, 2018 to September 26, 2018 because it could not be recovered in fall 2018. Seven individuals were removed from analyses because their status became unknown during the project (Eilers 2008). Individuals were excluded if they were consistently detected at a single receiver or were not detected for at least one year of the project. These detection patterns may be due to transmitter failure, natural or fishing mortality, or movements beyond an acoustic array.

Range tests showed that high detection rates could often be achieved between approximately 100 and 400m. With some exceptions, these distances provided detection probabilities greater than 50%, which is a suggested minimum threshold of where tags can be reliably detected under poor conditions (VEMCO 2107a). An intermediate detection range of 300m was chosen for measuring Hurdle model habitat values, which provided relatively high detection probability in many situations (Table B1).

Genetic ancestry

Genetic data best supported two genetically distinct groups (K=2) (Figure C1), consistent with the known stocking of Minnesota and Wisconsin Muskellunge strains (Table C2). Minnesota strain ancestry ranged from 0.02 to 0.99, with many individuals having estimates near each extreme, and another large group having intermediate estimates (Figure 2). Guided by STRUCTURE analyses of simulated data (Table C1), individuals were classified into ancestral groups based on their estimated Minnesota strain ancestry: >0.875 = Minnesota strain, <0.125 = Wisconsin strain, intermediate values = strain hybrid. Of the 60 tagged Muskellunge, 29 (48.3%) individuals were classified as Minnesota strain, 14 (23.3%) as Wisconsin, and 17 (28.3%) as hybrid. Out of 258 successfully genotyped individuals from all trapped individuals, 107 (41.5%) were categorized as Minnesota strain, 56 (21.7%) as Wisconsin, and 95 (36.8%) as hybrid. Tagged fish slightly overrepresented Minnesota strain and underrepresented hybrids in the total adult population; however, there was no significant difference between the tagged and total adult population sample (χ=1.9176, df=2, P=0.3833).

Movement patterns

Tagged individuals exhibited highly variable movements over time. For example, nine percent (5 individuals) stayed within two sections, while 30% (16 individuals) spent time in all six study sections. More than 60% of the tagged Muskellunge exhibited similar movement patterns in 2017 and 2018 (Figure 3, Supplementary materials). Similar between year movements consisted of Muskellunge moving past the same receivers within similar time periods in the spring and summer. Despite this individual variability, the majority of the tagged population showed seasonal shifts in movement, moving upstream in spring, dispersing downstream (and some individuals moving into Lake Superior) throughout summer, and returning to the middle river during fall and winter (Figure 4 and 5; Table 2). Males (P = 4.37E-7 based on M-F pairwise comparison) and WI strain individuals (P = 9.52E-4 based on WI-MN pairwise comparison) were more likely to spend time in section one (19 and 10 days more on average per male and WI strain, respectively). Hybrids used section 2 most often (P = 3.17E-6 for MN-H and WI-H pairwise comparisons; 12 days more on average per hybrid) and section 4 was most often used by hybrid and WI strain (P = 9.87E-6 for MN-H and MN-WI pairwise comparisons). Within sections five and six, summer use was greatest (P = 0.0026 and P = 4.27E-13 for all seasonal pairwise comparisons, respectively). Females spent on average

10 more days in section five than males (*P* = 0.001 based on M-F pairwise comparison). Lastly, MN strain spent on average 10 days more in section six (Lake Superior) than WI and hybrid individuals (*P* = 2.33E-5 for MN-H and MN-WI pairwise comparisons). Pinch points between river sections were fairly effective overall, with only ~10% of transitions resulting in both pinch point receivers being missed (Table F1). Pinch point effectiveness varied making estimates of residency times highly accurate for upper river sections 1 and 2 and section 6 (Lake Superior) but slightly less certain for sections 3, 4 and 5.

Lake Superior use

Forty-seven percent (25) of tagged Muskellunge visited Lake Superior (n=24 in 2017 and n=22 in 2018), with 21 individuals repeating their lake use both years. Individuals spent an average of 50.8 days (~1 day to 175 days, median 43.3 days) in Lake Superior per year, excluding an individual that never returned to the SLRE (Figure 6). The random forest model correctly assigned individuals that used Lake Superior 72% of the time. Strain appeared to be an important driver of Lake Superior use, while sex and length were weak predictors (Figure 7 and Figure 8). Eighty percent of the individuals that used Lake Superior were Minnesota strain.

Two individuals made long-distance movements to a USFWS acoustic receiver array (Figure 1). Fish 1 travelled at least 90km to Bark Point, Lake Superior, and returned to the SLRE in 2017 and 2018. Fish 1 also arrived at Bark Point and returned to the SLRE in 2018 within 7 days of its 2017 arrival and departure times. Fish 13 migrated at least 150km to Chequamegon Bay, Lake Superior in October 2017 and did not return to the SLRE during the project. This individual was not detected from December 1, 2017 to October 17, 2018, and reappeared on the Chequamegon Bay acoustic receiver array on October 18, 2018 (74 days after our study concluded).

Habitat and restored area use

The two-stage Hurdle model distinguished the probability of Muskellunge being detected in an area, a binary occupancy measure (n=1363 samples of detections per individual per receiver), from the frequency at which they were detected in an area, an occurrence measure (n=851 samples of detections per individual per receiver). Muskellunge were more likely to occupy a restored or soon-to-be restored site (i.e., a poor quality site) than a natural riverine site (*P* = 4.08E-6 and *P* = 0.0002, respectively). However, the frequency of detections was lower in poor quality areas (*P* = 0.003) and higher, but similar between restored and natural riverine areas. Muskellunge were less likely to occupy greater depths (*P* = 1.25E-10) and areas with SAV (*P* = 1.74E-27) and FLV (*P* = 0.012). However, detection frequency only decreased with depth (*P* = 0.0003; Theta = 0.0491, Table 1). The Binomial and Poisson Generalized Linear Mixed Effects model results were almost identical to the Hurdle model results (Table E1).

Discussion

Passive acoustic tracking of adult muskellunge in the SLRE revealed highly variable individual movements, but trends in population movements driven by season, sex, and strain. Almost 50% of the tagged Muskellunge utilized Lake Superior, a behavior that was most common among the MN strain. Additionally, restored areas had a similar number of detections as natural riverine sites, suggesting that restored areas are functionally similar to natural riverine habitat (i.e., Muskellunge are benefiting from this restoration). Furthermore, non-restored sites had fewer detections, indicating that Muskellunge presence is briefer when they use degraded sites. The probability of a Muskellunge being detected also decreased with depth, SAV and FLV, but this is not consistent with known Muskellunge habitat preferences (e.g., [Dombeck et al. 1984, Miller and Menzel 1986, Cook and Solomon 1987, Diana et al. 2015]).

Despite the variability in individual movements, many SLRE Muskellunge moved similarly throughout the year. Further, the generally consistent patterns for each individual between 2017 and 2018 suggest individual movements are persistent from year to year. In the spring, large upstream movements were likely related to spawning activities as observed in other systems (Dombeck 1979, Younk et al. 1996, Weeks and Hansen 2009, Morrison and Warren 2015). Dombeck (1979) believed that increased water temperature and dissolved oxygen (DO) levels initiated spawning activities. Spring coincides with warming water temperatures that reach ideal spawning temperature first in shallow habitats. The upper river of the SLRE contains many shallow, vegetated bays and wetlands, which would be suitable for spawning (Dombeck 1979, Dombeck et al. 1984). Males also spent significantly more time in the upper river across all seasons, which may indicate that males arrive early to their staging grounds in the fall and winter, and remain in the upper river longer than females during spawning season. Younk et al. (1996) found that male Muskellunge arrived to spawning areas first and lingered, whereas females staged away from spawning areas and only briefly entered spawning areas to spawn. This behavior has also been observed in Lake Sturgeon (Bruch and Binkowski 2002) and Walleye (Hayden et al. 2014).

Many SLRE Muskellunge moved downstream after the spawning season. Almost half of the tagged Muskellunge moved into Lake Superior, where some individuals also made long-distance movements. Similarly, almost half of tagged Muskellunge in the St. Lawrence River migrated to Eastern Lake Ontario during the summer (Farrell et al. 2003). Long distance migrations have been observed (Crossman 1990, Curry et al. 2007, Kerr and Jones 2017) up to 156km (Curtis Wagner, OH DNR, personal communication) in addition to the two individuals in this study. Other species in the Great Lakes exhibit this behavior as well. Hayden et al. (2014) reported Walleye migrating after spawning from the Saginaw River to Lake Huron, with some individuals migrating more than 350km, before returning back to the river for spawning.

Muskellunge commonly exhibit collective fall movements followed by relatively sedentary behavior in the winter (Dombeck 1979, Younk et al. 1996, Morrison and Warren 2015). Dombeck (1979) found that Muskellunge moved toward areas with higher levels of DO in overwintering grounds. Similarly, Striped Bass and Smallmouth Bass exhibit peak movement rates in the fall when returning to tributaries followed by relatively sedentary behavior in the winter months (Langhurst and Schoenike 1990, Young and Isely 2002, Able and Grothues 2007). These movements were driven by warmer water temperatures and increased DO levels in tributaries (Young and Isely 2002, Able and Grothues 2007). My study revealed that Muskellunge used the middle river (section 3) most during winter, suggesting that this is an important overwintering area. A number of tributary streams and rivers, such as the Pokegama River, flow into this section of the SLRE. Tributaries are important overwintering habitat for stream (Koizumi et al. 2017) and lake fishes (Jepsen and Berg 2002), which use these areas as thermal refuges, for their coarse habitat, or slower currents (Koizumi et al. 2017).

The spatial ecology of the SLRE Muskellunge population was influenced by strain. Different strains of Muskellunge have been shown to have diverse spawning behaviors (Dombeck 1979, Kapuscinski et al. 2013) and different maturation timing and length-weight relationships (Younk and Strand 1992, Margenau and Hanson 1996). I speculate that the SLRE WI and MN strains are predisposed to different habitats and waterbodies. The Minnesota strain originates from Leech Lake, a large lake (41,700 ha) with an irregular shoreline and numerous bays. The Wisconsin strain originates from small lakes and rivers, mostly in the Chippewa River drainage (Paul Piszczek, WDNR, personal communication). These vastly different environments may have selected for different behaviors between the strains.

The MN strain may have a genetic tendency to explore and move larger distances than the WI strain and hybrid. Exploratory behavior may enhance foraging opportunities (Farrell et al. 2003, Kerr 2016), which could lead to increased growth or reproductive success (Fraser et al. 2001). If prey are migratory, then Muskellunge may follow them into deeper water (Kerr 2016). For example, the Muskellunge that migrate upstream from their spawning grounds in the St. Lawrence River to Eastern Lake Ontario likely exploit foraging opportunities that are related to habitat or prey (Farrell et al. 2003). Similarly, Diana et al. (2015) speculated that Muskellunge migrated in summer to maximize feeding opportunities, specifically on schools of cisco in deeper waters. Dombeck (1979) believed that increased feeding during summer and fall contributed to gonadal maturation. The majority of SLRE Muskellunge that moved long-distances and used Lake Superior were MN strain individuals, which also tended to be larger than WI and hybrid individuals. Additionally, the MNDNR reported a high percentage of MN ancestry (largely pure MN strain) in juvenile (age-0) Muskellunge in years after stocking stopped (Loren Miller, MNDNR, unpublished data), indicating that MN strain were more successful at reproduction than the WI strain.

