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ARTICLE

Muskellunge Spatial Ecology 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 U.S. Environmental Protection Agency due to severe environmental degradation. The spatial ecology of Muskellunge *Esox masquinongy*, an indicator species, is uncertain within the estuary and the large, connected water body, Lake Superior. We collected genetic samples and used passive acoustic telemetry to track 60 adult 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 (WI) and Minnesota (MN)—and their hybrids. These genetic strains were previously stocked to restore a nearly extirpated population. 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 portions of the river, respectively. Movements were influenced by strain in that hybrids and the 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, highlighting the importance of understanding strain behavior when stocking different strains. Future research should include investigating Muskellunge habitat use (before, during, and after restoration), tracking juvenile Muskellunge, and connecting telemetry data with mark–recapture and stable isotope data. Our results provide new insight into Muskellunge spatial ecology and genetics that can inform management and restoration efforts within and beyond the Great Lakes.

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Monitoring fish populations is necessary to conserve biodiversity and ecosystem services. Traditional fishery monitoring techniques such as gill–net or trap-net sampling estimate population abundance or species richness as a "snapshot" in time and space (Brooks et al. 2007; Rous et al. 2017). Acoustic telemetry can gather fine- and broad-scale data on fish habitat requirements and responses to environmental change (Crossin et al. 2017). The Great Lakes of North America exemplify a region benefiting from enhanced monitoring tools. The Great Lakes are home to over 100 fish species (NOAA 2017) that play important ecological roles as predators, forage, and ecosystem engineers (McClenachan et al. 2015). Great Lakes fishes also generate ecosystem services that have economic and social benefits (Brooks et al. 2007; McClenachan et al. 2015). These ecosystem services are threatened by climate change, invasive species, industry, agriculture, and urban sprawl (Dudgeon et al. 2006; Brooks et al. 2007; Geist and Hawkins 2016). Research into the spatial ecology of Great Lakes fishes is contributing to our knowledge of fish reproductive biology, invasive species, and habitat use to inform restoration practices and better understand fisheries (Kelso and Gardner 2000; Caswell et al. 2004; Mucha and Mackereth 2008; Landsman et al. 2011; Hilts 2017; Binder et al. 2018). The application of acoustic telemetry to bioindicator fishes and economically important fishes is also vital to fisheries management and restoration planning and monitoring (Brooks et al. 2007).

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 in estuaries connected to the Great Lakes, resulting in economic, social, and aesthetic benefits (Boston et al. 2016; Piszczek et al. 2016). 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 (Steiger et al. 2015; Environmental Protection Agency 2019).

The Muskellunge *Esox masquinongy* is a large, popular freshwater game fish that was likely extirpated from the SLRE due to overexploitation and habitat degradation in the mid-19th century (Minnesota Department of Natural Resources [MNDNR], unpublished data). As a result, Muskellunge were reintroduced and stocked from 1983 to 2005 to meet AOC delisting goals and expand angling opportunities within the SLRE (MNDNR 2007). Muskellunge were then selected as one of three SLRE AOC indicator fish species (along with Walleye *Sander vitreus* and Lake Sturgeon *Acipenser fulvescens*) to monitor the effects of restoration (Steiger et al. 2015). Two strains were stocked: a strain of Minnesota (MN) origin and another of Wisconsin (WI) origin. Strain differences affect traits in Muskellunge, such as growth (Miller et al. 2009; Andree et al. 2018) and physiology (Clapp and Wahl 1996), and could also affect movement and habitat use.

Muskellunge are native to the Great Lakes region and south through the upper Mississippi and Ohio River basins (Kerr 2011). Adults are known to eat amphibians, insects, and small mammals, but they primarily consume fish (Kerr 2016). 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). Muskellunge establish home ranges and movement patterns that may vary by lake size, habitat characteristics, and season (Dombeck 1979; Miller and Menzel 1986; Younk et al. 1996; Morrison and Warren 2015). For restoration projects, progress can be measured and potential ecological impacts can be anticipated by monitoring Muskellunge movements and habitat use throughout the year.

Despite the importance of Muskellunge within the SLRE AOC as a valuable bioindicator and game species, little is known about their spatial ecology within the SLRE and how it varies with genetic strain, sex, and season. Additionally, the extent to which SLRE Muskellunge use Lake Superior proper is unknown. A Muskellunge sport fishery is managed within the SLRE, yet anglers report catch of the species nearshore in Lake Superior, and fisheries agencies cannot effectively sample Muskellunge within the lake. In this study, we investigated how many genetically distinct groups make up the SLRE Muskellunge population and the proportional contributions of these groups to the population. We then used passive acoustic telemetry to quantify Muskellunge habitat use within the SLRE and southwestern Lake Superior and compared use by season, sex, and strain.

METHODS

Study area.— The SLRE runs roughly 25 river kilometers from the upstream Fond du Lac Dam and flows into and exchanges water with Lake Superior through two connecting entry canals. This exchange often results in cooler water temperature in the lower estuary. We used narrow areas of the river (i.e., "pinch points") to demarcate six study sections: five within the SLRE itself and one in Lake Superior (Figure 1). The upper estuary has mostly natural, undeveloped shorelines, shallow aquatic habitat, and a narrow, unmaintained channel (river section 1). The river then deepens and transitions (river sections 2 and 3) to the lower half of the estuary, which largely consists of industrial development and shipping channels that are regularly

