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Telemetry and genetic data characterize lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) breeding ecology and spawning site fidelity in Green Bay Rivers of Lake Michigan

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Summary

The primary objective of this study was to use direct (acoustic telemetry) and indirect (genetic assignment) methods to characterize basic aspects of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) breeding ecology. Specifically, data on natal origin, spawning habitat, spawn sex-size structure, and sex-specific residence times, spawning site fidelity, seasonal movements and degree of straying between demographically and genetically independent populations. A secondary benefit of the project was the non-spawning period movements of tagged fish. The analysis was based on acoustic telemetry and genetic assignment tests for individuals captured from the Menominee, Peshtigo, Oconto and Fox rivers (draining into Green Bay) in Wisconsin, which represent the only spawning rivers in western Lake Michigan. Sturgeon ($N = 160$) were captured during the spring (18 April-25 May) of 2011-2015 using large dip nets (51%) and electro fishing (49%). Captured sturgeon were genotyped and assigned to a Great Lakes river population using likelihood-based estimators based on microsatellite ($N = 13$) genotype and mtDNA haplotype frequencies. Assignments revealed that captured adults from four Green Bay rivers were of an aggregate composition from the overall sample size ($N = 160$) of 38.2% assigned to the Fox-Wolf River population, 23.5% to the Menominee River population and 37.4% to the Peshtigo-Oconto River population. One adult female sturgeon was assigned to the Manistee River population (eastern Lake Michigan). Of the 160 captured adults, 115 spawning lake sturgeon were tagged with surgically inserted acoustic tags/transmitters (Vemco V-16). Collected lake sturgeon ranged in size from 114 cm to 185 cm total length, and girth from 43 cm to 74 cm. Visual examination during surgery confirmed the sex of each individually tagged fish. Timing of post-surgery departure from the rivers differed significantly between males (mean 35.6 days) and females (mean 8.9 days), but was not significant because of the large variability. Post-surgery residence time was longer for the Menominee River sturgeon compared to individuals from the other rivers. More than twice as many males versus females were detected in the four rivers during the non-spawning period. A subsample of 53 lake sturgeon returned to one of the four rivers 1.9-3.4 years after surgery. Eight males returned to one of the four rivers in successive springs but no female sturgeon returned in successive years. High straying (i.e., dispersal to a non-native stream to spawn) rates occurred among rivers. Transition probability was highest for lake sturgeon captured in the Peshtigo and Oconto Rivers moving to the Fox River (0.77), and Fox River captured lake sturgeon moving to the Peshtigo and Oconto rivers (0.21). Since these populations represent the only spawning sturgeon in western Lake Michigan, lake sturgeons associated with these rivers represent spawning populations of significant importance towards their restoration in Lake Michigan. This study improved the understanding of the species breeding ecology and movement patterns needed to guide management decisions, such as prioritizing habitats for restoration or protection.

1 | INTRODUCTION

Analyses of spawning migrations are critical to the management of lake sturgeon (*Acipenser fulvescens*) spawning populations in four Green Bay Rivers and towards restoration efforts for this species in the Great Lakes in general. Lake sturgeon populations in the Great Lakes declined in the early 20th century because of anthropogenic activities such as pollution, overharvesting (initially), followed by dam construction and habitat loss/fragmentation (primarily due to dam construction). (Auer, 1996). Lake Michigan populations were reduced to 1% of historic levels (Hay-Chmielewski & Whelan, 1997). Remnant spawning populations of lake sturgeon persist in Lake Michigan, including the Menominee, Peshtigo, Oconto and Fox rivers, but their abundance and reproductive success is unknown (Baker, Elliott, Holey, & Thuemler, 2000). In these rivers, spawning areas for lake sturgeon that reside in Green Bay or Lake Michigan are restricted to the lower section because of hydroelectric dams located 3.7 to 23 km upstream. Sturgeon spawning also occurs in the upper Menominee and Fox rivers by river-resident fish (Priegel and Wirth, 1975; Thuemler, 1985), but resident sturgeon are nonexistent in the upper Peshtigo and Oconto rivers.

Previous studies documented spawning activity in each Green Bay river (Benson, Elliott, Meronek, & Sutton, 2006; Caroffino, Donofrio, Elliott, & Sutton, 2010; Elliott & Gunderman, 2008). Spawning population sizes in each Green Bay River remain relatively small, with less than 100 spawners each in the Fox and Oconto rivers, approximately 500 in the Peshtigo River and about 1,000 in the Menominee River (Elliott & Gunderman, 2008). In addition, contemporary and asymmetrical straying rates among Lake Michigan lake sturgeon populations have been documented (Homola et al., 2012). However, fidelity to spawning areas in each river was unknown.

The tendency for fish species to return to spawn in their natal streams (homing) is important both from ecological and managerial perspectives. Although straying is important for the colonization of new or previously extirpated streams (Anderson, Kiffney, Press, & Quinn, 2008; Milner, 1987; Milner et al., 2000), homing allows for the growth and recovery of individual populations. For example, successful management of the Winnebago system lake sturgeon population is linked to a progressive harvest regulation program and protection of the adult population, which eventually enabled more fish to have access to spawning areas in the upper Fox and Wolf rivers (Binkowski & Bruch, 2002).