From a management perspective, there is a need to understand spatial ecology to assess management and stocking program goals. Muskellunge fisheries are managed for recreational fishing and often as a trophy fishery, like in the SLRE (Wingate and Younk 2007). Differences in behavior between strains may affect the development of SLRE versus Lake Superior Muskellunge fisheries. If stocking resumed, the use of WI strain could best enhance the SLRE fishery because few of this strain went to Lake Superior. However, a possible trade-off exists between abundance and fish size in that the WI strain was generally smaller than the MN strain, although age differences between strains could have been a factor (fish were not aged). SLRE hybrids were also less likely to be in Lake Superior. Ongoing natural reproduction, especially if stocking were to resume with both strains, could result in a greater hybrid proportion in the population and less Lake Superior use. Alternatively, stocking more MN strain could increase the proportion of Muskellunge in the population that uses Lake Superior, which also consists of the larger individuals, and could therefore support a Lake Superior trophy Muskellunge fishery.

Currently, WI and MN agency biologists are discussing supplemental Muskellunge stocking (J. Pinkerton, MNDNR and P. Piszczek, WIDNR. Personal communication). If stocking occurs with a new strain, I recommend acoustic tracking and other studies to determine how this strain behaves and performs (i.e., growth and return to anglers) in the SLRE. These findings have important implications for many fisheries (e.g., Muskellunge, Lake Trout, Lake Sturgeon, etc.) throughout the Great Lakes, especially where multiple strains may be present and are sustained through stocking.

Restoration and remediation projects in the SLRE have worked toward reestablishing aquatic habitat, removing contaminated soils, softening the shoreline and recreating natural bathymetric contours (Steiger et al. 2015). This study found that Muskellunge were detected more often in restored and natural riverine areas than in non-restored sites. The Binomial and Poisson Generalized Linear Mixed Effects models results were almost identical to the hurdle model results, which provided further support that Muskellunge were utilizing restored areas and natural river habitats more often than poor quality areas. Restored sites had similar numbers of detections compared to natural riverine sites, suggesting that restored areas supported Muskellunge as effectively as natural river habitat. Likewise, Tupper and Able (2000) concluded that Striped Bass utilized a restored marsh similar to a control marsh within Delaware Bay, New Jersey. Rous et al. (2017) also determined that Northern Pike and Yellow Perch had a higher daily site fidelity in restored sites than non-restored sites across all seasons in the Toronto Harbour of Lake Ontario, Canada. Conversely, Muskellunge have been documented repeatedly using degraded habitat during spawning season, likely due to spawning site fidelity (Weller et al. 2016, Diana et al. 2017). Continued and finer-scale evaluation of habitat use during this critical time will be needed to better understand how restoration projects can enhance Muskellunge sustainability.

The conclusion that Muskellunge are more likely to occupy restoration sites (completed and uncompleted) than natural riverine sites could be due to site placement. Many restoration and natural riverine sites are located in bays and flats, which are known to support suitable Muskellunge habitat (Miller and Menzel 1986). However, natural riverine sites are also along a regularly dredged channel, which may deter Muskellunge. Also, restoration sites are chosen because they are highly degraded, not for the sole purpose of benefiting Muskellunge. For instance, the soil in a non-restored site may be highly contaminated, but there may also be suitable coarse woody habitat and aquatic vegetation on top of that soil. In that case, Muskellunge may not be negatively affected by this non-restored site (at least behaviorally).

The finding that Muskellunge detections decreased with depth, SAV and FLV in the SLRE is inconsistent with known Muskellunge habitat preference. Seasonal movements are commonly associated with areas of different depths. In the spring, Muskellunge often occupy shallow habitats (Dombeck 1979, Diana et al. 2017). Some researchers have shown that Muskellunge inhabit deeper water in the summer (Diana et al. 2015, Spooner 2016), while others argue that they occupy shallow water from mid to late summer (Dombeck 1979, Younk et al. 1996) before moving to deeper waters in the fall and winter (Miller and Menzel 1986, Gillis et al. 2010, Morrison and Warren 2015). Future work would benefit from assessing restored habitat use during Muskellunge spawning season and using tags that indicate depth at the time of detection. Additionally, many studies confirm that Muskellunge use SAV and FLV for foraging and spawning activities (Dombeck et al. 1984, Miller and Menzel 1986, Cook and Solomon 1987, Diana et al. 2015). The lower frequency of detections at varying depths and around vegetation may have been partly due to transmitter signal interference, especially during the summer when vegetation can be dense.

Attempts to better understand receiver detection range in the SLRE with range testing was informative, but still contained uncertainty. Variability in detection range is a common problem in biotelemetry studies (Kessel et al. 2014). Many environmental factors such as vegetation, wind speed, motorboat traffic and rain affect detection range (Kessel et al. 2014, Mathies et al. 2014). Range also varies among water bodies, fish behavior and receiver array design (Shroyer and Logsdon 2009). Detection interference likely occurred during this present study due to high boat traffic and thick vegetation in some areas. Range tests determined that vegetation interfered with and sometimes substantially reduced transmitter detections. The VR2Tx receivers also indicated that moderate to high levels of background noise, likely from shipping traffic, occurred during the study, which has a known negative effect on acoustic communication (Mathies et al. 2014). To minimize biases related to detection uncertainty in the SLRE, I analyzed data by section based on pinch-point passage to evaluate seasonal movement patterns and Lake Superior use. Future studies would benefit from longer-term range tests throughout a biotelemetry project.

This study provided baseline information regarding Muskellunge movement patterns, restoration site use, and related habitat use within the SLRE AOC. Results were based on only 15 months of data. For further confirmation, multiple years of data are needed to verify trends. All transmitters will remain active until approximately April 2022, and a subset of receivers will continue to collect acoustic telemetry data during that time. I recommend deploying some receivers strategically in restored and non-restored sites to better understand if a restoration project is effective. For instance, more than one receiver could be deployed to better detect tagged individuals throughout an entire restoration site. A receiver could also be altered to block transmitter signals from 180 degrees of its 360 degree range, creating a hemi-directional receiver (see [Kendall et al. 2016]). By facing a hemi-directional receiver toward a restoration site, detections would be limited to fish located within a restoration site. Although this study compared use in both restored and non-restored sites, it does not include multiple years of data and lacked before and after restoration data for any site. Continuing to analyze telemetry data in the SLRE pre- and post- restoration will allow managers to inform restoration practices and identify opportunities for habitat enhancement, creation, and restoration in the SLRE.

Future work would also benefit from linking telemetry data with agency mark-recapture data. Combining these data will improve understanding of Muskellunge movements relative to where they are managed to better develop population estimates and management practices. In the past, MNDNR has used a closed population model (no births, immigration, deaths, emigration) to estimate Muskellunge population size (Pine et al. 2012). My acoustic telemetry study suggests that this assumption was violated (e.g., Lake Superior migrations) which may have biased estimates of SLRE Muskellunge population size. Future population size estimates should use an open population model to account for individuals that leave the SLRE (Pine et al. 2012). Further, MNDNR has recently explored using anglers to assist with recaptures for population estimates (Miller et al. 2015, Ward et al. 2017a). In this study system, anglers focus efforts in the SLRE itself and much of the angling occurs during the summer when Muskellunge make most use of Lake Superior. Angler samples should be treated with caution because the strain differences in use of the lake assure the entire marked population is not equally susceptible to recapture, another violation of assumptions for population estimation. Researchers would also benefit from a study incorporating telemetry and stable isotope data to investigate the influence of prey on movement patterns and estimate the contribution of their dietary sources. Lastly, more work is needed to determine if juvenile Muskellunge (<763 mm) exhibit similar patterns of movement and habitat use.

This study demonstrated that Muskellunge movements are related to season, sex and strain in the SLRE and southwestern Lake Superior. Muskellunge appear to benefit from the AOC restoration projects by similarly using restored and natural riverine areas. Restoration projects also appear to be restoring habitat function in degraded areas. Overall, my results provide a more thorough understanding of Muskellunge ecology in the SLRE and southwestern Lake Superior, while also giving insight on restoration project progress. The maintenance of this project by the MNDNR will continue to increase our knowledge of Muskellunge ecology to guide future management and restoration efforts of Muskellunge in the SLRE and other areas of the Great Lakes.

Table 1. Negative Binomial Hurdle model results for the number of muskellunge detections per individual per hectare meters within the St. Louis River Estuary. A Hurdle model is a two-stage model assessing the probability of detection (zero hurdle model) and the number of detections (count model) at a receiver. Predictor variables were proportion of submerged aquatic vegetation (SAV), average depth, proportion of floating leaf vegetation (FLV), and restoration status (restored [n=3], proposed for restoration but not yet restored [n=6], and natural riverine habitat [n=24]). Depth, SAV, and FLV were calculated within the area available of a 300m radius of each receiver.

Count model (truncated negbin with log link):

Coefficient	Estimate	p-value
(Intercept)	-7.6304	0.947
SAV	-0.4383	0.436
Depth	-0.4337	3.14E-12
FLV	0.19057	0.612
Not restored	-0.7233	0.003
Restored	0.69041	0.073
Log(theta)	-14.721	0.899

Zero hurdle model (binomial with logit link):

Coefficient	Estimate	p-value
(Intercept)	4.95271	1.90E-23
SAV	-4.7841	1.74E-27
Depth	-0.3944	1.25E-10
FLV	-0.655	0.012
Not restored	0.65939	1.60E-04
Restored	1.12285	4.08E-06

Table 2. ANOVA and Tukey–Kramer HSD post hoc test results used to evaluate the differences in residency time (days) in each section with sex, strain, and season. Sex included males (M) and females (F) and strain included Minnesota (MN), Wisconsin (WI), and hybrid (H) genetic groups. Seasons were defined as spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February).

						Effect size	
River section	**Variable**	**ANOVA p-value**	**Tukey pairwise comparison**	**Tukey p-value**		**Category**	**Mean number of days**
1	Sex	4.37E-07	M-F	4.00E-07	*	M	28.8
						F	9.8
	Strain	0.000952	MN-H	0.078		WI	25.6
			WI-H	0.335		H	23.3
			WI-MN	2.15E-03	*	MN	15.6
	Season	0.353717	—				
2	Sex	0.1707	—				
	Strain	3.17E-06	MN-H	1.23E-05	*	H	19.9
			WI-H	4.41E-05	*	MN	7.4
			WI-MN	0.817		WI	7.3
	Season	0.0469	Spring-Fall	0.133		Spring	15.1
			Summer-Fall	0.974		Summer	10.1
			Winter-Fall	0.963		Fall	8.8
			Summer-Spring	0.300		Winter	7.4
			Winter-Spring	0.041	*		
			Winter-Summer	0.801			
3	Sex	0.549	—				
	Strain	0.314	—				
	Season	0.685	—				
4	Sex	0.1935	—				
	Strain	9.87E-06	MN-H	2.86E-05	*	H	18.0
			WI-H	0.122		WI	10.7
			WI-MN	0.045	*	MN	6.2
	Season	0.0279	Spring-Fall	0.925		Summer	14.8
			Summer-Fall	0.230		Fall	9.2
			Winter-Fall	0.847		Spring	7.3
			Summer-Spring	0.058		Winter	6.8
			Winter-Spring	0.997			
			Winter-Summer	0.035	*		

Table 2. (continued)

River section	Variable	ANOVA p-value	Tukey pairwise comparison	Tukey p-value		Effect size: Category	Effect size: Mean number of days
5	Sex	0.0011	M-F	0.001	*	F	21.1
						M	11.1
	Strain	0.34325	–				
	Season	0.00262	Spring-Fall	0.979		Summer	26.3
			Summer-Fall	0.005	*	Winter	13.7
			Winter-Fall	0.978		Spring	13.7
			Summer-Spring	0.017	*	Fall	12.0
			Winter-Spring	1.000			
			Winter-Summer	0.018	*		
6	Sex	0.812	–				
	Strain	2.33E-05	MN-H	0.014	*	MN	13.6
			WI-H	0.991		H	3.5
			WI-MN	0.008	*	WI	2.9
	Season	4.27E-13	Spring-Fall	1.000		Summer	27.9
			Summer-Fall	0.000	*	Fall	5.2
			Winter-Fall	0.998		Spring	5.0
			Summer-Spring	0.000	*	Winter	4.6
			Winter-Spring	0.999			
			Winter-Summer	0.000	*		