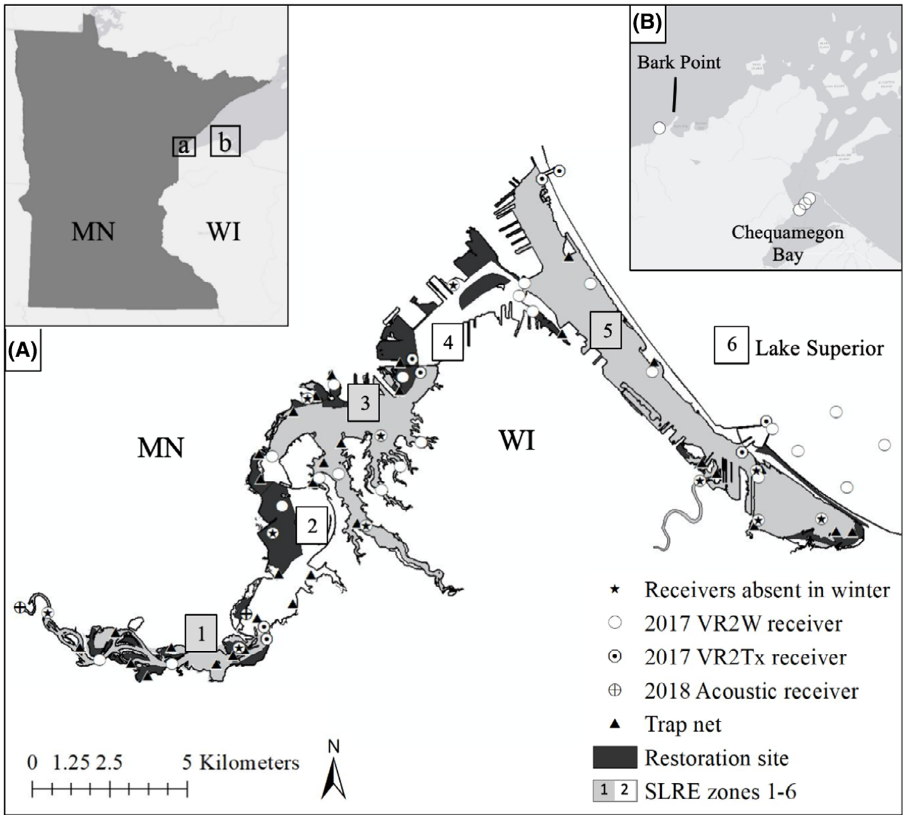

FIGURE 1. Map of the **(A)** St. Louis River estuary (SLRE) receiver array, trapping locations, restoration sites, and six river zones; and **(B)** a portion of the U.S. Fish and Wildlife Service receiver array that detected tagged SLRE Muskellunge. The SLRE is a border water between Minnesota (MN) and Wisconsin (WI) that eventually flows into the southwestern corner of Lake Superior. [Color figure can be viewed at afsjournals.org.] [Color figure can viewed at afsjournals.org.]

dredged to 8.2 m deep (Angradi et al. 2013) and are flanked by shallow aquatic habitat (river sections 4 and 5). Each section in the SLRE contains sites with a previous, ongoing, or future restoration project (Figure 1). Restoration activities at these sites include remediation (the removal of nonnative 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). Common game fishes include Muskellunge, Northern Pike *Esox lucius*, Yellow Perch *Perca flavescens*, Walleye, Smallmouth Bass *Micropterus dolomieu*, Black Crappie *Pomoxis nigromaculatus*, and Channel Catfish *Ictalurus punctatus* (MNDNR, unpublished data).

Fish capture, sampling, and tagging.— Our study complemented the 2017 spring Muskellunge population assessment that was conducted by MNDNR and the Wisconsin Department of Natural Resources. All Muskellunge were captured and sampled following MNDNR Muskellunge sampling guidelines (Muskellunge Technical Committee 2017). Thirty large-frame trap nets (1.5- × 1.8-m frame, 19.05-mm mesh, 30.5-m lead line) were arranged throughout the SLRE. Trap nets were set during Muskellunge spring spawning from April 14 to May 11, 2017, and checked every 24 h, weather permitting. Trapping began when water temperatures warmed to approximately 7.2°C and ended when water temperatures neared 15.5°C and Muskellunge were no longer being caught (MNDNR, unpublished data).

All captured Muskellunge were measured for total length and weight. Approximately 10 scales and a pectoral fin clip (<2-cm section) were collected for genetic and stable isotope analyses, respectively. Each fish was also marked with an internal PIT tag for individual identification (Muskellunge Technical Committee 2017).

Adult Muskellunge were tagged with coded acoustic transmitters (VEMCO; V16-4H, 16-mm diameter × 68 mm, 24-g mass in air). Each tag had an output frequency of 69 kHz and an estimated tag life of 5 years and was powered by a lithium battery (158-decibel output power). Tags emitted short pulses at random, with a nominal delay of 60 s for 8 months during spring, summer, and fall. The transmitters shifted to a 90-s ping rate during the four winter months to maximize tag life span during a period when Muskellunge tend to exhibit reduced movement

(Miller and Menzel 1986; Younk et al. 1996; Pankhurst et al. 2016). We selected adults to obtain equal numbers of both sexes and a representative sample of adult Muskellunge lengths. Adult Muskellunge were defined as individuals at least 762 mm in total length (Muskellunge Technical Committee 2017). The target size distribution for males and females in the sample was based on sex-specific mean lengths from all previous Muskellunge assessments on the SLRE (1997–2014). Muskellunge larger than 1,219 mm were also tagged because they are considered "trophy"-sized individuals that are targeted by anglers.

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 Aqui-S 20E at 15 mg/L (10% eugenol) before surgery. 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 2–3-cm incision. The incision was closed with two to four non-absorbable sutures (polyamide pseudomonofilament, 3/8 cutting needle). Surgeries lasted an average of 3.5 min (maximum = 5 min). All tagged fish were marked with an external, individually numbered spaghetti tag (Floy Tag and Manufacturing, Seattle) 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 400–1,000 m from their capture trap net to avoid immediate recapture (J. J. Pinkerton, personal observation; D. 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 (Ward et al. 2017; Abrams et al. 2018; Reid et al. 2019). The gloves transmitted a low-amperage and low-voltage electric current that ranged between 0.016 and 0.0063 A and was independently controlled. The fish was immobilized when both electric gloves touched opposite ends of the fish, completing the electric circuit. Muskellunge recovered soon after release from the gloves.

Genetic laboratory analysis.— The DNA for genetic analysis was extracted from scale samples by boiling in a chelating resin and was amplified by 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 MN populations, including those in the SLRE. Miller et al. (2012) detected two distinct genetic groups in the SLRE, consistent with the known stocking of MN and WI Muskellunge strains (Table S.1 available in the Supplement in the online version of this article), and strong differentiation between these source populations (genetic differentiation index F_{ST} = 0.24).

Passive acoustic telemetry array.— Tagged Muskellunge were tracked via an array of 40 acoustic receivers (VEMCO; Model VR2W and VR2Tx; 69 kHz) that were deployed prior to tagging in March and April 2017 in the SLRE and western Lake Superior (Figure 1). We worked with agency biologists to deploy two types of acoustic receivers: VR2W (32 receivers) and VR2Tx (8 receivers). Each receiver was positioned vertically, with the hydrophone about 0.5 m above the river or lake floor. Acoustic receivers were moored to a rebar spike that was secured within a 30–40-kg concrete anchor. These anchors were then attached to a smaller, 14-kg anchor by galvanized wire rope to aid receiver retrieval.

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

Receivers were retrieved, downloaded, fitted with new batteries, and redeployed in the same location in fall 2017 and 2018. Eleven, non-pinch-point receivers in depths less than 1.8 m were retrieved in late September 2017 for the winter to prevent ice damage or loss and then were redeployed in April 2018. Acoustic receiver data were uploaded to the Great Lakes Acoustic Telemetry Observation System (GLATOS) database of tag detections (https://glatos.glos.us/projects; project code: SLRMU).