Lake sturgeon populations have also utilized river habitat for year round residency. Lake sturgeon resided in the Kettle River, Minnesota, year round (Borkholder et al., 2011). Adult Sturgeon are also known to be present in the Wolf River, Wisconsin, during non-spawning periods (Lyons & Kempinger, 1992).

Telemetry is one of the traditional methods to document lake sturgeon movement patterns and straying rates (Auer, 1999). Advances in acoustic telemetry, including longer transmitter life that allows the tracking of individual fish for multiple years, are applicable for a long-lived, iteroparous species like lake sturgeon and allow researchers to better evaluate spawning periodicity and straying rates.

The use of genetic techniques for a species like lake sturgeon is particularly important to develop information on straying because of the species' reproductive ecology. *Acipenser fulvescens* are a long-lived potamodromous fish species that reaches sexual maturity at age

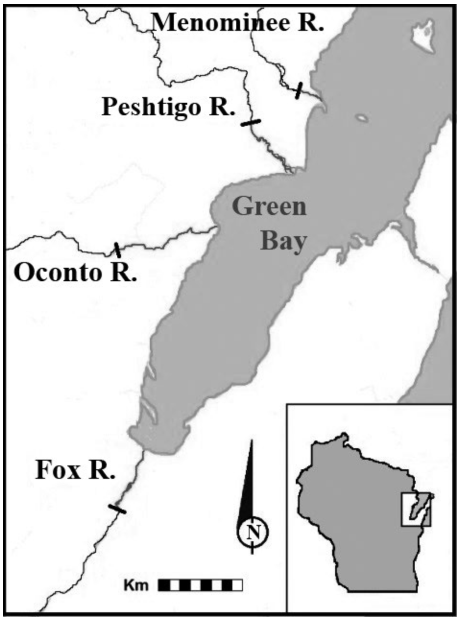

FIGURE 1 Location of the four rivers in study area within Green Bay, Lake Michigan. Bars indicate the location of the lowest dam on each river

15-25 years (Harkness & Dymond, 1961; Houston, 1987). All Green Bay lake sturgeon are highly genetically differentiated from the lake sturgeon originating from eastern (Michigan) rivers to Lake Michigan (DeHaan, Elliott, Libants, & Scribner, 2006; Homola et al., 2012; Hill, May, Quinlan, Robinson, & Welsh, 2003). Genetic analysis has recently allowed scientists to study straying rates and gene flow in *A. fulvescens* (Homola et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area includes geographically proximal but physically distinct Wisconsin rivers (Menominee, Peshtigo, Oconto, and Fox) of Green Bay in western Lake Michigan (Figure 1). In the Menominee River, the first dam is located 3.7 km from the river mouth. The Menominee River has a mean daily discharge of 85 m^3s^{-1} and a 10,178 km^2drainage area. The first dam on the Peshtigo River is 19.2 km from the river mouth. The Peshtigo River has a mean daily discharge of 29 m^3s^{-1} and a drainage area of 2,800 km^2. The first dam on the Oconto River is 23 km from the river mouth. Its drainage size is similar to the Peshtigo with a drainage area of 2,500 km^2 but the daily mean discharge is approximately half the discharge of the Peshtigo River, 15 m^3s^{-1}. The Fox River is the largest of the four rivers, with a watershed size of 16,394 km^2 and a daily mean discharge of 112 m^3s^{-1}. The first dam on the Fox is 10.8 km from the river mouth (Figure 1).

2.2 | Field collection methods

From 2011-2015, adult lake sturgeon were captured in the spring (mid-April to late May) at known spawning areas in each river. Fifteen surveys were conducted on the Menominee, Peshtigo, Oconto, and Fox rivers from late April to late May, 2011-2015 (Table 1), where water temperatures ranged from 11.1 to 21.1°C and the mean was 14.1°C. The relatively shallow spawning areas of the two studied rivers allowed the capture of lake sturgeon with large dip nets (Peshtigo *N* = 55 and Fox *N* = 27). The remaining 49% of 160 were captured from deeper waters with electrofishing.

Fish were collected with large dip nets on the Fox and Peshtigo rivers when adults congregated to spawn in relatively shallow water (<1 m). Fish were collected from deeper water using electro fishing on the Menominee, Peshtigo and Oconto rivers. Pulsed DC electro fishing settings were 6-10 amps, 25% duty cycle, and 150-250 volts. The date and location were recorded for each captured sturgeon. All fish were measured for total length (TL) and girth to the nearest centimeter. A small piece of caudal or dorsal fin tissue was retained for genetic analysis. A Biomark pocket reader was used to scan each fish for a passive integrated transponder (PIT) tag (both 125 kHz and 134.5 kHz tags). If no PIT tag was detected, then a new 12.5 mm 134.5 kHz tag was inserted. PIT tags were used to individually identify all fish. Sex was determined by visual examination of the gonads during surgical insertion of acoustic transmitters.