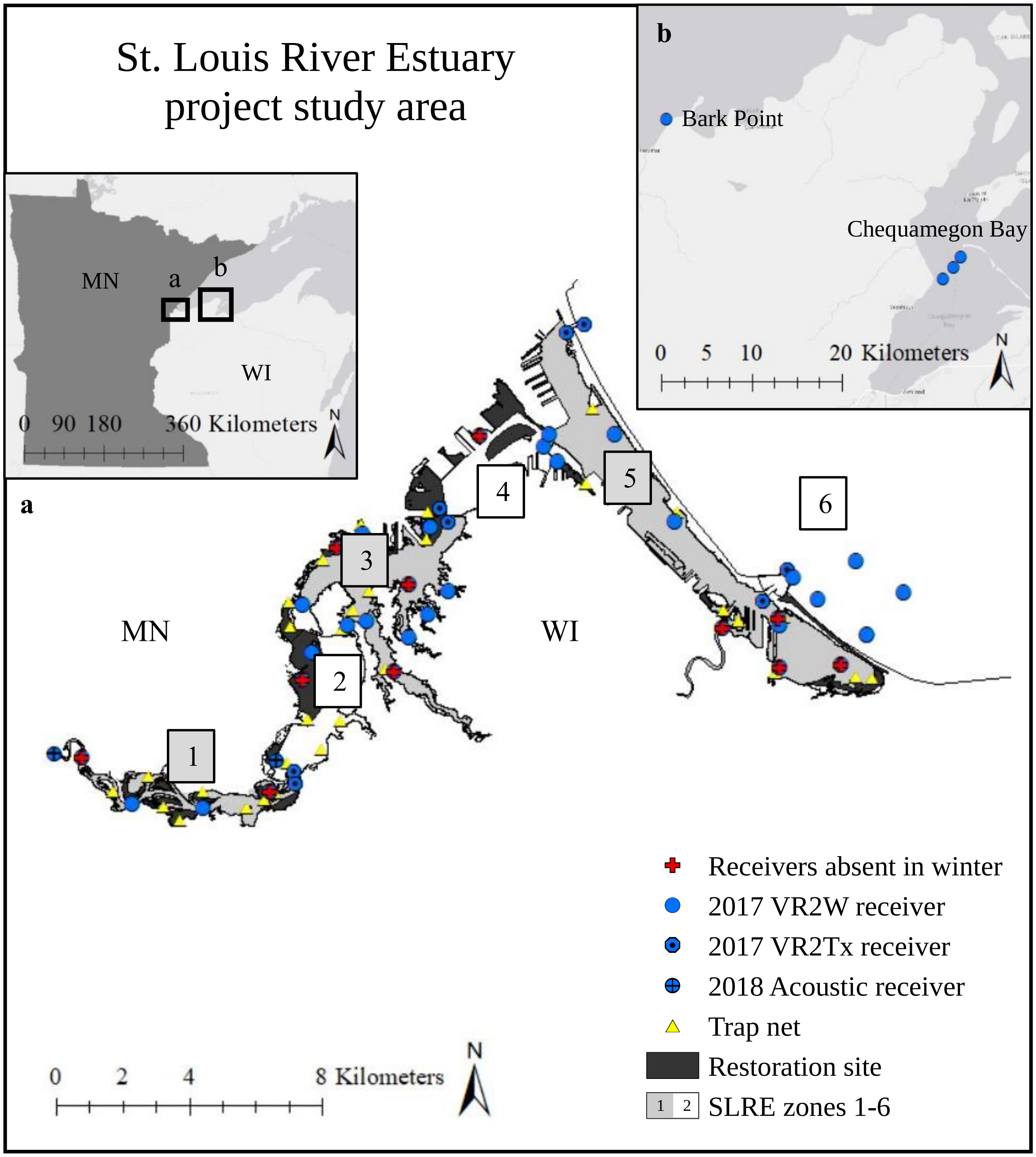


Figure 1. Map of the St. Louis River Estuary (SLRE) receiver array, trapping locations, restoration sites, six river zones (a) and a portion of the United States Fish and Wildlife Service's receiver array that detected tagged SLRE Muskellunge (b). The SLRE is a border water between Minnesota (MN) and Wisconsin (WI) that eventually flows into the southwestern corner of Lake Superior.

a.

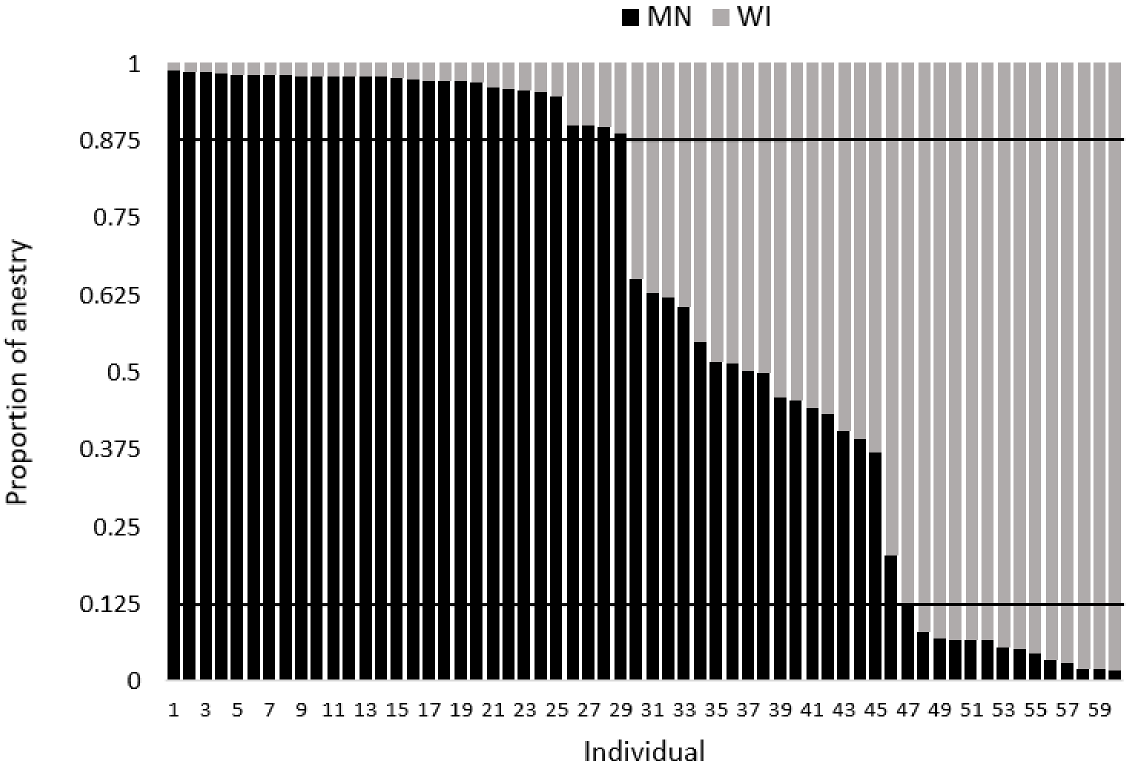
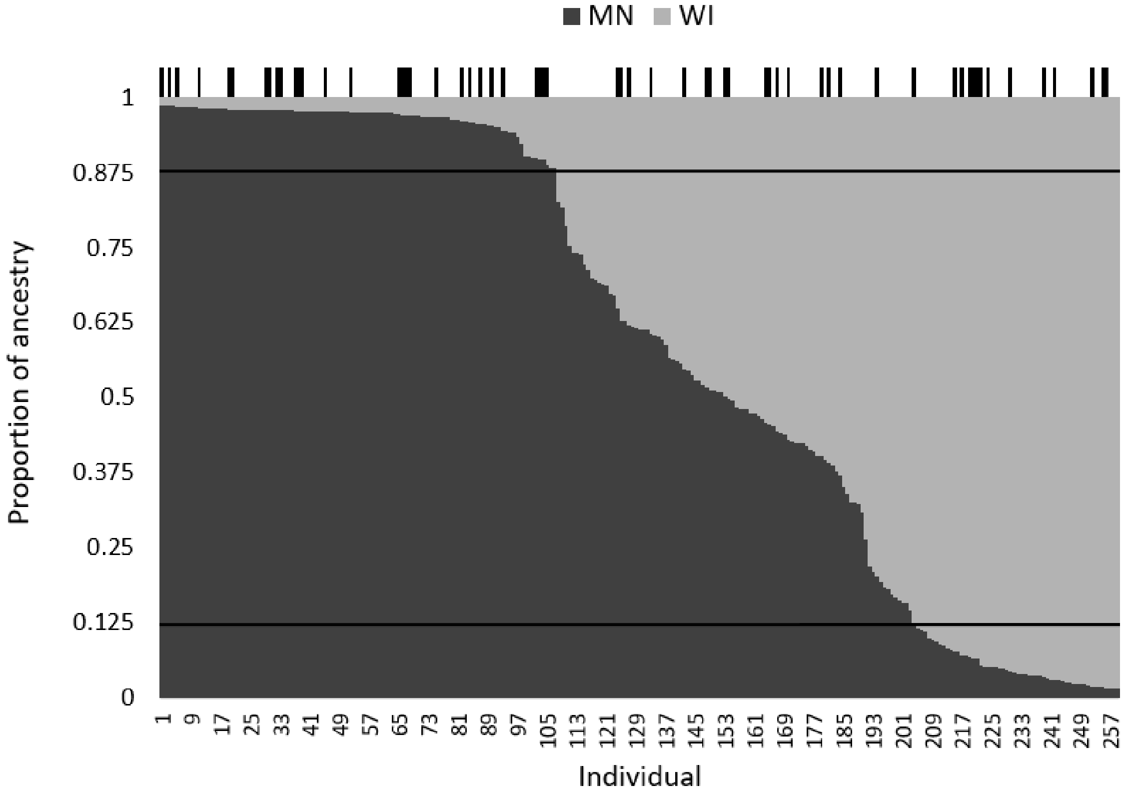


Figure 2. Proportion of ancestry for 60 acoustically tagged individuals (a) and all Muskellunge caught in spring 2017 (b) in the St. Louis River Estuary. Horizontal lines represent classification thresholds where >0.875 = Minnesota strain, <0.125 = Wisconsin strain, and intermediate values = strain hybrid. Tick marks above the figure in panel b indicate each of the 60 acoustically tagged individuals.

Figure 2. (continued)

b.