Data analysis.— We analyzed the microsatellite genetic data using a clustering method in Bayesian Analysis of Population Structure (BAPS) version 6.0 (Corander et al. 2003) to classify individuals categorically into three ancestral groups: pure MN strain, pure WI strain, or hybrid crosses between strains. Archived genetic data from MN and WI Muskellunge strains were included to associate these known stocked strains with distinct genetic groups identified by BAPS. The nonspatial population mixture subcomponent was run with the number of clusters fixed at two, based on the finding of two genetic groups in the SLRE by Miller et al. (2012). The population admixture subcomponent (Corander and Marttinen 2006) was then run with input parameters of 200 reference individuals and 100 and 20 iterations to estimate admixture coefficients for unknown and reference individuals, respectively. Strain hybrids were those individuals with admixture coefficients indicating that the probabilities of being pure strain were 0.05 or less based on simulations in BAPS. A chi-square test was used to determine if there was a significant difference in the proportion of strain groups between tagged and untagged individuals.

The study period began when all Muskellunge were acoustically tagged and continued until the first day that acoustic receivers were downloaded (May 9, 2017, to August 6, 2018, or 455 d). All analyses were performed using R version 1.1.423 (R Core Team, Vienna). We used VEMCO VUE version 2.3.0 and the glatos package developed by GLATOS (available at https://gitlab.oceantrack.org/GreatLakes/glatos) to identify false detections (based on the time between individual transmitter detections: Pincock 2012) and to correct for each receiver's internal time lag (VEMCO 2017).

We calculated the residence time of each individual within each study section of the SLRE to evaluate if sex, strain, or season affected spatial use. Zones were assigned per individual with 1-h time bins and the last observation carried forward 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 the fish's time was split evenly between the zones within that 1-h time bin. An initial subset of telemetry data was 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. We used ANOVAs to evaluate the differences in residency time in each section with sex, strain (categorical), and season. A Tukey–Kramer honestly significant difference 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).

We used a random forest model (Breiman 2001; Cutler et al. 2007) from the randomForest package (Liaw and Wiener 2002) to determine if Muskellunge presence in Lake Superior varied by sex, strain, or length. We determined whether a Muskellunge was using Lake Superior with the last observation carried forward residency code. An individual was considered to have used Lake Superior if it spent at least one full 1-h time bin in Lake Superior.

RESULTS

Sixty Muskellunge were surgically implanted with acoustic transmitters (Table S.2). All recaptured individuals in 2017 and 2018 had healed incisions. The sample was composed of 30 females (mean = 1,123 mm; range = 905–1,280 mm) and 28 males (mean = 993 mm; range = 791–1,132 mm), and two individuals of unknown sex. The length distributions of the tagged sample and the total sample population were analogous (two-sample Kolmogorov–Smirnov test: $P = 0.91$). Individuals logged 4,161–230,180 detections, with an average of 109,546 detections over the 15 months or 455 d of this project. Every receiver within the SLRE array detected at least one tagged Muskellunge. Two of our Muskellunge were also detected by four U.S. Fish and Wildlife Service receivers on the south shore of Lake Superior (Figure 1). Two receivers failed to collect data during parts of the study period due to battery or equipment failure. Seven individuals were removed from analyses because their status became unknown during the project (e.g., consistent detection at a single receiver or not detected for at least 1 year). These detection patterns may be due to transmitter or suture failure, natural or fishing mortality, or movements beyond an acoustic array.

Genetic Ancestry

The Muskellunge population of the SLRE had substantial proportions of each pure strain and hybrid individuals. The BAPS program estimated high admixture coefficients for most individuals that were classified as pure strain (high coefficients for one strain indicate a lack of admixture). Admixture coefficients were 1.00 for all but three of the individuals that were classified as pure strain (Figure 2); three MN strain individuals had coefficients from 0.81 to 0.89 for the MN strain, but these did not have significant evidence of admixture. Individuals that were classified as hybrids had admixture coefficients for the MN strain ranging from 0.27 to 0.80. Of the 60 tagged Muskellunge, 29 (48.3%) individuals were classified as MN strain, 14 (23.3%) as WI strain, and 17 (28.3%) as hybrid. Out of 258 successfully genotyped individuals from all trapped individuals, 107 (41.5%) were categorized as MN strain, 56 (21.7%) as WI strain, and 95 (36.8%) as hybrid. Tagged fish slightly overrepresented MN strain and underrepresented hybrids in the total adult population; however, there was no significant difference between the tagged and total adult population sample ($\chi^2 = 0.4339$, df = 2, $P = 0.80$).

Spatial Use

Tagged individuals exhibited highly variable spatial use over time. For example, 9% of the tagged individuals (5 individuals) stayed within two sections, while 30% (16 individuals) spent time in all six study sections. Despite this individual variability, the majority of the tagged population showed seasonal shifts in spatial use, moving upstream in spring, dispersing downstream (and some

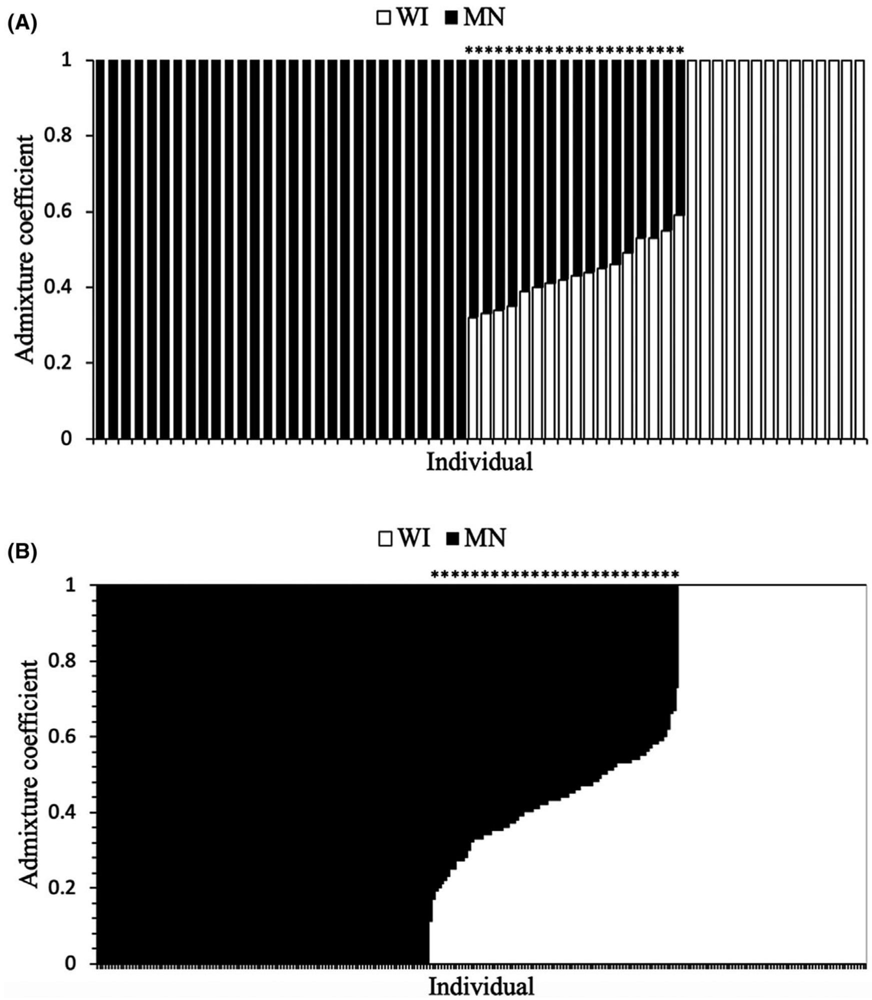

FIGURE 2. Bayesian Analysis of Population Structure (BAPS) estimated admixture coefficients for **(A)** 60 acoustically tagged individuals and **(B)** all 258 Muskellunge caught in spring 2017 in the St. Louis River estuary. Each thin vertical bar represents an individual. Asterisks above the bars indicate individuals classified as admixed (i.e., hybrids) at $P < 0.05$.