Fish were placed ventral side up in a fabric sling supported by a metal frame. One end of the sling had a folded pouch for the head of the fish. Fresh river water was continually poured into the pouch to irrigate the gills. Transmitters were inserted into the abdomen of each sturgeon through an approx. 40 mm mid-ventral incision. Upon reaching the peritoneum, a retractor was placed into the incision to spread the musculature and enable a clear view of the opening into the abdomen including gonadal area (Fox et al., 2000). The incision was closed with 3-5 simple, interrupted Vicryl brand sutures and surgical materials were disinfected with 0.02% Chlorhexiderm before and after surgery. The surgery was completed in less than three minutes and fish were either released directly into the river or held temporarily

Date	River	Temperature (°C)	Genetic sample size	Transmitter sample size
May 21, 2012	Menominee	21.1	15	15
May 16, 2013	Menominee	14.4	10	8
May 25, 2011	Peshtigo	NA	8	8
April 18, 2012	Peshtigo	11.1	7	7
May 10, 2013	Peshtigo	13.3	8	7
May 17, 2013	Peshtigo	15.6	8	0
May 21, 2014	Peshtigo	14.1	20	0
April 30, 2015	Peshtigo	12.8	12	10
April 24, 2012	Oconto	12.2	12	11
May 8, 2012	Oconto	13.9	8	8
May 22, 2013	Oconto	15.5	8	8
May 8, 2014	Oconto	13.9	8	0
April 29, 2015	Oconto	12.8	9	8
May 7, 2013	Fox	12.8	11	10
May 13, 2014	Fox	13.3	16	15
		Totals	160	115

TABLE 1 Dates and location of lake sturgeon sampling from Green Bay Rivers, 2011-15, with total number of individuals sampled (genetics) and number that received acoustic transmitters

in a net pen for no more than two hours, depending on fish condition following surgery.

Vemco 69 kHz V16-6L acoustic tags weighing 17.3 *g* had a maximum length of 98 mm, a 16 mm Ø and an 8-10 year battery life. Transmission delay varied randomly between 60 s and 180 s (mean 120 s). Transmitter viability was determined with a Vemco VR-100 mobile receiver before and after surgery.

Acoustic tags were inserted into 115 of 160 spawning lake sturgeon (39 females and 76 males). Acoustic tags were allocated to the four rivers as follows: 23 for Menominee River, 32 for Peshtigo River, 35 for Oconto River and 25 for the Fox River. A Vemco VR100 receiver verified that all transmitters were active before and after surgery. Following the surgery, a sturgeon was deemed to have departed from the river if it was not detected on any receivers for a period of 30 days; the date that a fish departed the river was set as the date of last detection.

Sturgeon movements were detected with 18 Vemco 69 kHz VR2W stationary receivers in the lower reaches of each river to detect directional movement. One of the receivers in each river was located within 20-150 meters of each spawning site in the waters immediately below each dam (tail water) and maintained for 2-4 years for each river (Menominee and Fox rivers 2015-2016, Oconto River 2014-2016, and Peshtigo River 2013-2016). Additional stationary receivers were deployed further downriver to determine timing and direction of movements for each tagged sturgeon. A total of three receivers were maintained in the Fox, four in the Oconto, five in the Peshtigo and six in the Menominee (Figure 2).

A test V16 transmitter at the Menominee dam tailwater was used to verify the relative detection range of a stationary receiver in a turbulent environment. The test range for that receiver was highly variable from 20 to 100 m. No additional testing of receivers was conducted. Any sturgeon had a spawning opportunity if it was detected by any tailwater receiver during the months of April and May, but actual spawning activity was not verified.

2.3 | Laboratory methods

DNA was extracted from fin samples using QIAGEN DNeasy® kits (QIAGEN Inc.) using protocols recommended by the manufacturer. DNA concentrations were quantified using a NanoDrop® ND-1000 spectrophotometer. Samples were diluted to a concentration of 20 ng/ml for use in PCR (polymerase chain reaction) reactions.

All individuals collected from spawning locations and individuals with telemetry tags ($N = 115$) were genotyped at 13 disomic microsatellite loci. Loci included *LS-68* (May et al., 1997), *Afu68b* (McQuown, Graham, & May, 2002), *Spl120* (McQuown et al., 2000), *Aox27* (King, Lubinksi, & Spidle, 2001), *AfuG9*, *AfuG56*, *AfuG63*, *AfuG74*, *AfuG112*, *AfuG160*, *AfuG195*, *AfuG204* (Welsh et al., 2003), and *Atr113* (Rodzen & May, 2002). PCR reactions were carried out using either an Applied Biosystems (ABI) SimpliAmp or a Startagene Robocycler PCR machine. PCR conditions were as described in Homola et al. (2012). PCR products were subjected to electrophoresis on 6% denaturing polyacrylamide gels. Genotypes were visualized using a Hitachi FMBIOII scanner. Several individuals of known genotype were run on each gel to serve as standards to assign genotypes. All genotypes were scored by two experienced people. Ten percent of all individuals were regenotyped at all 13 loci as a blind test to determine scoring error rate. The error rate for this project was 0%.

A region of the mitochondrial (mt) DNA control region 410 bp in length as described by Breckenbach, Breckenbach, Brown, and Smith (1996) and Debus, Ludwig, May, and Jenneckens (2000) was sequenced for all individuals collected from all spawning locations and for the individuals with telemetry tags using PCR conditions described in DeHaan et al. (2006). PCR products were purified using QIAquick kit (QIAGENE). Sanger sequencing was conducted as described by DeHaan et al. (2006). Electrophoresis was conducted using a capillary electrophoresis ABI 3730xl platform.