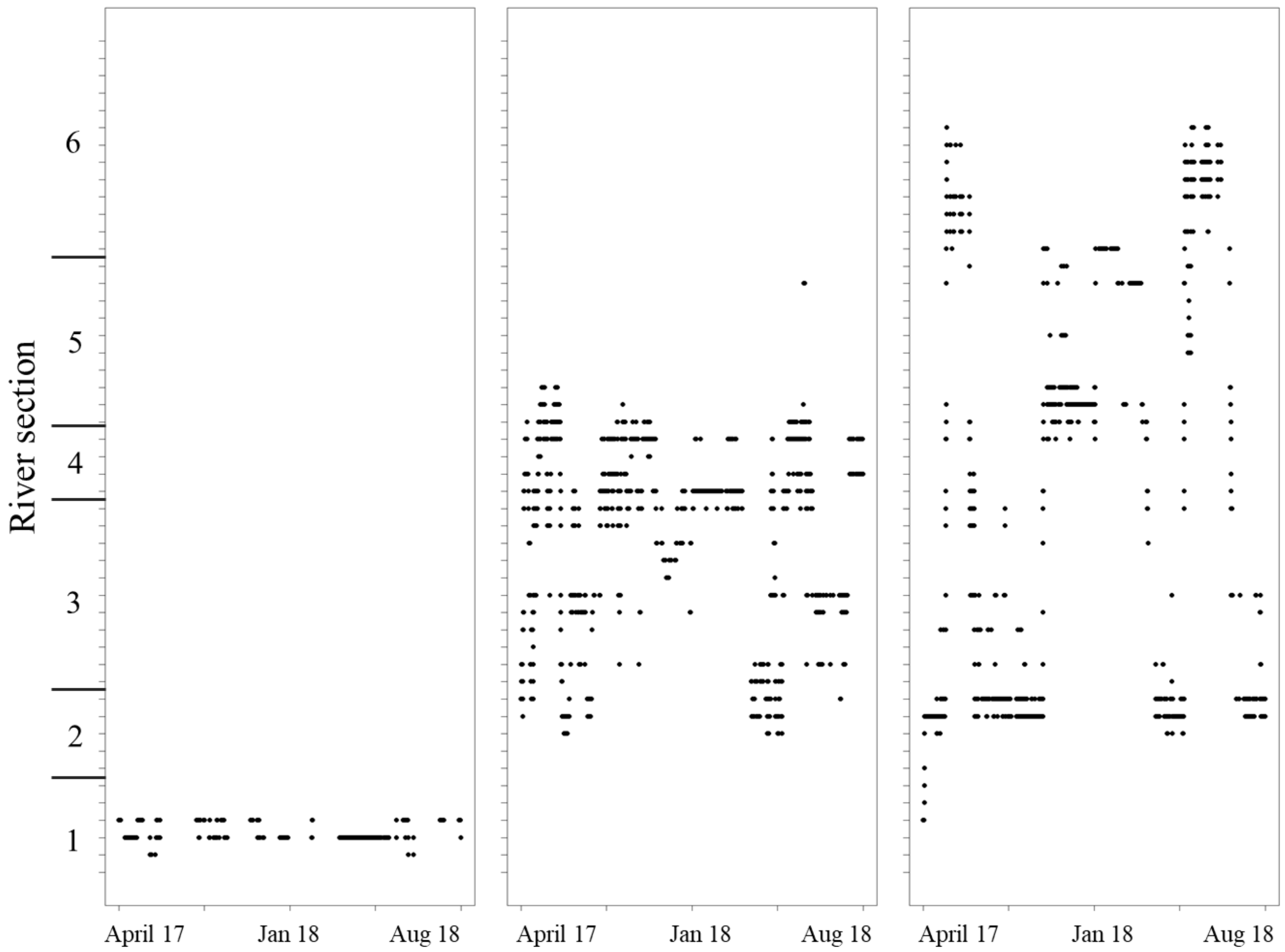


Figure 3. Abacus plots for three Muskellunge that are representative of a wide range of movement over a 15-month study in the St. Louis River Estuary and southwestern Lake Superior. Each dot indicates a detection. Tick marks on the y-axis indicate individual receivers and numbers on the y-axis correspond to the river sections shown in Figure 1.

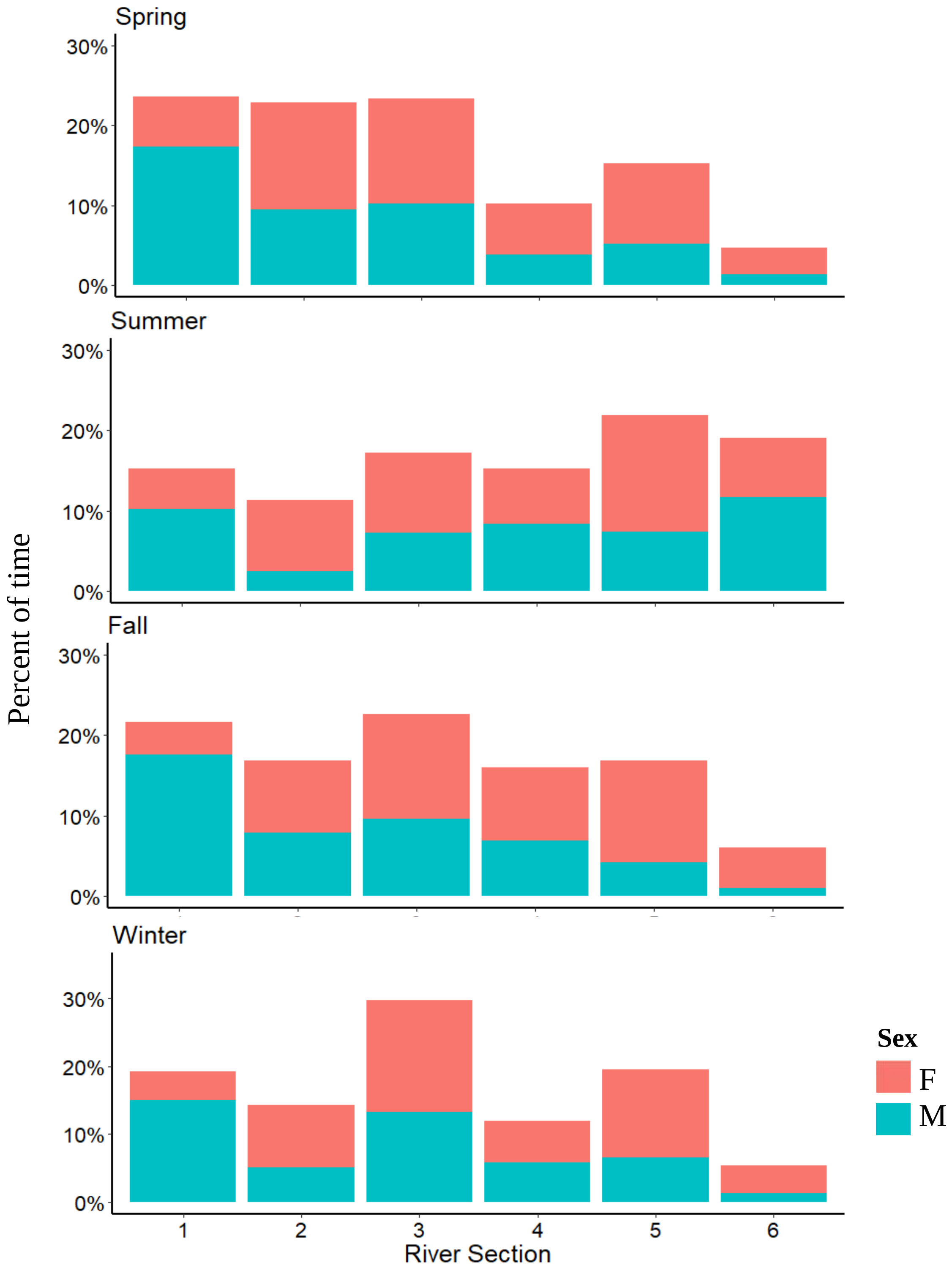


Figure 4. Percent of time that male (M) and female (F) Muskellunge were detected in each river section per season during the 15 month study on the St. Louis River Estuary. Numbers on the x-axis correspond to the river sections shown in Figure 1.

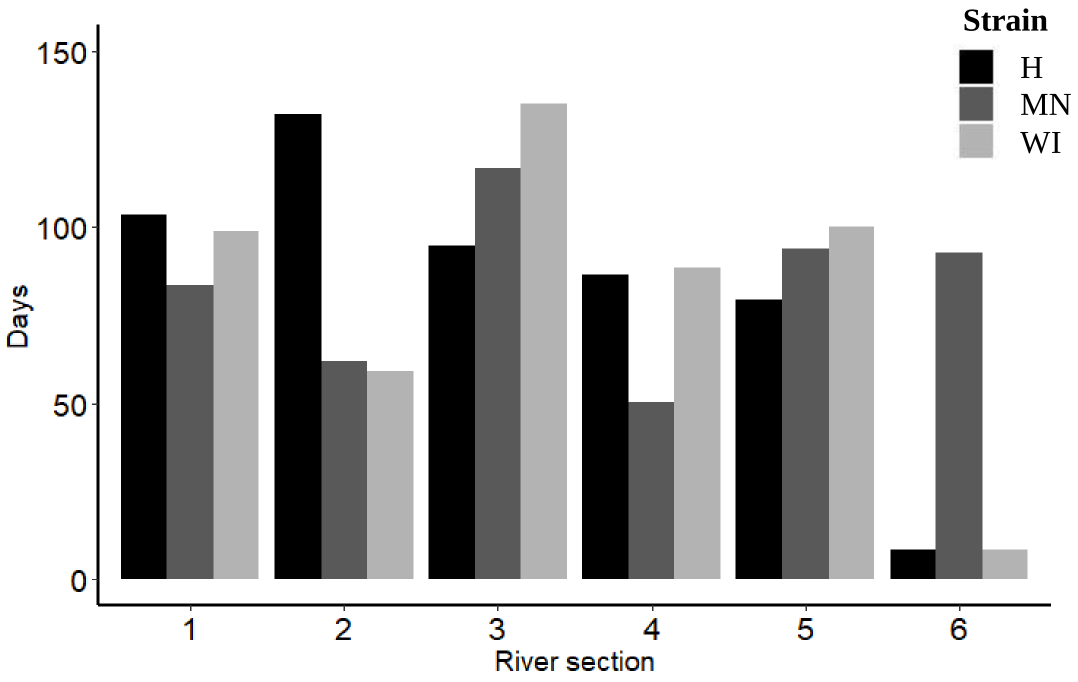


Figure 5. Total number of days that Minnesota (MN), Wisconsin (WI), and MN x WI hybrid (H) Muskellunge were detected in each river section during the 15 month study on the St. Louis River Estuary. Numbers on the x-axis correspond to the river sections shown in Figure 1.

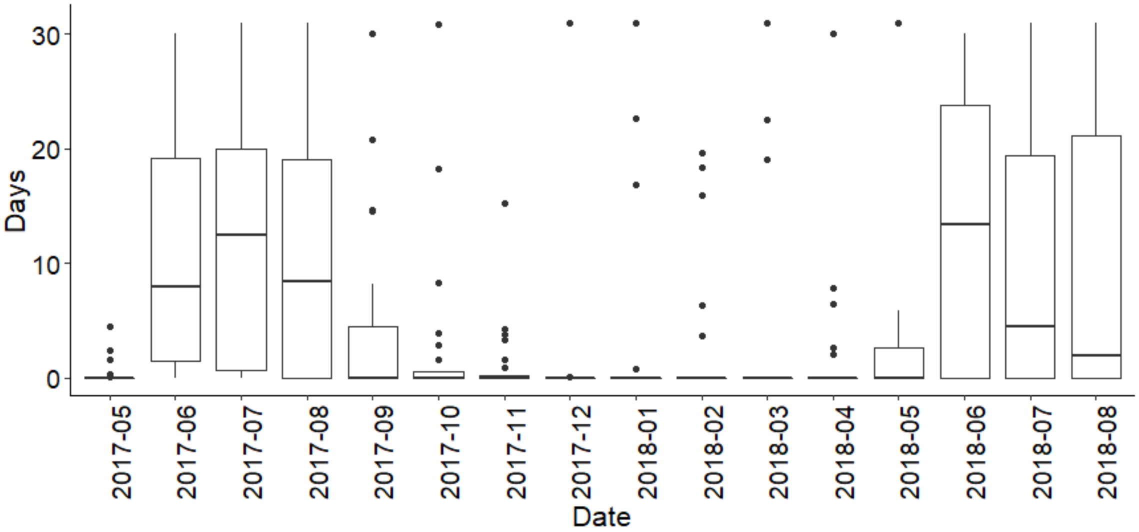


Figure 6. Box plot showing the number of days that each Muskellunge spent in Lake Superior each month over the 15-month study. The Muskellunge included are only individuals that spent time in Lake Superior and returned to the St. Louis River Estuary (n=24). One additional individual left the estuary, was detected in Chequamegon Bay, Wisconsin, and never returned to the estuary.