individuals moving into Lake Superior) throughout summer, and returning to the middle river during fall and winter (Figures 3, 4; Table 1).

Sex, strain, and season were statistically significant factors affecting the use of various sections. Males were more likely than females and WI strain individuals were more likely than MN strain individuals to spend time in section 1 (19 and 10 d more on average per male and WI strain, respectively). Hybrids used section 2 more than other strains (12 d more on average per hybrid), and section 4 was more often used by hybrid and WI strain Muskellunge than by MN strain individuals. Summer use was greatest within sections 5 and 6. Females spent, on average, 10 d more in section 5 than males. Lastly, MN strain individuals spent on average 10 d more in section 6 (Lake Superior) than hybrid and WI strain individuals. Many of the tagged Muskellunge exhibited similar movement patterns in 2017 and 2018. Similar between-year movements consisted of Muskellunge moving past the same receivers within similar time periods in the spring and summer, which was apparent in abacus plots of individual Muskellunge movements (Figure S.1 available in the Supplement in the online version of this article). Pinch points between river sections were effective overall, with only about 10% of transitions resulting in both pinch point receivers being missed (Table S.3).

Lake Superior Use

Forty-seven percent of acoustically tagged Muskellunge (25 individuals) visited Lake Superior ($n = 24$ in 2017; $n = 22$ in 2018), with 21 individuals using the lake in both years. Individuals spent an average of 50.8 d (~1 to 175 d; median = 43.3 d) in Lake Superior per year, excluding an individual that never returned to the SLRE (Figure 5).

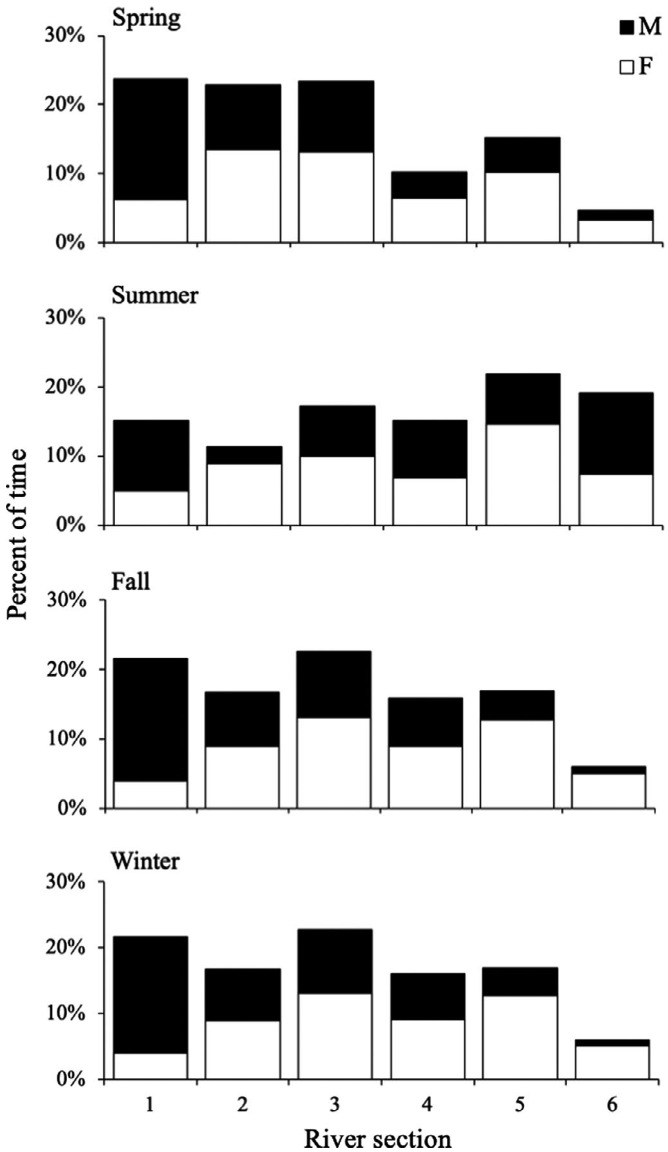

FIGURE 3. Percentage of time that male (M) and female (F) Muskellunge were detected in each river section per season during the 15-month study on the St. Louis River estuary (SLRE). Numbers on the *x*-axis correspond to the river sections in Figure 1. Sections 1–5 are within the SLRE, and section 6 is Lake Superior proper.

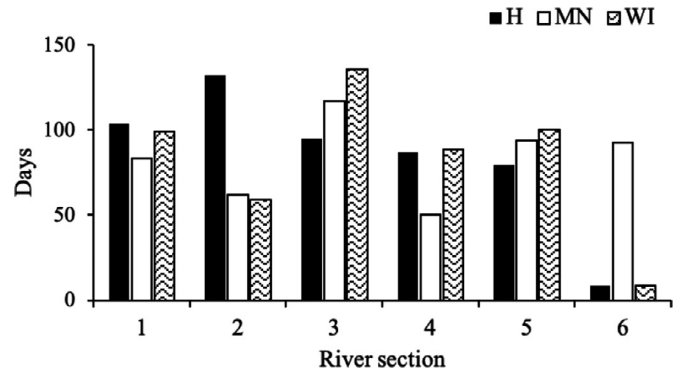

FIGURE 4. Total number of days that Minnesota (MN) strain, Wisconsin (WI) strain, and MN × WI hybrid (H) Muskellunge were detected in each river section during the 15-month study on the St. Louis River estuary (SLRE). Numbers on the *x*-axis correspond to the river sections shown in Figure 1. Sections 1–5 are within the SLRE, and section 6 is Lake Superior proper.

The random forest model correctly assigned individuals that used Lake Superior 72% of the time. Strain was an important driver of Lake Superior use, while sex and length were weak predictors (Figures 6, S.2). Eighty percent of the individuals that used Lake Superior were MN strain, despite making up only 48% of the tagged fish.