All individual sequences were aligned manually. We used the program Collapse (Crandaysdaysll, Posadaysdays, & Templeton, 2000) to assign each mtDNA sequence a haplotype based on homology to previously characterized haplotypes generated by DeHaan et al. (2006). We used the numerical haplotype designations described in DeHaan et al. (2006) (GeneBank accession numbers AY947813 to AY947834).

2.4 | Telemetry data analysis

Acoustic receivers were downloaded twice annually (summer and autumn) from 2011 to 2016. Vemco VUE software was used to identify detections. Suspected false positive detections were identified and removed. False detections were those for which the minimum time between the last or next detection for the same transmitter on the same receiver was greater than 30x the average tag delay (= 3600 S in our study) (Pincock, 2012).

We used two criteria to determine that a fish was considered to be spawning versus simply present in a river, including (i) a tagged fish was detected by any tailwater receiver when known spawning activity was occurring in several sturgeon, or (ii) WDNR/MDNR staff handled a sturgeon that was expressing gametes and an acoustic tagged fish was detected at that same location on the same day. The presence of adult sturgeon on spawning grounds during temperatures documented in our study can reasonably infer that spawning activity occurred in these Green Bay rivers (Binkowski & Bruch, 2002).

2.5 | Statistical analyses

Genetic markers used were previously confirmed to be independent (i.e., no evidence for gametic disequilibrium: DeHaan et al., 2006; Homola et al., 2012). For each lake sturgeon tributary population we estimated the degree of deviation of observed and expected heterozygosities to test observed genotype frequencies in each of 13 microsatellite loci for deviations from Hardy to Weinberg expectations.

F-statistics (Weir, 1996) were calculated using the program *F*-STAT (Goudet, 2001) to estimate the degree of genetic differentiation among spawning populations. Measures of variance in allele frequency among baseline populations were summarized as pair-wise estimates of inter-population F_{st}. Significance of mean inter-population F_{st} values