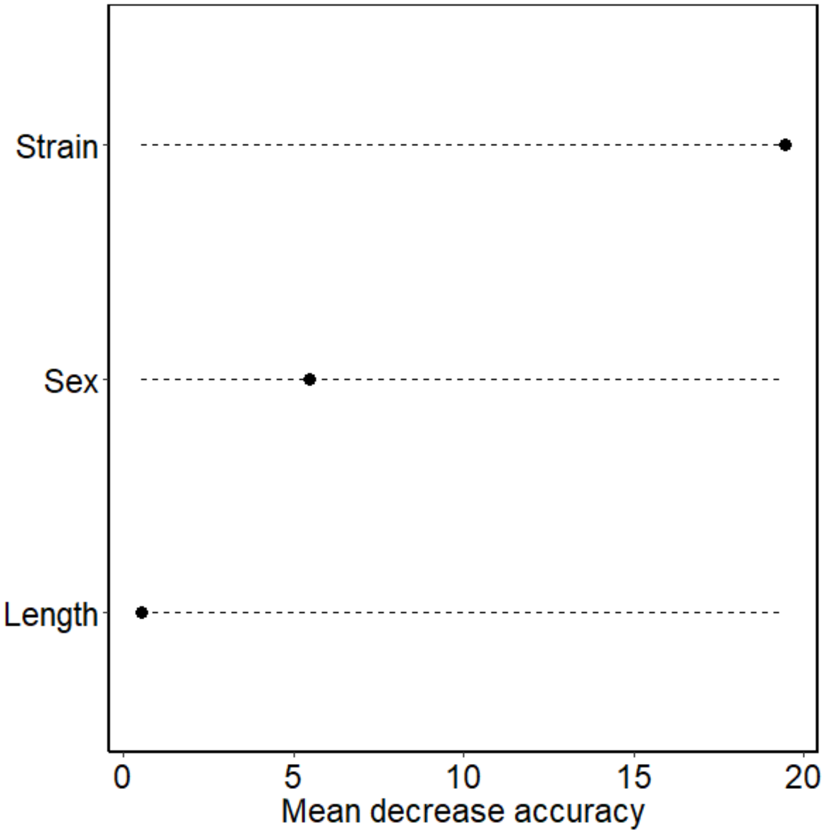


Figure 7. Importance of strain, sex and length in explaining Lake Superior use by Muskellunge tagged in the St. Louis River Estuary, based on a random forest model. The x-axis indicates the predictive accuracy for each variable. A higher mean decrease in accuracy indicates greater importance for a given variable when explaining Lake Superior use.

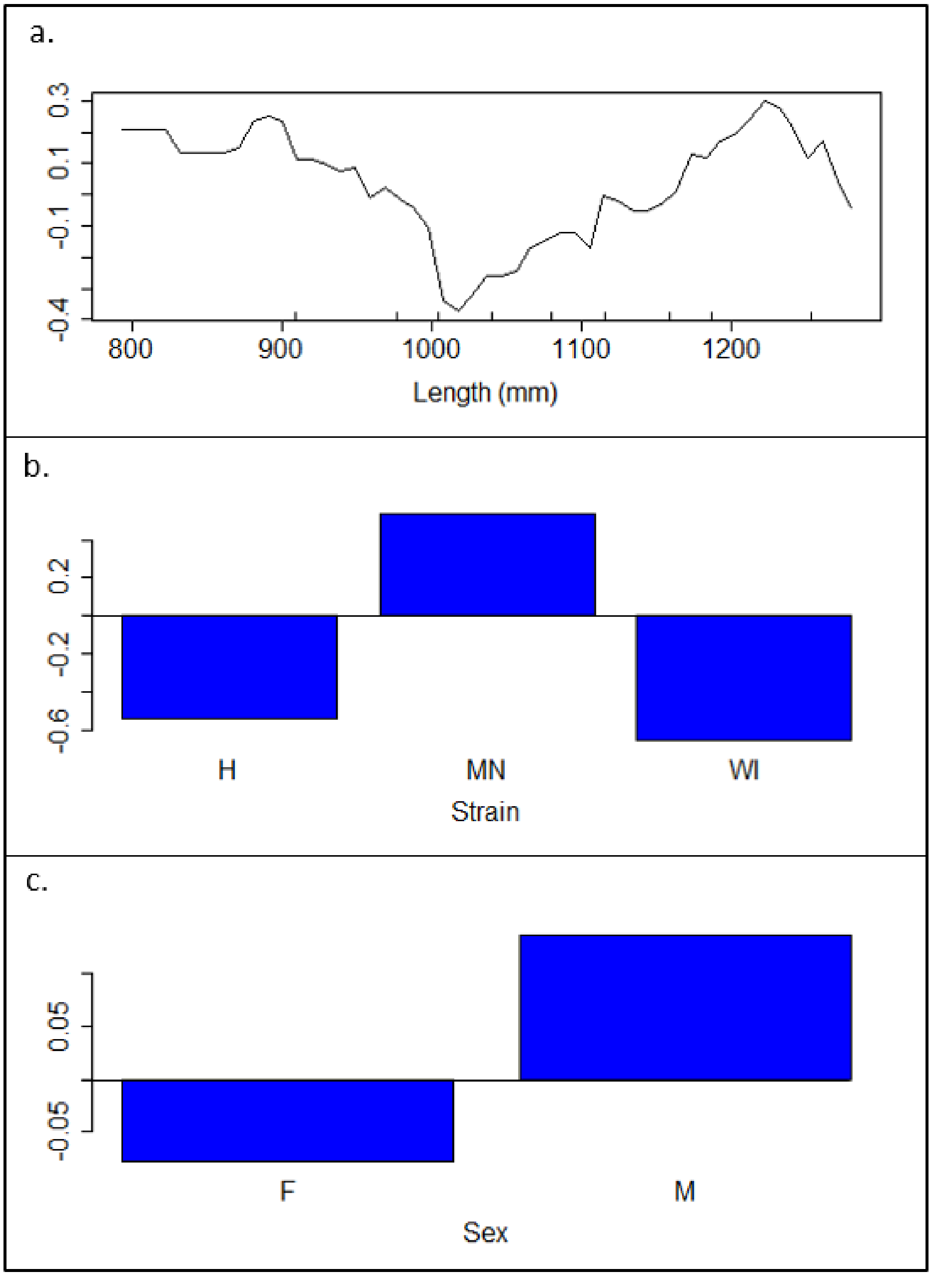


Figure 8. Random forest partial dependence plots showing how length (a), strain (b), and sex (c) influence Lake Superior use by Muskellunge tagged in the St. Louis River Estuary. Strain (b) was the only signficant predictor. The y-axis details the marginal effect of a variable. Note that the y-axes scales vary among plots.

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Appendix A: Passive acoustic array deployment locations and timeline

Table A1: Summary table of acoustic telemetry array deployed in the St. Louis River Estuary and southwestern Lake Superior. Station numbers refer to a geographic location and serial numbers identify receivers individually. Thirteen receivers remained deployed at the end of the project (—).

Station	Latitude	Longitude	Deployment date	Recovery date	Receiver type	Serial number
SLR-000	46.77979	-92.08674	4/4/2017 19:55	10/16/2017 18:47	VR2Tx	481071
SLR-000	46.77974	-92.08676	10/16/2017 19:27	8/6/2018 19:41	VR2Tx	481071
SLR-000	46.7798	-92.08668	8/6/2018 20:06	—	VR2Tx	481071
SLR-001	46.65934	-92.20319	4/6/2017 17:00	9/26/2017 19:40	VR2Tx	481070
SLR-001	46.65935	-92.20314	9/26/2017 20:02	8/8/2018 14:24	VR2Tx	481070
SLR-001	46.65916	-92.20298	8/8/2018 14:39	—	VR2Tx	481070
SLR-002	46.72541	-92.14927	4/3/2017 19:10	9/29/2017 17:53	VR2W	131205
SLR-003	46.69947	-92.01198	4/3/2017 18:00	9/25/2017 20:15	VR2W	111090
SLR-003	46.69965	-92.01161	4/27/2018 18:48	9/25/2018 17:00	VR2W	111090
SLR-004	46.69696	-92.03404	4/5/2017 18:00	9/28/2017 14:02	VR2W	127689
SLR-004	46.69694	-92.03405	4/27/2018 19:07	—	VR2W	127689
SLR-005	46.74664	-92.10307	4/3/2017 17:10	9/29/2017 14:05	VR2W	103405
SLR-005	46.74666	-92.10305	9/29/2017 14:21	9/25/2018 19:18	VR2W	103405
SLR-006	46.75009	-92.10095	4/3/2017 16:55	9/28/2017 18:01	VR2W	131203
SLR-006	46.75004	-92.10097	9/28/2017 18:15	8/8/2018 20:20	VR2W	131203
SLR-008	46.71041	-92.00551	5/24/2016 17:00	8/7/2017 20:00	VR2W	127687
SLR-009	46.7497	-92.1285	4/5/2017 19:26	9/29/2017 18:13	VR2W	127686
SLR-009	46.74966	-92.12834	4/27/2018 19:50	9/26/2018 19:27	VR2W	127686
SLR-010	46.7426	-92.09792	4/3/2017 17:20	9/29/2017 18:30	VR2W	103398
SLR-010	46.74267	-92.09791	9/29/2017 18:52	9/27/2018 16:40	VR2W	103398
SLR-011	46.70994	-92.15715	4/3/2017 19:30	9/29/2017 15:35	VR2W	103397
SLR-011	46.70991	-92.15722	4/29/2018 14:45	9/26/2018 16:42	VR2W	103397
SLR-012	46.68609	-92.1632	4/7/2017 18:45	9/27/2017 18:30	VR2W	131421
SLR-012	46.68611	-92.16318	4/30/2018 20:05	9/26/2018 15:00	VR2W	131421
SLR-013	46.69989	-92.17375	4/7/2017 18:25	9/27/2017 16:35	VR2W	131415
SLR-013	46.69993	-92.17376	9/27/2017 17:05	9/24/2018 19:50	VR2W	131415
SLR-015	46.73023	-92.14458	4/3/2017 18:56	9/29/2017 14:36	VR2Tx	481072
SLR-015	46.73019	-92.14452	9/29/2017 14:54	8/7/2018 18:31	VR2Tx	481072
SLR-015	46.73013	-92.14451	8/7/2018 18:44	—	VR2Tx	481072
SLR-016	46.72361	-92.17502	4/7/2017 19:46	9/27/2017 19:10	VR2W	131417
SLR-016	46.72357	-92.17509	9/27/2017 19:26	9/24/2018 18:55	VR2W	131417
SLR-017	46.7199	-92.18538	4/5/2017 20:10	9/27/2017 18:51	VR2W	127692
SLR-018	46.70479	-92.19929	4/7/2017 17:30	9/27/2017 15:14	VR2W	131419
SLR-018	46.70467	-92.19922	9/27/2017 15:40	9/26/2018 16:02	VR2W	131419

Table A1. (continued)