Two individuals made long-distance movements to U.S. Fish and Wildlife Service acoustic receivers that were located along the southern shore of Lake Superior (Figure 1). One Muskellunge traveled at least 90 km to Bark Point and returned to the SLRE in both 2017 and 2018. A second Muskellunge migrated at least 150 km to Chequamegon Bay during October 2017 and did not return to the SLRE during the study. This individual was not detected from December 1, 2017, to October 17, 2018, but it reappeared on the Chequamegon Bay acoustic receiver array on October 18, 2018 (74 d after our study concluded).

DISCUSSION

This project is an important first step in building a foundation of Muskellunge movement ecology data in the SLRE to inform fishery management decisions and guide restoration efforts within an AOC. Passive acoustic tracking of adult Muskellunge in the SLRE revealed highly variable individual movements but also highlighted trends in population movements that were driven by season, sex, and strain. These general population trends have also been observed in Muskellunge in other areas of their range (Younk et al. 1996; Kapuscinski et al. 2013; Morrison and Warren 2015). Almost 50% of the tagged Muskellunge utilized Lake Superior, a behavior that was most common among the MN strain. The continuous data provided by the acoustic array revealed Muskellunge habitat use within the SLRE throughout the year. Restoration projects may provide critical habitat for reproduction, whereas other habitats may be crucial for Muskellunge growth and survival, all of which are important for conserving and enhancing esocid populations (Crane et al. 2015; Morrison and Warren 2015).

Despite the variability in individual movements, many individual SLRE Muskellunge exhibited fairly consistent patterns between 2017 and 2018, suggesting that individual movements are persistent from year to year. Large upstream movements in spring were likely related to

TABLE 1. Results of ANOVA and Tukey–Kramer honestly significant difference post hoc tests used to evaluate the differences in residency time (d) in each section with Muskellunge sex, strain, and season. Values were considered significant at $P < 0.05$ (*). 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	
Variable	ANOVA *P*-value	Tukey pairwise comparison	Tukey *P*-value	Category	Mean number of days
		River section 1			
Sex	4.37×10^{-7}	M–F	4.00×10^{-7}*	M	28.8
				F	9.8
Strain	0.001	MN–H	0.078	WI	25.6
		WI–H	0.335	H	23.3
		WI–MN	2.15×10^{-3}*	MN	15.6
Season	0.354	—	—		
		River section 2			
Sex	0.171	—	—		
Strain	3.17×10^{-6}	MN–H	1.23×10^{-5}*	H	19.9
		WI–H	4.41×10^{-5}*	MN	7.4
		WI–MN	0.817	WI	7.3
Season	0.047	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		
		River section 3			
Sex	0.549	—	—		
Strain	0.314	—	—		
Season	0.685	—	—		
		River section 4			
Sex	0.194	—	—		
Strain	9.87×10^{-6}	MN–H	2.86×10^{-5}*	H	18.0
		WI–H	0.122	WI	10.7
		WI–MN	0.045*	MN	6.2
Season	0.028	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*		
		River section 5			
Sex	0.001	M–F	0.001*	F	21.1
				M	11.1
Strain	0.343	—	—		
Season	0.003	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*		

TABLE 1. Continued.

Variable	ANOVA *P*-value	Tukey pairwise comparison	Tukey *P*-value	Effect size	
				Category	Mean number of days
		River section 6			
Sex	0.812	—	—		
Strain	2.33×10^{-5}	MN–H	0.014*	MN	13.6
		WI–H	0.991	H	3.5
		WI–MN	0.008*	WI	2.9
Season	4.27×10^{-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		

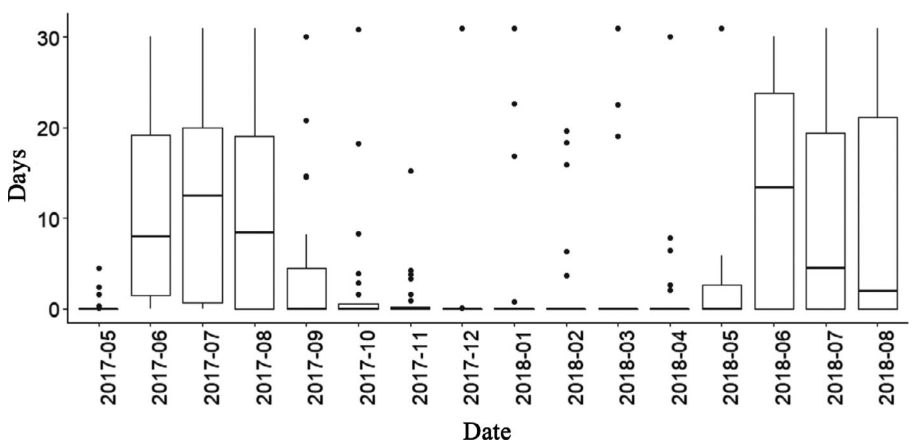

FIGURE 5. Box plot showing the number of days that Muskellunge spent in Lake Superior each month over the 15-month study. The Muskellunge included are only individuals that spent time in Lake Superior and returned to the St. Louis River estuary ($n = 24$). One additional individual left the estuary, was detected in Chequamegon Bay, Wisconsin, and never returned to the estuary.

spawning activities as observed in other systems (Dombeck 1979; Younk et al. 1996; Weeks and Hansen 2009; Morrison and Warren 2015). Dombeck (1979) proposed that spawning activities were initiated by increased water temperatures and dissolved oxygen levels. Spring coincides with warming water temperatures that reach ideal spawning temperature first in shallow habitats. The upper river of the SLRE (sections 1 and 2) contains many shallow, vegetated bays and wetlands—as well as two AOC restored habitat sites—that would be suitable for spawning (Dombeck 1979; Dombeck et al. 1984). Males also spent significantly more time than females 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 the spawning season. This result is consistent with evidence that male Muskellunge in the upper Mississippi River arrived to spawning areas first and lingered, whereas females staged away from spawning areas and only briefly entered spawning areas to spawn (Younk et al. 1996).

Many SLRE Muskellunge moved downstream after the spring spawning season. The lower river may provide a cooler refuge or additional forage during the warm summer months (Farrell et al. 2003). Almost half of the acoustic-tagged Muskellunge moved into Lake Superior, and two of these individuals subsequently made long-distance movements. Similarly, almost half of the tagged Muskellunge in the St. Lawrence River migrated to eastern Lake Ontario during the summer (Farrell et al. 2003). Muskellunge have been observed migrating up to 156 km in other systems during the summer (Crossman 1990; Curry et al. 2007; Kerr and Jones 2017; C. Wagner, Ohio

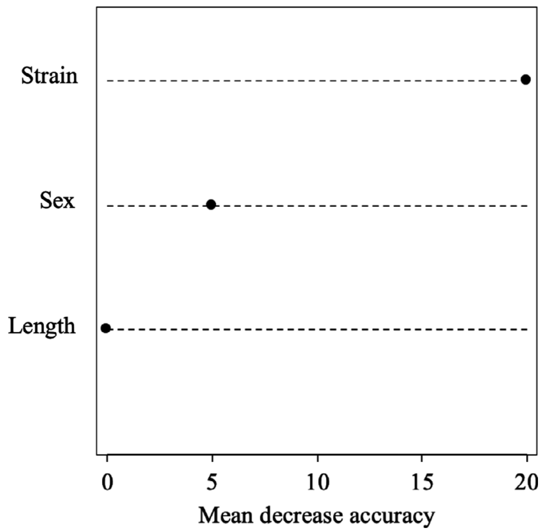

FIGURE 6. The importance of strain, sex, and length in explaining Lake Superior use by Muskellunge tagged in the St. Louis River estuary based on a random forest model. The *x*-axis indicates the predictive accuracy for each variable. A higher mean decrease in accuracy indicates greater importance for a given variable when explaining Lake Superior use.