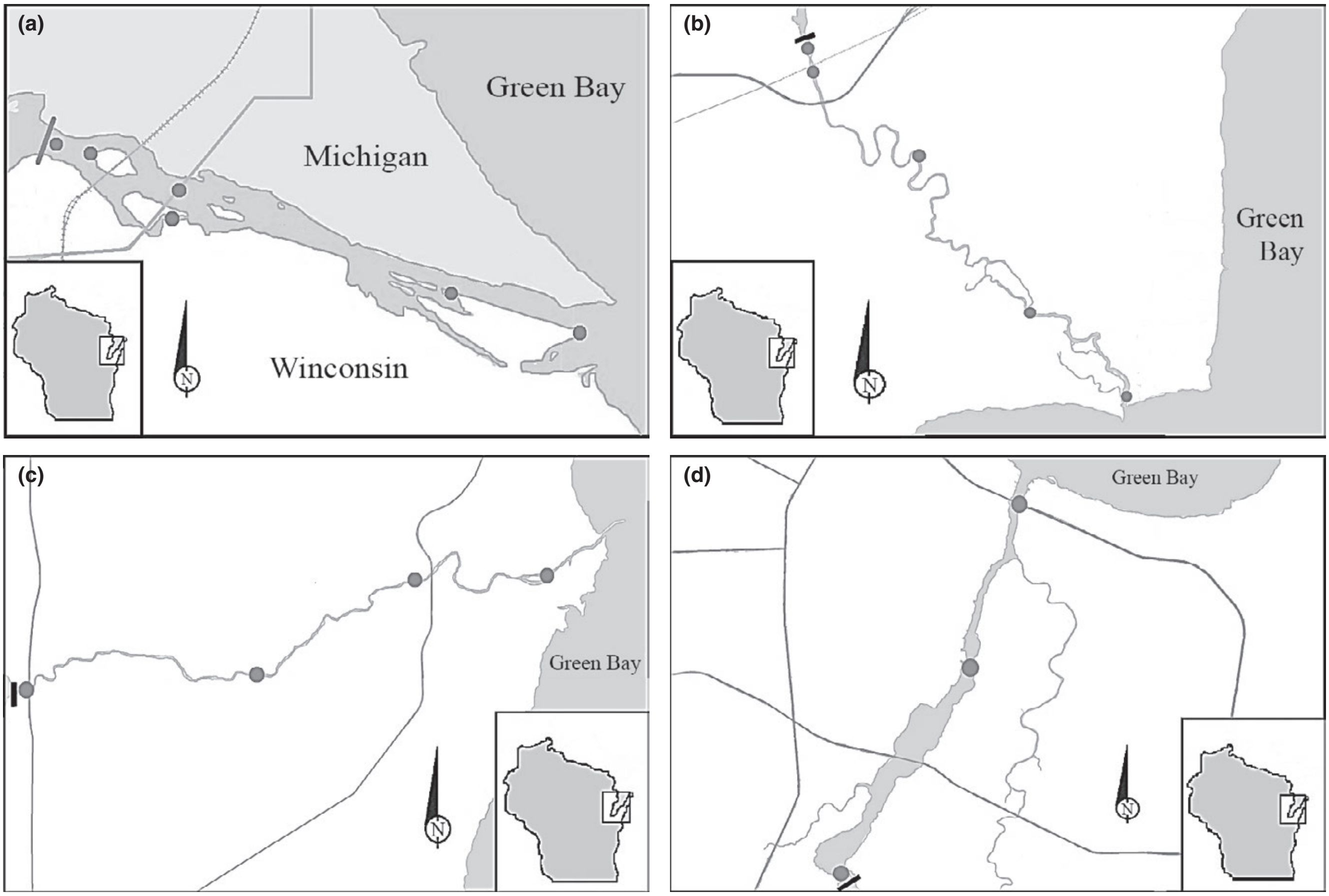

FIGURE 2 Green Bay rivers from the lowest dam to the river mouth with bars indicating dams and solid dots depicting receiver locations: (a) Menominee River; (b) Peshtigo River; (c) Oconto River; (d) Fox River

(across microsatellite loci) was determined by jackknifing procedures (Weir, 1996). To account for multiple testing, sequential Bonferroni procedures (Rice, 1989) were used to adjust nominal significance levels in tests of Hardy-Weinberg and *F*-statistics. A comparable measure of inter-population variance ($_{st}$) was estimated using the program Arlequin (Excoffier, Quattro, & Smouse, 1992) for mtDNA sequence data. Baseline genetic data for the individuals from the Peshtigo and Oconto rivers were combined as allele frequencies were not distinguishable (DeHaan et al., 2006).

Likelihood based individual assignment tests were used to assign spawning individuals to a natal tributary as described (Calvert, Paetkau, Stirling, & Strobeck, 1995). Assignment tests are a likelihood decision rule, where probabilities over all loci scored for an individual are conditioned on the genetic characteristics of each potential contributing population. Estimates of the expected frequency of an individual's multi-locus genotype were made for each of the putative source populations from Wisconsin and from the Manistee River in eastern Lake Michigan. For example, given estimates of allele frequencies $\hat{\theta}_A$ and $\hat{\theta}_B$ determined from samples in two populations (A and B), the goal was to use the genotype of an individual of unknown origin to assign it to one of the two potential source populations. An individual is assigned to population A if the ratio:

$$\frac{L_A}{L_B} = \frac{\text{Prob(genotype)}|\hat{\theta}_A}{\text{Prob(genotype)}|\hat{\theta}_B}$$

is >1, or individuals were assigned to population B if the ratio is <1. Here L_A is the probability of the individual's multi-locus genotype (assuming both Hardy-Weinberg and linkage equilibrium within the source population), conditional on its origin being in a population with estimated allele frequencies $\hat{\theta}_A$. Estimates of statistical confidence in individual assignment decisions can be estimated as the ratio of likelihood of the 'most likely' population of origin divided by the sum of the likelihoods of origin over all populations (Cornuet, Piry, Luikart, Estoup, & Solignac, 1999). We used a program developed by our group (MLE; Topchy et al., 2004) for population assignment and cross-validation because it allows use of both Mendelian (e.g., microsatellite loci) and other discrete (non-Mendelian) character data such as mitochondrial DNA haplotype. The accuracy of population assignments was determined using the leave-one-out method of cross-validation (Shao, 1993) for each baseline population.

A *t* test was used to determine the significant difference of total length and girth between sexes. A two-way ANOVA using type III sum of squares (to account for uneven groups), alpha level set at 0.05, was used to compare post-surgery residence time among locations and between sexes. A Tukey test was used to perform post-hoc pairwise comparisons of residence times among rivers and sexes and river-sex combinations. Chi-square and Cohen's kappa tests (alpha set at 0.05) were conducted to assess spawning site-fidelity based on the degree of association between genetically determined river of origin and capture location (or the difference between observed spawning returns to a given river and the expected returns under assumption of random movement). We combined the data on the river of inferred genetic origin and the river of capture with the telemetry detection (spring activity) data (2011–2015) to create 'encounter histories' of individual fish for movement analysis using the program MARK. We employed the multi-state (aka multi-strata) model in MARK, analyzing survival and/or detection probabilities of fish from one year to the next, just as with the Cormack-Jolly-Seber (CJS) model. Transition probabilities described movements of fish among spawning locations. For multi-state models, the 'encounter history' is a contiguous series of letters to indicate the particular state or strata in which the individual was encountered, and '0's to indicate if the individual was not encountered in any of the states or strata on a particular occasion. For example, F0F00FM represented a fish that was genetically assigned to be originally from the Fox River, was not detected in the 2nd, 4th, and, 5th years, detected in the Fox River in the 3rd and 6th years, and was detected in the Menominee River in the 7th year. We conducted the analysis using the data on all 115 acoustically tagged fish together and for males and females separately.

3 | RESULTS

3.1 | Population characteristics

Sample sizes were inconsistent among the four rivers but represented an adequate sample size for each river (Table 1). Our objectives were 25-50 fish/river for genetic analysis; the results were Menominee *N* = 25, Peshtigo *N* = 63, Oconto *N* = 45, and Fox *N* = 27). The transmitter sample size target was 25-35 per river, with the results Menominee *N* = 23, Peshtigo *N* = 32, Oconto *N* = 35, and Fox *N* = 25.