Station	Latitude	Longitude	Deployment date	Recovery date	Receiver type	Serial number
SLR-019	46.69879	-92.18112	4/7/2017 18:17	9/27/2017 16:19	VR2W	131208
SLR-019	46.70466	-92.18117	9/27/2017 16:19	9/26/2018 15:30	VR2W	131208
SLR-020	46.65386	-92.21282	4/6/2017 17:55	9/26/2017 18:30	VR2W	103406
SLR-020	46.65367	-92.21324	4/29/2018 15:50	8/8/2018 17:51	VR2W	103406
SLR-021	46.64971	-92.23878	4/6/2017 15:45	9/26/2017 17:50	VR2W	127691
SLR-021	46.64974	-92.23877	9/26/2017 18:20	8/8/2018 17:05	VR2W	127691
SLR-022	46.65088	-92.26672	4/6/2017 16:00	9/26/2017 17:05	VR2W	106312
SLR-022	46.65082	-92.26666	9/26/2017 17:34	8/8/2018 16:35	VR2W	106312
SLR-023	46.68425	-92.19939	4/7/2017 18:02	9/27/2017 14:08	VR2W	131422
SLR-023	46.68425	-92.19936	4/29/2018 15:17	8/8/2018 19:23	VR2W	131422
SLR-024	46.69141	-92.19573	4/7/2017 17:45	9/27/2017 14:25	VR2W	127688
SLR-024	46.69142	-92.19581	9/27/2017 14:50	9/24/2018 18:05	VR2W	127688
SLR-025	46.72606	-92.05193	3/31/2017 19:20	9/28/2017 16:04	VR2W	131204
SLR-025	46.726	-92.05193	9/28/2017 16:23	9/25/2018 18:40	VR2W	131204
SLR-026	46.74973	-92.07537	3/31/2017 19:36	9/28/2017 16:37	VR2W	131209
SLR-026	46.74975	-92.07537	9/28/2017 16:58	9/25/2018 18:58	VR2W	131209
SLR-027	46.69759	-92.01137	4/3/2017 17:50	9/28/2017 14:35	VR2W	111091
SLR-027	46.6975	-92.01137	9/28/2017 14:40	9/25/2018 16:50	VR2W	111091
SLR-028	46.77725	-92.09439	10/25/2016 17:15	4/4/2017 20:20	VR2W	127692
SLR-028	46.77765	-92.0936	4/5/2017 17:17	9/28/2017 17:30	VR2Tx	481074
SLR-028	46.77763	-92.0935	9/28/2017 17:41	8/7/2018 14:25	VR2Tx	481074
SLR-028	46.77771	-92.09343	8/7/2018 14:38	–	VR2Tx	481074
SLR-029	46.71254	-92.0078	3/31/2017 18:11	10/16/2017 20:25	VR2Tx	481076
SLR-029	46.71251	-92.00783	10/16/2017 20:52	9/28/2018 16:25	VR2Tx	481076
SLR-029	46.71256	-92.00777	9/28/2018 17:44	–	VR2Tx	481076
SLR-030	46.70439	-92.01728	3/31/2017 18:53	9/28/2017 15:09	VR2Tx	481075
SLR-030	46.70438	-92.01728	9/28/2017 15:28	8/7/2018 15:22	VR2Tx	481075
SLR-030	46.70439	-92.01729	8/7/2018 15:33	–	VR2Tx	481075
SLR-031	46.72667	-92.14147	4/4/2017 16:40	9/27/2017 15:08	VR2Tx	481073
SLR-031	46.72666	-92.14154	9/29/2017 15:23	8/7/2018 19:06	VR2Tx	481073
SLR-031	46.72667	-92.14142	8/7/2018 19:22	–	VR2Tx	481073
SLR-032	46.65534	-92.2022	7/20/2016 19:30	4/6/2017 15:45	VR2W	127688
SLR-032	46.65607	-92.20222	4/6/2017 16:55	9/26/2017 18:55	VR2Tx	481069
SLR-032	46.65608	-92.20226	9/26/2017 19:15	8/8/2018 18:27	VR2Tx	481069
SLR-032	46.65584	-92.20228	8/8/2018 18:41	–	VR2Tx	481069
SLR-033	46.66353	-92.28678	7/20/2016 17:27	10/10/2016 16:00	VR2W	127690
SLR-033	46.66366	-92.28673	4/6/2017 17:15	11/3/2017 18:14	VR2W	127690
SLR-033	46.66365	-92.28672	4/29/2018 16:26	8/8/2018 16:00	VR2W	127690
SLR-034	46.69549	-92.15722	4/11/2017 19:10	9/29/2017 15:50	VR2W	131416
SLR-034	46.69554	-92.15706	9/29/2017 16:02	9/26/2018 17:02	VR2W	131416
SLR-035	46.70166	-92.14965	4/11/2017 19:20	9/29/2017 16:18	VR2W	131418
SLR-035	46.70166	-92.14962	9/29/2017 16:30	9/26/2018 18:15	VR2W	131418

Table A1. (continued)

Station	Latitude	Longitude	Deployment date	Recovery date	Receiver type	Serial number
SLR-036	46.70798	-92.14144	4/11/2017 19:50	9/29/2017 16:56	VR2W	131420
SLR-036	46.70798	-92.14144	9/29/2017 17:09	9/26/2018 19:40	VR2W	131420
SLR-037	46.7045	-91.99581	3/31/2017 17:00	10/25/2017 19:00	VR2W	110398
SLR-037	46.7045	-91.9959	10/25/2017 19:33	9/28/2018 17:15	VR2W	110398
SLR-038	46.69474	-91.97697	3/31/2017 17:15	10/26/2017 20:08	VR2W	103403
SLR-038	46.69474	-91.97688	11/3/2017 16:51	8/6/2018 16:16	VR2W	131205
SLR-038	46.69479	-92.00831	8/7/2018 17:24	—	VR2W	131205
SLR-039	46.71478	-91.98091	3/31/2017 17:50	10/27/2017 19:23	VR2W	131207
SLR-039	46.71109	-91.97732	11/3/2017 16:30	8/6/2018 18:25	VR2W	131207
SLR-039	46.71127	-91.97793	8/7/2018 17:49	—	VR2W	131207
SLR-040	46.70584	-91.96228	3/31/2017 17:32	10/19/2017 21:30	VR2W	103400
SLR-040	46.70592	-91.96228	11/3/2017 16:40	8/6/2018 17:03	VR2W	103400
SLR-040	46.70582	-91.96211	8/6/2018 17:20	—	VR2W	103400
SLR-041	46.68619	-92.01156	4/5/2017 18:48	9/28/2017 18:39	VR2W	106311
SLR-041	46.68612	-92.01145	5/4/2018 13:35	9/25/2018 16:25	VR2W	106311
SLR-042	46.68643	-91.98704	4/5/2017 18:33	9/28/2017 18:51	VR2W	127685
SLR-042	46.68547	-91.98367	4/27/2018 18:29	9/25/2018 16:12	VR2W	127685
SLR-043	46.66509	-92.29734	5/3/2018 13:59	8/8/2018 16:35	VR2W	103403
SLR-044	46.66266	-92.20979	4/30/2018 20:05	8/8/2018 19:01	VR2W	127687
SLR-045	46.74559	-91.60684	6/6/2018 19:23	—	VR2W	127692
SLR-291	46.71249	-92.00728	11/8/2017 21:00	9/25/2018 15:35	VR2W	131206

Appendix B. **Range tests to determine receiver detection range**

Detection range tests were conducted throughout the St. Louis River Estuary during the summer of 2016 and 2017. Range tests confirmed that the signal was blocked 100% of the time when there was no line-of sight between the receiver and the tag. Tests where line-of-sight was blocked were excluded from detection range analysis. Percent of successful transmissions also decreased with variable bottom topographically and as the vertical distance between a tag and receiver increased. Analysis determined that detection range was variable, fluctuating between approximately 200m – 400m. Greater than 50% of tag transmissions were generally detected at these distances, with some exceptions (Table B1).

Table B1. Detection range test results for 12 tests completed in 2016 and 2017. Results of range tests where line-of-sight was obstructed were not included in the detection range analysis (*). The latitude and longitude data for range tests 8, 9, and 10 conducted by the Minnesota Department of Natural Resources are approximate (**) because the data were lost (—), but tests were located at the Highway 23 bridge, Blatnik bridge (~6m deep set), and Blatnik bridge (~2m shallow set), respectively.

Range test number	Test length	Distance to Receiver (m)	Percent of successful transmissions	Latitude	longitude
1	10 min	0	—	46.65367	-92.21324
		180	4.5%	46.65365	-92.21041
2	10 min	0	—	46.72541	-92.14927
		210	41.7%	46.72400	-92.14637
		400	0%*	46.72241	-92.14370
3	10 min	0	—	46.74970	-92.12850
		140	90.0%	46.74849	-92.12793
		250	0%*	46.75049	-92.12543
4	10 min	0	—	46.70994	-92.15715
		200	71.7%	46.70923	-92.15477
		410	0%*	46.70850	-92.15219
5	10 min	0	—	46.69989	-92.17375
		260	83.3%	46.70111	-92.17089
6	10min	0	—	46.69141	-92.19573
		210	93.3%	46.68966	-92.19523
		300	96.7%	46.69149	-92.19567
		400	76.7%	46.68950	-92.19135
7	10 min	0	—	46.70479	-92.19929
		150	13.3%	46.70415	-92.19755

Table B1. (continued)

Range test number	Test length	Distance to Receiver (m)	Percent of successful transmissions	Latitude	longitude
8**	5 days	0	–	46.658411	-92.28283
		100	95%	–	–
		200	89%	–	–
		300	89%	–	–
		400	87%	–	–
		500	65%	–	–
		600	5%	–	–
9**	5 days	0	–	46.74935	-92.10216
		210	82%	–	–
		400	50%	–	–
		510	7%	–	–
10**	5 days	0	–	46.74935	-92.10216
		100	95%	–	–
		350	11%	–	–
11	5 days	0	–	46.69465	-92.00990
		130	88%	46.69350	-92.00977
		200	86%	46.69288	-92.00980
12	5 days	0	–	46.701047	-92.18071
		550	84%	46.70186	-92.17351

Appendix C. Simulations to determine thresholds for categorical assignment to ancestral groups.

I simulated genotypes in HybridLab (Nielsen et al. 2006) using archived baselines to determine the thresholds for categorical assignment to ancestral groups. Ten input files were created, each with 100 of Minnesota (MN) and Wisconsin (WI) and 50 of each hybrid group: first-generation (WxL), second-generation (F2 and backcrosses L-BC and W-BC). Structure was run at K=2. Based on a >87.5% composition threshold, 12% of simulated pure Minnesota strain and 8% of pure Wisconsin strain were falsely assigned as hybrids. Zero to 1% of F1 or F2 hybrids and up to 19-24% of backcrosses were incorrectly classified as pure strains (Table C1). These simulations did not consider further advanced generations of hybrids, which would be more difficult to distinguish from pure strain individuals. However, the likelihood of advanced-generation hybrids within the St. Louis River Estuary Muskellunge population is low because of its recent stocking history and the relatively old age at maturity, which begins at 5-7 years old (Crossman 1990) (Table C2).

Table C1. The number and proportion of simulated individuals assigned to the incorrect genetic group for ten replicated simulations. Simulated group represents pure strain (WI and MN) four categories of hybrids, first-generation (WxL) and second-generation (F2 and backcrosses L-BC and W-BC).