Department of Natural Resources, personal communication).

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 concentrations of dissolved oxygen in overwintering grounds. Long-distance migration with coordinated peak movement in fall and sedentary behavior in winter are also common among other fishes, such as Striped Bass *Morone saxatilis* and Smallmouth Bass (Langhurst and Schoenike 1990; Young and Isely 2002; Able and Grothues 2007). The Muskellunge in our study used the middle river (section 3) most during winter, suggesting that this is an important overwintering area. Several tributary streams and rivers, such as the Pokegama River, flow into this section of the SLRE. Tributary outfalls are important overwintering habitat for stream fishes (Koizumi et al. 2017) and lake fishes (Jepsen and Berg 2002), which use these areas as thermal refuges, for their coarse habitat, or for slower flow velocity (Koizumi et al. 2017).

The spatial ecology of the SLRE Muskellunge population was also influenced by strain. Interestingly, the strains did not differ in their use of SLRE section 5 that connects to Lake Superior, yet WI strain fish and hybrids infrequently moved into the lake (section 6). 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). We speculate that the WI and MN strains were predisposed to different habitats and waterbodies, which has also been suggested for other fishes, such as Brook Trout *Salvelinus fontinalis* (Van Offelen et al. 1993). The MN strain originated from Leech Lake, a large lake (41,700 ha) with an irregular shoreline and numerous bays. The WI strain originated from small lakes and rivers, mostly in the Chippewa River drainage (P. Piszczek, Wisconsin Department of Natural Resources, personal communication). These contrasting 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 hybrids. 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, Muskellunge that migrated upstream from their spawning grounds in the St. Lawrence River to eastern Lake Ontario likely exploited foraging opportunities that were 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 *Coregonus artedi* in deeper waters. Cisco are abundant in Lake Superior but uncommon in the SLRE (Gorman 2012; Yule et al. 2013). Dombeck (1979) hypothesized 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 of the MN strain. Additionally, naturally produced juvenile (age-0) Muskellunge had a high percentage of MN ancestry (largely pure MN strain; L. M. Miller, unpublished data), indicating that the MN strain may be more successful at reproduction than the WI strain, although strain differences in spawning or early rearing locations could not be ruled out because the entire estuary was not sampled.

It is important to understand Muskellunge spatial ecology and behavioral differences to assess regulations and stocking goals. The differential movement by strain shown in this study supports the idea of carefully considering the strain and habitat in the source system when introducing or re-introducing Muskellunge. For example, a strain that is more likely to move large distances may be more prone to escapement from reservoirs, which has been shown to be an issue in Muskellunge management (Wolter et al. 2013; Morrison and Warren 2015), including the introduction of Muskellunge to a large watershed (Kerr and Jones 2017). Differences in strain behaviors and performance have important implications for many fisheries, especially where multiple strains may be present and are sustained through stocking (Wagner and Wahl 2011; Diana and

Wagner 2017). Managers would also benefit from linking telemetry data with mark–recapture data to improve our understanding of Muskellunge movements relative to where they are managed to better develop population estimates and guide management.

When restoration projects are scheduled, fine-scale telemetry data from indicator species pre- and post-restoration paired with data on the aquatic environmental conditions will provide managers with a more integrated approach to inform restoration practices and will identify opportunities for habitat enhancement, creation, and restoration. Future Muskellunge research would benefit from a study incorporating telemetry and stable isotope data to investigate the influence of prey on movement patterns and quantify prey contribution to the Muskellunge diet (Eggenberger et al. 2019). Lastly, more work is needed to determine patterns of movement and habitat use by juvenile Muskellunge (<763 mm). Although studies have characterized habitats of age-0 Muskellunge, little is known about habitat use and movements by subadults of older ages (Wagner and Wahl 2011; Farrell et al. 2014; Crane et al. 2015).

This study demonstrated that Muskellunge spatial use is related to season, sex, and strain in the SLRE and southwestern Lake Superior. Overall, our results provide a more thorough understanding of Muskellunge ecology in the SLRE and southwestern Lake Superior. The maintenance of this project by the MNDNR will continue to increase our knowledge of Muskellunge ecology to guide future management efforts of Muskellunge in the SLRE and in other freshwater systems.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Supplementary materials

Table S.1. 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. The MNDNR and WIDNR stocked WI strain in 1986 (*).

	MNDNR		WIDNR	
Year	Muskellunge stocked	Strain	Muskellunge stocked	Strain
1983	0	—	500	WI
1984	0	—	500	WI
1986*	800	WI	2000	WI
1987	0	—	3039	WI
1988	0	—	2500	WI
1989	346	MN	5000	WI
1990	0	—	5000	WI
1991	5002	MN	4658	WI
1992	5000	MN	2500	WI
1993	0	—	2500	WI
1994	5000	MN	0	—
1994	0	—	0	—
1995	0	—	0	—
1996	0	—	0	—
1997	5500	MN	2500	WI
1998	0	—	0	—
1999	0	—	0	—
2000	5000	MN	2500	WI
2001	5000	MN	3500	WI
2002	0	—	2500	WI
2003	5001	MN	0	—
2004	0	—	2500	WI
2005	5005	MN	0	—
2015	2189	MN	0	—
Strain total	43,843		41,697	

Table S.2. Summary of tagging and biological data for 60 muskellunge acoustically tagged in the St. Louis River Estuary, Lake Superior. Individuals were passively tracked from May 9, 2017 to August 6, 2018. Receivers detected (RD) indicates how many of the 40 receivers detected each 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 (*).

Table S.2.