The following statistics are from the genetic sample size of *N* = 160: total length ranged from 114 to 185 cm (mean ± *SD* 146 ± 16 cm (Figure 3); mean ± *SD* TL of female lake sturgeon was 160.5 ± 13.3 cm; mean ± *SD* TL of male lake sturgeon was 140.2 ± 14.2 cm; mean TL differed significantly between sexes (*t* test = 8.3, *df* = 92, *p* < .001); girth for females ranged from 48.3 to 86.4 cm (mean ± *SD* 67.1 + 9.4 cm); male girth ranged from 43.2 to 73.7 cm (mean ± *SD* 53.9 + 7.2 cm); mean girth differed significantly between sexes (*t* test= 8.4, *df* = 70, *p* < .001).

3.2 | Movement patterns

Tagged sturgeon exited from a river a median of 11 days following surgery, with exit day values highly variable from 0 to 149 days after surgery. Duration of river occupancy following surgery varied between males (0-149 days) and females (1-43 days). Menominee River males (mean ± *SD* 45.3 ± 52.9 days) and females (mean ± *SD* 17.4 ± 16.5 days) exhibited longer average post-surgery resident times compared to adults tagged in the other three rivers (male mean ± *SD* 10.8 ± 8.8; female mean ± *SD* 6.7 ± 6.2 days). Two-way ANOVA showed that post-surgery residence times overall varied significantly (*p* < .005) among locations and between sexes, with no significant interactions between the two. Based on Tukey pair-wise comparisons, residence time in the Menominee River was significantly higher (*p* < .005) than in any of the other three rivers, with the difference being only among males; the differences in residence times among the other three rivers were not significant (overall or by sex). In addition, Menominee River males showed significantly higher (*p* < .005) residence times than did males in the other three rivers.

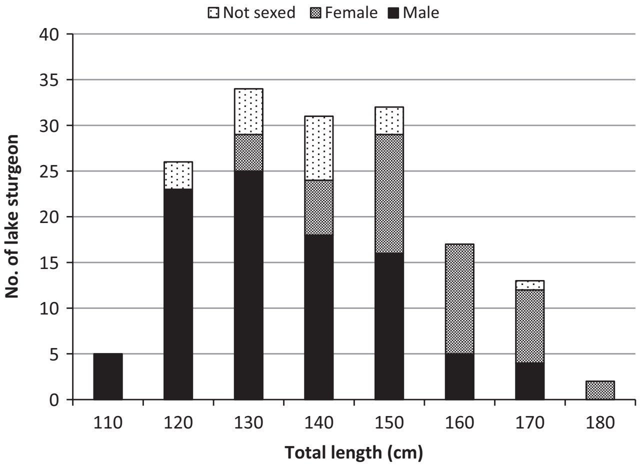

FIGURE 3 Length frequency distribution (total length, cm) for lake sturgeon in Green Bay Rivers sampled from 2011 to 2015. *N* = 160 (Male *N* = 96, Female *N* = 45, and Unknown *N* = 19). Sex was determined by visual examination of gonads

The Peshtigo River receivers detected 57 (49.6%) of the 115 lake sturgeon, followed by the Menominee River receivers (44; 38.3%), Oconto River receivers (42; 36.5%), and the Fox River receivers (38; 33%). The majority of the detections (62%) came from lake sturgeon that received their transmitters in a genetically determined natal river. However, a total of 10, 13, 21, and 25 sturgeon of a different natal origin were detected in the Oconto, Fox, Menominee, and Peshtigo rivers, respectively.

Many Sturgeons (45%) returned at least once for assumed subsequent spawning events or spawning opportunities as indicated by spring (early-April through mid-May) detections at receivers, located in the tail waters (identified spawning area) below an impassable dam. An average spawning frequency was determined for fish initially detected on spawning grounds and then subsequently detected on spawning grounds between mid-April and mid-May in later years. The mean ± *SD* inter-spawning interval for 14 females was 3.4 ± 0.17 years and for 39 males 1.9 ± 0.11 years.

For sturgeon returning to spawn on the Peshtigo River, the average first detection date at the tailwaters (closest to the lowest dam) varied from 23 April to 10 May (Table 2). Sturgeon staged 2-9 days before the actual date when spawning activity was observed by Wisconsin and Michigan DNR staff. Sturgeon entered the river earlier in years when discharge was lower when compared to higher discharge years.

TABLE 2 2013-16 Description of river residency for lake sturgeon as determined by a Vemco VR2W receiver below the lowest dam in the Peshtigo River, Wisconsin during the spawning season. Average daily discharge calculated from April 23-May 23. *N* = sample size

Year	*N*	Ave. detected enter date	First observed spawn date	Ave. daily discharge	Ave. water temp	Ave. detected leave date	Ave. detected days at spawn site
2013	5	May 3	May 10	57.5	12.2	May 23	20
2014	5	May 10	May 12	50.1	12.1	May 23	13
2015	6	April 23	April 30	26.8	12.9	May 18	25
2016	12	April 25	May 4	31.9	12.3	May 10	16

TABLE 3 Comparison of occupancy within each study river (Menominee, Peshtigo, Oconto, and Fox) of capture versus detected river from 2012 to 2016

		Detected River			
Capture River	Sample size	Menominee	Peshtigo	Oconto	Fox
Menominee	23	19	0	0	2
Peshtigo	32	6	1	1	1
Oconto	35	5	4	2	2
Fox	25	1	1	0	10

TABLE 4 Summary of occupancy during non-spawning period by sex from 2012 to 2016

	Males	Females
Capture River	22	11
Other River	15	8

Peshtigo River temperatures at the time of spawning ranged from 12.1 to 12.9°C. Lake Sturgeon were last detected at the spawning site receiver from the second to fourth week of May. Duration of an adult sturgeon detected at this spawning site ranged from 13 to 25 days.