		Simulation												
Incorrect Group	**Simulated Group**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Total Incorrect**	**Standard Deviation**	**Percent Incorrect**
Hybrid	WI	6	8	11	8	11	4	7	10	10	9	84	2.271	8.4%
	MN	8	7	15	13	13	11	12	17	8	20	124	4.169	12.4%
WI	WxL	0	0	1	1	0	0	0	0	0	0	2	0.422	0.4%
	L-BC	0	0	0	0	0	0	0	0	0	0	0	0.000	0.0%
	W-BC	12	8	9	9	10	14	10	7	13	4	96	2.951	19.2%
	F2	3	0	0	0	0	2	1	1	1	1	9	0.994	1.8%
MN	WxL	0	0	0	0	1	0	0	0	0	1	2	0.422	0.4%
	L-BC	18	15	11	10	12	11	14	10	9	8	118	3.048	23.6%
	W-BC	0	0	0	0	0	0	0	0	0	0	0	0.000	0.0%
	F2	0	2	0	1	0	0	1	2	0	0	6	0.843	1.2%

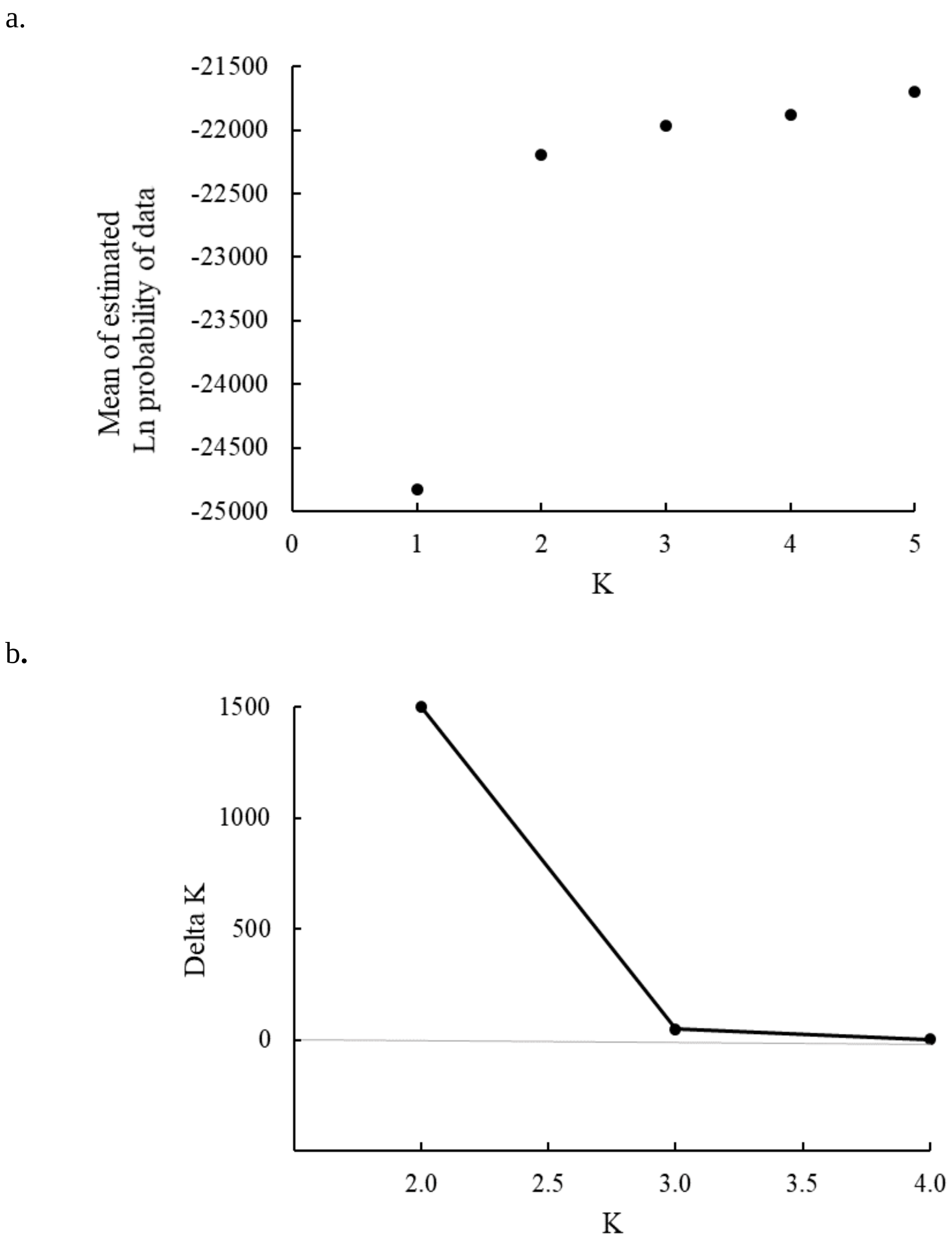

Figure C1. Mean likelihoods (a) and delta K values (b) for ten runs in STRUCTURE at K=1-5. The presence of two genetically distinct sources (K=2) is supported by a plateauing of likelihood values in (a) and peak delta K at K=2 in (b).

Table C2. Stocking history of Minnesota and Wisconsin strain Muskellunge in the St. Louis River Estuary by the Minnesota (MN) and Wisconsin (WI) Departments of Natural Resources (DNR) 1983-2015.

	MNDNR		**WIDNR**	
Year	**Number**	**Strain**	**Number**	**Strain**
1983			500	WI
1984			500	WI
1986	800	WI	2,000	WI
1987			3,039	WI
1988			2,500	WI
1989	346	MN	5,000	WI
1990			5,000	WI
1991	5002	MN	4,658	WI
1992	5000	MN	2,500	WI
1993			2,500	WI
1994	5000	MN		
1994				
1995				
1996				
1997	5500	MN	2,500	WI
1998				
1999				
2000	5000	MN	2,500	WI
2001	5000	MN	3,500	WI
2002			2,500	WI
2003	5001	MN		
2004			2,500	WI
2005	5005	MN		
2015	2189	MN		
Total	**43843**		**41697**	

Appendix D. Summary of tagging and biological data for 60 acoustically tagged individuals

Table D1. Summary of tagging and biological data for 60 muskellunge acoustically tagged in the St. Louis River Estuary, United States. Individuals were passively tracked from May 9, 2017 to August 6, 2018. Receivers detected (RD) indicates how many receivers detected each individual. Minnesota Ancestry (MNA) refers to the proportion of MN ancestry in an individual. Status, active (A) or unknown (U), was determined at the end of the project. Seven individuals were removed from analyses because their status became unknown during the project. An unknown status may be due to death, transmitter failure, angler morality, or uncertain due to lack of movement over time or moving beyond the array. Last detection indicates the time of the last detection within the study period, even if an individual was detected after that timeframe (*).
L= total length from front of head to tip of tail, W= weight (kg)

ID	L (mm)	Sex	W (kg)	Strain	MNA	RD	Number of Detections	First Detection	Last Detection	Days Tracked	Status
1	1162	M	13.25	MN	0.987	17	112869	5/9/17	6/10/18*	397	A
2	1215	F	14.5	MN	0.98	5	102224	5/9/17	8/6/18	454	U
3	1254	F	15.25	WI	0.017	22	98003	5/9/17	8/1/18*	449	A
4	1002	F	8.75	H	0.458	17	180300	5/9/17	8/6/18	454	A
5	1203	F	14.5	WI	0.079	14	54731	5/9/17	8/6/18	454	A
6	1170	F	13.25	MN	0.986	34	110451	5/9/17	8/6/18	454	A
7	1181	F	12.5	H	0.498	9	114246	5/9/17	8/6/18	454	A
8	1235	F	17.25	WI	0.052	32	101194	5/9/17	8/6/18	454	A
9	1006	M	6.5	H	0.549	21	171276	5/9/17	8/6/18	454	A
10	885	M	4	MN	0.97	35	123392	5/9/17	7/29/18	446	A
11	793	M	3.5	MN	0.945	32	110506	5/9/17	6/27/18*	414	A
12	1147	F	13.75	WI	0.019	11	84094	5/9/17	8/6/18	454	A
13	1190	F	14	MN	0.897	24	48100	5/9/17	10/26/17*	170	A
14	905	F	5	H	0.391	31	112869	5/9/17	8/6/18	454	A
15	1255	F	15.75	MN	0.978	30	120211	5/9/17	8/3/18*	451	A
16	791	U	3.5	MN	0.953	6	230180	5/9/17	8/6/18	454	U
17	1212	F	17	MN	0.887	30	122176	5/9/17	8/3/18	451	A
18	1062	M	12.75	MN	0.898	25	177394	5/9/17	8/6/18	454	A
19	1008	F	8	H	0.513	11	105312	5/9/17	7/1/18*	418	A
20	1251	F	15.5	MN	0.983	12	167308	5/9/17	8/5/18*	453	A
21	991	M	8.25	H	0.65	10	97294	5/9/17	8/6/18	454	A
22	1090	M	9.25	MN	0.97	38	80804	5/9/17	8/6/18	454	A

Table D1. (continued)

ID	L (mm)	Sex	W (kg)	Strain	MNA	RD	Number of Detections	First Detection	Last Detection	Days Tracked	Status
23	1111	M	12.75	MN	0.96	28	112140	5/9/17	8/6/18	454	A
24	1097	M	14	MN	0.899	26	36856	5/9/17	8/6/18	454	A
25	907	F	6.5	MN	0.976	32	131824	5/9/17	5/20/18	376	A
26	1053	M	8.75	H	0.204	2	167144	5/9/17	8/6/18	454	A
27	865	M	4	H	0.606	9	24123	5/9/17	7/31/18	448	U
28	1018	F	—	WI	0.03	20	112978	5/9/17	8/6/18	454	A
29	1136	F	14	WI	0.02	23	129929	5/9/17	8/6/18	454	A
30	1120	F	11.25	WI	0.054	15	108880	5/9/17	8/6/18	454	A
31	1036	F	8.25	WI	0.044	5	82686	5/9/17	8/6/18	454	U
32	1159	F	12.75	H	0.37	12	33979	5/9/17	8/4/18*	452	A
33	1270	F	18.75	MN	0.956	38	147318	5/9/17	8/6/18	454	A
34	1064	F	12.25	WI	0.067	17	82355	5/9/17	8/6/18	454	A
35	987	F	7.5	H	0.516	26	151405	5/9/17	8/6/18	454	A
36	1158	M	13.25	MN	0.959	32	125175	5/9/17	8/6/18	454	A
37	1265	F	16.75	MN	0.981	19	162078	5/9/17	8/6/18	454	A
38	863	M	4.75	H	0.455	15	115453	5/9/17	8/6/18	454	A
39	1280	F	14.2	MN	0.972	16	69485	5/9/17	8/6/18	454	A
40	1080	M	8	MN	0.985	3	31215	5/9/17	8/6/18	454	A
41	1020	M	8.5	H	0.443	3	70463	5/9/17	8/6/18	454	A
42	1164	F	10.75	WI	0.035	14	15902	5/9/17	6/7/18	394	A
43	954	F	7.5	H	0.431	16	185405	5/9/17	8/6/18	454	A
44	807	U	4	WI	0.066	18	7295	5/9/17	7/9/17	61	U
45	832	M	4.5	H	0.627	2	4161	5/9/17	6/1/17	23	U
46	984	M	6.5	MN	0.971	10	37631	5/9/17	7/2/18	419	A
47	1114	M	12.5	MN	0.981	26	108350	5/9/17	7/18/18*	435	A
48	1105	M	9.5	MN	0.978	19	89052	5/9/17	8/3/18*	451	A
49	856	M	5.5	WI	0.068	6	9559	5/9/17	5/27/18*	383	A
50	971	M	8.5	MN	0.968	25	37811	5/9/17	8/4/18*	452	A
51	1259	F	17.75	MN	0.979	36	122658	5/9/17	8/6/18	454	A
52	1039	M	8	MN	0.978	31	101398	5/9/17	8/6/18	454	A
53	962	F	8.75	H	0.404	8	177817	5/9/17	8/6/18	454	A
54	1074	M	9.5	MN	0.979	26	76269	5/9/17	8/5/18*	453	A
55	1040	F	9	WI	0.122	29	47865	5/10/17	7/14/18	430	A
56	912	M	6	H	0.621	16	26007	5/10/17	8/6/18	453	A
57	951	M	6	H	0.502	2	60036	5/11/17	8/6/18	452	A
58	964	F	8	WI	0.07	2	12147	5/11/17	8/6/18	452	U
59	996	M	8	MN	0.98	16	164503	5/11/17	8/6/18	452	A
60	1121	M	10	MN	0.977	36	108616	5/14/17	8/3/18*	446	A

Appendix E. Binomial and Poisson Generalized Linear Mixed Effects model results

Table E1. Results of a Binomial and Poisson Generalized Linear Mixed Effects models to determine if specific characteristics of each acoustic receivers' deployment site within the St. Louis River Estuary influenced Muskellunge occupancy or transmitter detection number over a 15-month study. Individual was the random effect in both models. The response variable was the number of detections per individual per hectare meters within a 300m detection radius for a given receiver. Average depth, floating leaf vegetation (FLV), submerged aquatic vegetation (SAV), and restoration status (i.e., restored, proposed for restoration, but not yet restored, and natural riverine habitat) were explanatory variables. Depth, SAV, and FLV were calculated within the area available of a 300m radius of each receiver.