ID	Length (mm)	Sex	Weight (kg)	Strain	RD	Number of detections	First detection	Last detection	Days tracked	Status
1	1162	M	13.25	MN	17	112869	5/9/17	6/10/18*	397	A
2	1215	F	14.5	MN	5	102224	5/9/17	8/6/18	454	U
3	1254	F	15.25	WI	22	98003	5/9/17	8/1/18*	449	A
4	1002	F	8.75	H	17	180300	5/9/17	8/6/18	454	A
5	1203	F	14.5	WI	14	54731	5/9/17	8/6/18	454	A
6	1170	F	13.25	MN	34	110451	5/9/17	8/6/18	454	A
7	1181	F	12.5	H	9	114246	5/9/17	8/6/18	454	A
8	1235	F	17.25	WI	32	101194	5/9/17	8/6/18	454	A
9	1006	M	6.5	H	21	171276	5/9/17	8/6/18	454	A
10	885	M	4	MN	35	123392	5/9/17	7/29/18	446	A
11	793	M	3.5	MN	32	110506	5/9/17	6/27/18*	414	A
12	1147	F	13.75	WI	11	84094	5/9/17	8/6/18	454	A
13	1190	F	14	MN	24	48100	5/9/17	10/26/17*	170	A
14	905	F	5	H	31	112869	5/9/17	8/6/18	454	A
15	1255	F	15.75	MN	30	120211	5/9/17	8/3/18*	451	A
16	791	U	3.5	MN	6	230180	5/9/17	8/6/18	454	U
17	1212	F	17	MN	30	122176	5/9/17	8/3/18	451	A
18	1062	M	12.75	MN	25	177394	5/9/17	8/6/18	454	A
19	1008	F	8	H	11	105312	5/9/17	7/1/18*	418	A
20	1251	F	15.5	MN	12	167308	5/9/17	8/5/18*	453	A
21	991	M	8.25	H	10	97294	5/9/17	8/6/18	454	A
22	1090	M	9.25	MN	38	80804	5/9/17	8/6/18	454	A
23	1111	M	12.75	MN	28	112140	5/9/17	8/6/18	454	A
24	1097	M	14	MN	26	36856	5/9/17	8/6/18	454	A
25	907	F	6.5	MN	32	131824	5/9/17	5/20/18	376	A
26	1053	M	8.75	H	2	167144	5/9/17	8/6/18	454	A
27	865	M	4	H	9	24123	5/9/17	7/31/18	448	U
28	1018	F	–	WI	20	112978	5/9/17	8/6/18	454	A
29	1136	F	14	WI	23	129929	5/9/17	8/6/18	454	A
30	1120	F	11.25	WI	15	108880	5/9/17	8/6/18	454	A
31	1036	F	8.25	WI	5	82686	5/9/17	8/6/18	454	U
32	1159	F	12.75	H	12	33979	5/9/17	8/4/18*	452	A
33	1270	F	18.75	MN	38	147318	5/9/17	8/6/18	454	A

Table S.2. (continued)

ID	Length (mm)	Sex	Weight (kg)	Strain	RD	Number of detections	First detection	Last detection	Days tracked	Status
34	1064	F	12.25	WI	17	82355	5/9/17	8/6/18	454	A
35	987	F	7.5	H	26	151405	5/9/17	8/6/18	454	A
36	1158	M	13.25	MN	32	125175	5/9/17	8/6/18	454	A
37	1265	F	16.75	MN	19	162078	5/9/17	8/6/18	454	A
38	863	M	4.75	H	15	115453	5/9/17	8/6/18	454	A
39	1280	F	14.2	MN	16	69485	5/9/17	8/6/18	454	A
40	1080	M	8	MN	3	31215	5/9/17	8/6/18	454	A
41	1020	M	8.5	H	3	70463	5/9/17	8/6/18	454	A
42	1164	F	10.75	WI	14	15902	5/9/17	6/7/18	394	A
43	954	F	7.5	H	16	185405	5/9/17	8/6/18	454	A
44	807	U	4	WI	18	7295	5/9/17	7/9/17	61	U
45	832	M	4.5	H	2	4161	5/9/17	6/1/17	23	U
46	984	M	6.5	MN	10	37631	5/9/17	7/2/18	419	A
47	1114	M	12.5	MN	26	108350	5/9/17	7/18/18*	435	A
48	1105	M	9.5	MN	19	89052	5/9/17	8/3/18*	451	A
49	856	M	5.5	WI	6	9559	5/9/17	5/27/18*	383	A
50	971	M	8.5	MN	25	37811	5/9/17	8/4/18*	452	A
51	1259	F	17.75	MN	36	122658	5/9/17	8/6/18	454	A
52	1039	M	8	MN	31	101398	5/9/17	8/6/18	454	A
53	962	F	8.75	H	8	177817	5/9/17	8/6/18	454	A
54	1074	M	9.5	MN	26	76269	5/9/17	8/5/18*	453	A
55	1040	F	9	WI	29	47865	5/10/17	7/14/18	430	A
56	912	M	6	H	16	26007	5/10/17	8/6/18	453	A
57	951	M	6	H	2	60036	5/11/17	8/6/18	452	A
58	964	F	8	WI	2	12147	5/11/17	8/6/18	452	U
59	996	M	8	MN	16	164503	5/11/17	8/6/18	452	A
60	1121	M	10	MN	36	108616	5/14/17	8/3/18*	446	A