Tagged sturgeon were commonly detected on all receivers during the non-spawning period (mid-June to early April, 41%; 47 fish), but the number of fish detected during the non-spawning period was highest (91%; 21 of 23 fish) for fish receiving transmitters in the Menominee River. Sturgeon initially captured and tagged in the other rivers were far less likely to be detected by any river receiver during the non-spawning period (Fox 40%, Oconto 26% and Peshtigo 21% of total detections), implying greater tendencies for these fish to reside in Green Bay. Of all sturgeon detected during the non-spawning period, 68%, i.e., 78 fish were males and 32%, i.e., 37 fish were females in all rivers. Lake sturgeon were significantly more likely to be detected in rivers where they were initially sampled ($X^2 = 39.69$; $df = 12$, $p < .0001$), indicating fidelity to spawning rivers even during non-spawning periods (Table 3). The degree of fidelity to spawning rivers during non-spawning periods did not differ between males and females ($X^2 = 0.0127$; $df = 4$, $p < .91$) (Table 4).

3.3 | Genetic assignments

Each lake sturgeon was assigned genetically to a Great Lakes tributary population based on likelihood scores and confidence (likelihood ratios) that is an indicator of the accuracy of each assignment. Of all individuals captured at all spawning locations from 2011 to 2015, 38.2% were assigned to the Fox-Wolf population, 23.5% to the Menominee population, and 37.4% to the Peshtigo-Oconto population. One adult female sturgeon was assigned to the Manistee River in eastern Lake Michigan. Genotype assignments by capture river depicts a mixed population in each river, but the capture river explains most of the assignment for each river (72% Menominee River, 58% Peshtigo River, 56% Oconto River, and 73% Fox River [Figure 4]).

The estimated confidence in population assignment for individuals that were captured at the spawning sites varied from 44% to 99% (note that with four baseline populations, an assignment confidence of 50% would mean that an individual was no more likely of having originated in one river population than of another). Seventy-six (48%) of the sturgeon were assigned to a river of origin with a confidence of 90% or greater. Based on cross validation re sampling of the baseline populations, nearly 100% of the baseline individuals were correctly reassigned to their natal population when the estimated statistical confidence was at or exceeded 90% (data not shown).

Of the tagged individuals assigned to natal populations with a high (>90%) confidence, 39.5% were assigned to the Fox-Wolf, 27.6% to the Menominee, and 31.6% to the Peshtigo-Oconto. One sturgeon (< 1% of the number tagged) was assigned to the Manistee River in eastern Lake Michigan. Genetic assignments by river for tagged individuals made with high confidence were (i) for individuals tagged in the Menominee River: 5.3% Manistee River, 10.5% Fox–Wolf rivers, 15.8% Peshtigo–Oconto rivers, and 68.4% Menominee River; (ii) for individuals tagged in the Peshtigo River: 20.8% Menominee River, 37.5% Fox–Wolf rivers, and 41.7% Peshtigo–Oconto rivers; (iii) for individuals tagged in the Oconto River: 15.8% Menominee River, 36.8% Fox–Wolf rivers, and 47.4% Peshtigo–Oconto rivers; (iv) for individuals tagged in the Fox River: 14% Peshtigo–Oconto rivers, and 86% Fox–Wolf rivers (Figure 5).

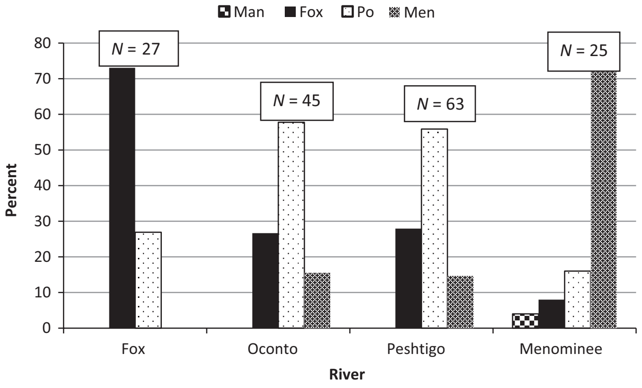

FIGURE 4 Genetic assignments for all lake sturgeon from Green Bay rivers, N = 160. (Legend: natal rivers MAN = Manistee River, FOX = Fox-Wolf Rivers, PO = Peshtigo-Oconto Rivers, and MEN = Menominee River), 2011-2015