	Binomial model		**Poisson model**	
	Estimate	p-value	Estimate	p-value
(Intercept)	5.07031	< 2e-16	6.55444	<2e-16
SAV	-4.9325	< 2e-16	-1.19	<2e-16
Depth	-0.40637	1.08E-10	-0.7173	<2e-16
FLV	-0.66678	0.012	-0.182	7.08E-16
Not restored	0.6826	0.000	-0.7544	<2e-16
Restored	1.16187	3.31E-06	0.37527	<2e-16

Appendix F. Pinch point efficiency

Table F1. Pinch point efficiency of five pinch points that divide the St. Louis River Estuary into six different sections. An initial subset of telemetry data were used to determine pinch point efficiency by dividing the number of transitions missed by the number of transitions at each pinch point. Transitions missed were identified when an individual was detected in a new section without being detected on both pinch point receivers.

Section	Missed transitions
1 – 2	0
2 – 3	0
3 – 4	44
4 – 5	44
5 – 6	0
Total number of transitions	840
Percent of transitions missed	10.47%

Appendix G. Mobile acoustic telemetry tracking

Mobile tracking with a VHTx omni-directional transponding hydrophone and VH110 directional hydrophone occurred from May to September 2017 with the goal of locating as many tagged individuals through triangulation as possible while the river was ice-free. The entire SLRE was systematically covered over 2-4 days twice during May and once per month thereafter. The same tracks, which generally ran parallel to shore, were followed during every monthly excursion. A VEMCO VR-100 receiver and deck box was used to detect and record all tag detections.

When searching for individual transmitters, sonar equipment was turned off, the boat was stopped, and the transponding hydrophone was placed into the water to listen for pinging transmitters. When a transmitter was detected, the VR-100 recorded the transmitter number, a GPS point at the VR-100's location, date, time, gain level (dB) and signal strength (dB). To determine the most accurate location for each individual detected, multiple detections of a single muskellunge on the same day were eliminated based on lowest signal strength and highest gain.

Mobile tracking was unsuccessful in triangulating locations with the directional hydrophone and provided limited data with the omni-directional hydrophone. Mobile tracking detected 19 unique individuals per sampling period on average, with the lowest during the first attempt in May and the highest in June. Detection issues likely arose due to the small detection window built into a directional hydrophone combined with variable bottom topographically. The project did not continue mobile tracking during summer 2018 or incorporate these data into analyses.

Table G1. Acoustic telemetry mobile tracking data of tagged Muskellunge from May, 2017 to September, 2017 on the St. Louis River Estuary.

Date	Time	Acoustic tag number	Latitude	Longitude
5/15/2017	15:13:37	50866	46.65929	-92.28275
5/15/2017	15:29:31	50873	46.65451	-92.27757
5/17/2017	07:41:41	50864	46.65446	-92.25801
5/17/2017	06:51:03	50866	46.65915	-92.28233
5/17/2017	07:41:05	50867	46.6544	-92.25874
5/17/2017	07:04:45	50873	46.65525	-92.27953
5/17/2017	06:38:44	50875	46.65845	-92.28407
5/17/2017	07:37:37	50878	46.65318	-92.26245
5/17/2017	06:58:27	50895	46.65755	-92.28284
5/24/2017	12:19:37	50866	46.65222	-92.27271
5/24/2017	13:10:07	50867	46.65342	-92.25047
5/24/2017	13:07:39	50880	46.65446	-92.24966

Table G1. (continued)

Date	Time	Acoustic tag number	Latitude	Longitude
5/24/2017	14:33:05	50881	46.65248	-92.23714
5/24/2017	15:19:30	50882	46.65663	-92.20189
5/24/2017	12:05:20	50912	46.65487	-92.27817
5/24/2017	15:05:43	50920	46.65336	-92.20994
5/25/2017	10:19:44	50862	46.69054	-92.17632
5/25/2017	11:11:47	50865	46.7073	-92.17899
5/25/2017	11:03:06	50869	46.70203	-92.18061
5/25/2017	11:48:15	50871	46.70086	-92.20657
5/25/2017	09:11:51	50882	46.66769	-92.20348
5/25/2017	11:07:12	50892	46.70426	-92.17775
5/25/2017	11:07:09	50894	46.70423	-92.17778
5/25/2017	09:07:58	50897	46.66536	-92.20521
5/25/2017	09:27:12	50911	46.67509	-92.19295
6/5/2017	11:19:44	50872	46.72941	-92.14812
6/5/2017	11:05:07	50873	46.66256	-92.28678
6/5/2017	14:03:16	50874	46.75209	-92.10713
6/5/2017	11:05:18	50875	46.66247	-92.28684
6/5/2017	12:14:42	50878	46.65615	-92.28164
6/5/2017	12:50:31	50887	46.73905	-92.13945
6/5/2017	12:16:46	50900	46.73819	-92.14959
6/5/2017	14:33:00	50908	46.74524	-92.12331
6/5/2017	14:30:03	50908	46.74659	-92.12489
6/5/2017	15:04:33	50910	46.73725	-92.13558
6/5/2017	15:13:10	50913	46.7324	-92.14308
6/5/2017	10:32:41	50919	46.66715	-92.29181
6/5/2017	14:50:19	50920	46.65298	-92.20744
6/6/2017	12:57:11	50869	46.71484	-92.04039
6/6/2017	11:09:06	50871	46.75552	-92.08897
6/6/2017	13:16:14	50880	46.70941	-92.18266
6/6/2017	10:14:48	50881	46.67709	-92.19057
6/6/2017	11:15:46	50884	46.75216	-92.08324
6/6/2017	11:23:40	50886	46.7495	-92.07586
6/6/2017	14:14:53	50892	46.70244	-92.17553
6/6/2017	13:14:31	50893	46.71029	-92.18222
6/6/2017	12:47:31	50896	46.70448	-92.20311
6/6/2017	09:47:40	50897	46.6688	-92.20209
6/6/2017	10:24:03	50903	46.77589	-92.1017
6/6/2017	11:31:49	50904	46.74391	-92.07317

Table G1. (continued)

Date	Time	Acoustic tag number	Latitude	Longitude
6/6/2017	14:29:15	50906	46.70025	-92.17091
6/6/2017	10:12:52	50911	46.67621	-92.19133
6/6/2017	14:30:29	50916	46.69939	-92.1703
6/6/2017	10:37:28	50917	46.77576	-92.09597
6/6/2017	10:14:56	50918	46.7776	-92.0976
6/6/2017	10:21:21	50921	46.77689	-92.09956
6/7/2017	09:59:17	50865	46.71711	-92.19036
7/10/2017	13:53:21	50872	46.77781	-92.09753
7/10/2017	13:52:00	50876	46.77798	-92.09731
7/10/2017	14:45:08	50882	46.74953	-92.07646
7/10/2017	13:54:02	50884	46.7777	-92.0976
7/10/2017	15:08:44	50886	46.73604	-92.06578
7/10/2017	14:44:38	50901	46.7498	-92.07668
7/10/2017	14:57:32	50904	46.74187	-92.06961
7/10/2017	14:39:23	50913	46.75174	-92.07958
7/11/2017	10:19:48	50871	46.78113	-92.0863
7/11/2017	09:39:22	50873	46.6622	-92.2873
7/11/2017	09:32:37	50875	46.66532	-92.28593
7/11/2017	09:25:49	50883	46.7191	-92.05338
7/11/2017	10:12:45	50884	46.77697	-92.09468
7/11/2017	09:44:33	50886	46.73532	-92.07328
7/11/2017	12:15:46	50887	46.72984	-92.1465
7/11/2017	12:46:09	50889	46.73847	-92.15002
7/11/2017	11:05:07	50895	46.65541	-92.26113
7/11/2017	09:38:26	50901	46.73007	-92.06689
7/11/2017	10:21:33	50903	46.78218	-92.08681
7/11/2017	13:27:29	50908	46.74426	-92.1245
7/11/2017	11:24:52	50910	46.74615	-92.11134
7/11/2017	09:54:20	50912	46.74204	-92.08254
7/11/2017	12:00:03	50916	46.73313	-92.14243
7/11/2017	08:57:55	50918	46.70644	-92.0328
7/11/2017	12:49:27	50920	46.65316	-92.20459
7/11/2017	10:13:33	50921	46.77726	-92.09475
7/12/2017	11:41:39	50874	46.7209	-92.15391
7/12/2017	13:42:32	50893	46.69618	-92.19418
7/12/2017	12:27:31	50907	46.72322	-92.14235
8/7/2017	14:41:48	50880	46.73699	-92.06535
8/7/2017	13:49:10	50882	46.75323	-92.07768

Table G1. (continued)

Date	Time	Acoustic tag number	Latitude	Longitude
8/7/2017	14:46:04	50883	46.73627	-92.06397
8/7/2017	13:33:34	50884	46.75714	-92.08822
8/7/2017	15:03:58	50886	46.72922	-92.05939
8/7/2017	16:03:48	50887	46.73009	-92.14495
8/7/2017	16:48:29	50889	46.73835	-92.15225
8/7/2017	16:50:01	50900	46.73843	-92.1516
8/7/2017	10:20:01	50901	46.71491	-92.04752
8/7/2017	14:03:25	50904	46.7486	-92.07394
8/7/2017	17:11:18	50908	46.74529	-92.1241
8/7/2017	16:16:28	50910	46.75342	-92.11182
8/7/2017	12:23:50	50912	46.75209	-92.09015
8/7/2017	17:01:28	50917	46.74774	-92.11918
8/8/2017	11:03:22	50862	46.7099	-92.17568
8/8/2017	12:14:47	50864	46.64978	-92.24313
8/8/2017	13:35:07	50867	46.65381	-92.25229
8/8/2017	09:47:48	50873	46.66867	-92.2905
8/8/2017	10:15:16	50875	46.6592	-92.28591
8/8/2017	13:10:51	50878	46.65521	-92.2692
8/8/2017	11:28:53	50893	46.70753	-92.19566
8/8/2017	13:17:20	50895	46.65663	-92.26551
8/8/2017	10:30:42	50909	46.69502	-92.1718
8/8/2017	14:05:21	50920	46.65314	-92.20466
9/13/2017	17:17:34	50874	46.7505	-92.12543
9/13/2017	15:22:35	50887	46.73892	-92.1496
9/13/2017	14:20:29	50894	46.74754	-92.12659
9/13/2017	14:37:43	50908	46.74452	-92.12509
9/14/2017	08:56:27	50871	46.70091	-92.20647
9/14/2017	08:55:02	50896	46.70107	-92.20663
9/14/2017	08:59:55	50903	46.6989	-92.20603
9/14/2017	10:42:59	50909	46.7011	-92.17087