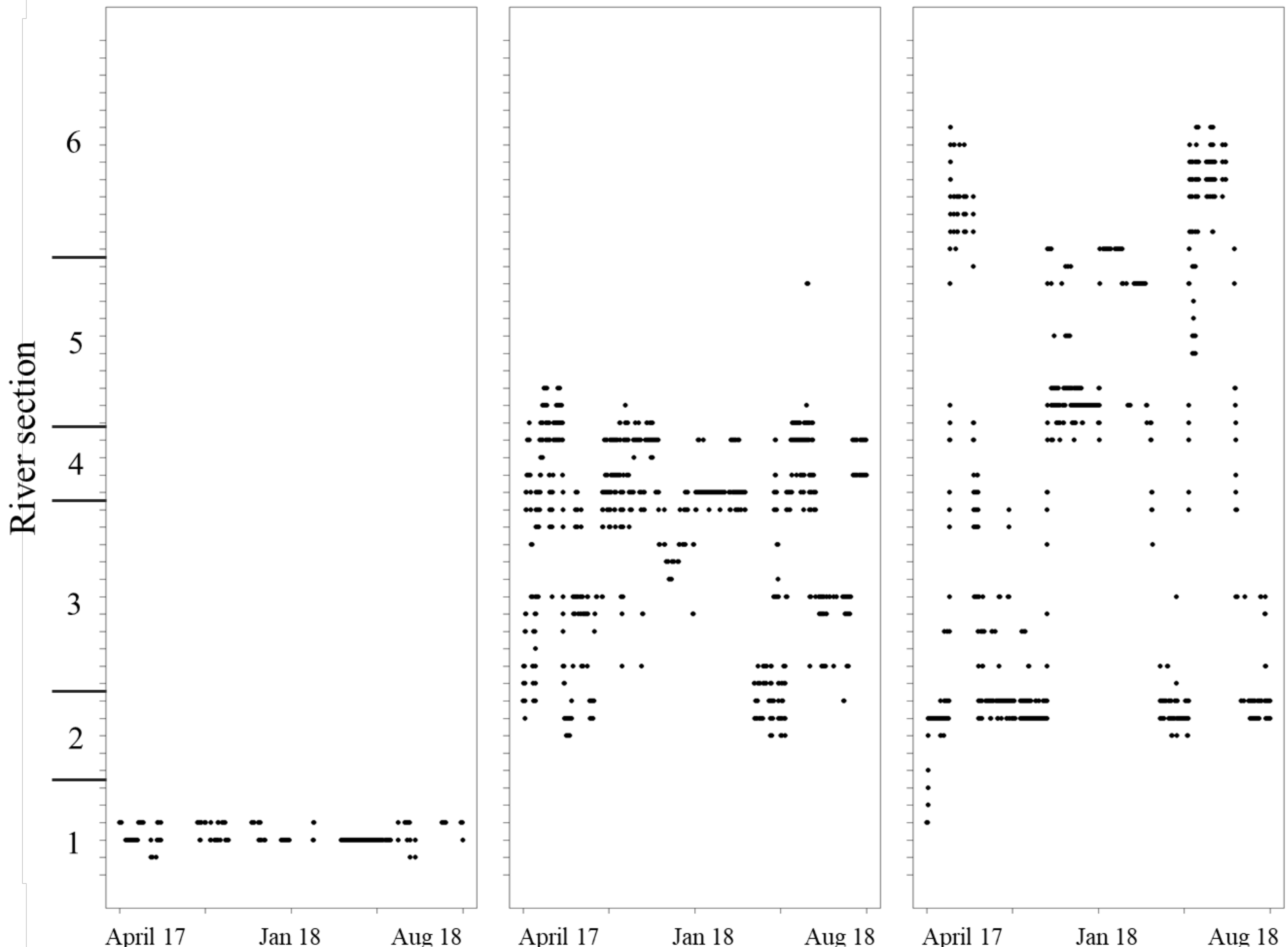
Table S.3. Pinch point efficiency of five pinch points that divide the St. Louis River Estuary into six different sections. An initial subset of telemetry data were used to determine pinch point efficiency by dividing the number of transitions missed by the number of transitions at each pinch point. Transitions missed were identified when an individual was detected in a new section without being detected by either pinch point receiver.

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%

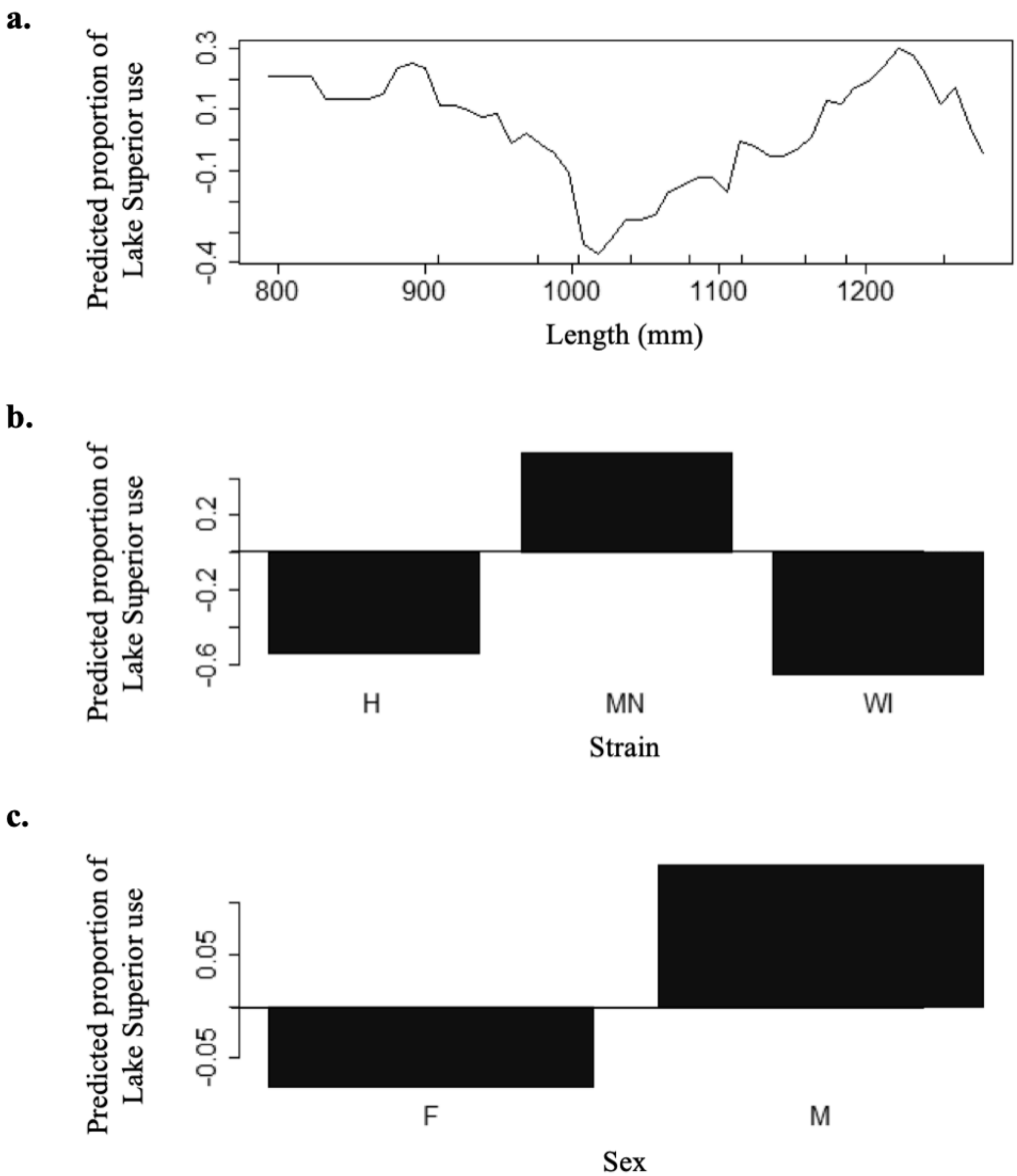
Supplementary figure captions

Figure S.1. 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. All abacus plots can be viewed at the University of Minnesota-Twin Cities Digital Conservancy (https://conservancy.umn.edu/handle/11299/208285).

Figure S.2. 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.



River section
6
5
4
3
2
1
April 17
Jan 18
Aug 18
April 17
Jan 18
Aug 18
April 17
Jan 18
Aug 18


a.
Predicted proportion of Lake Superior use
0.3
0.1
-0.1
-0.4
800
900
1000
1100
1200
Length (mm)
b.
Predicted proportion of Lake Superior use
0.2
-0.2
-0.6
H
MN
WI
Strain
c.
Predicted proportion of Lake Superior use
0.05
-0.05
F
M
Sex