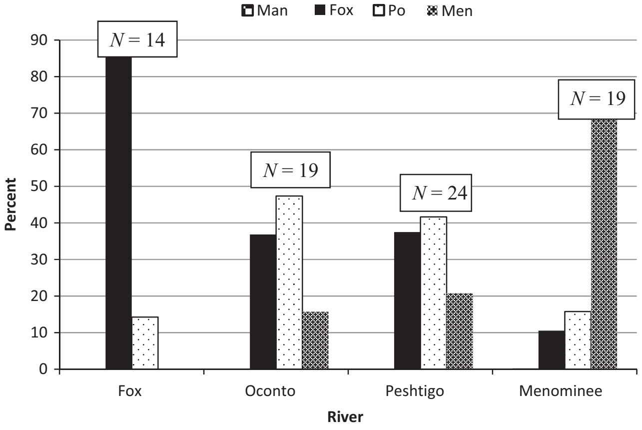

FIGURE 5 Genetic assignments by percent with high likelihood (> 90%) lake sturgeon from Green Bay Rivers, N = 76 (Legend: natal rivers MAN = Manistee River, FOX = Fox-Wolf Rivers, PO = Peshtigo-Oconto Rivers, and MEN = Menominee River), 2011-2015

TABLE 5 Genotype match of tagged fish (2011-2015) captured in one of the study rivers that were subsequently assigned by genotype to the river of capture or to a different river

	All transmitter fish genotype match		High confidence transmitter fish genotype match	
River of capture	Same	Different	Same	Different
Menominee	16	7	13	6
Peshtigo-Oconto	34	33	19	24
Fox	19	6	12	2

Site fidelity varied significantly among rivers, with Peshtigo-Oconto rivers showing the least site fidelity, especially when considering samples with high confidence genetic assignments (X^2 = 8.62, p = 0.01, df = 4; Table 5). Variations in site fidelity were statistically less significant when using all tagged lake sturgeon samples (all fish X^2 5.934 *p*-value .05, *df* = 4).). However, there was an association between genotype and surgery location, when considering all tagged sturgeon (X^2 = 51.24, *df* 4, *p* = 1.991e-10) as well as the high confidence assignments (X^2 = 33.69, *df* 4, *p* = 8.619e-7, Table 6), suggesting spawning site fidelity.

The transition movement probability was highest for lake sturgeon captured in the Peshtigo and Oconto rivers moving into the Fox River (0.77) and the Fox River captured lake sturgeon moving into the Peshtigo and Oconto rivers (0.21) (Table 7). Fewer movements were observed for lake sturgeon from the Menominee River moving into the Peshtigo and Oconto rivers (0.07) and lake sturgeon from the Peshtigo and Oconto rivers moving into the Menominee River (0.11). The movement probability was lowest for sturgeon from the Fox River and detected in the Menominee River (0.01) or from the Menominee River and detected in the Fox River (0.02).

The analysis using the program MARK showed varying transition probabilities, suggesting varying levels of site-fidelity across spawning rivers (Table 7). The MARK results indicated that by far the largest movement probabilities were from lake sturgeon captured in the Peshtigo-Oconto Rivers moving to the Fox River. The results also indicated 100% survival (S) for acoustically tagged individuals from all rivers, but the model was unable to differentiate between survival and detection (p) and the data were not sufficiently large enough to differentiate probabilities associated with both variables. Estimates of detection and transition probabilities for males and females were similar to the estimates based on combined data (Table 7).

4 | DISCUSSION

4.1 | Genetic aspects

Genetic population assignments and acoustical telemetry were used to characterize basic aspects of breeding ecology and probabilities of inter-river movements during breeding and non-breeding seasons

TABLE 6 Capture river for lake sturgeon and corresponding genotype assignment i.e., Pes-Oco equals the Peshtigo-Oconto population, 2011-2015

	Capture river-all transmitter fish			Capture river- high confidence transmitter fish		
Genotype	Menominee	Pes-Oco	Fox	Menominee	Pes-Oco	Fox
Menominee	16	11	0	13	8	0
Pes-Oco	4	35	6	3	19	2
Fox- Wolf	2	22	19	2	16	12
Manistee	1			1		

TABLE 7 Estimates of Lake Sturgeon survival (S), detection (p), and transition (psi) probabilities based on Multi-Strata Analysis using Program MARK, with parameters estimated for each river, i.e., Model = {S(g)p(g)psi(g)}. (a) all Fish, (b) males, and (c) females

(a) All fish

	Parameter	Estimate	Standard error	95% Confidence interval	
				Lower	Upper
1	S F:Fox	1.000000	0.000000	1.000000	1.000000
2	S M:Menominee	1.000000	0.000000	1.000000	1.000000
3	S O:Peshtigo-Oconto	1.000000	8.65E-09	1.000000	1.000000
4	P F:Fox	0.100354	0.015335	0.074041	0.134658
5	P M:Menominee	0.328777	0.041533	0.253014	0.414634
6	P O:Peshtigo-Oconto	1.000000	0.000000	1.000000	1.000000
7	Psi F to M	0.012214	0.008376	0.003161	0.045996
8	Psi F to O	0.212037	0.021850	0.172357	0.258004
9	Psi M to F	0.026039	0.025456	0.003724	0.160514
10	Psi M to O	0.075916	0.025691	0.038533	0.144130
11	Psi O to F	0.770012	0.047951	0.663219	0.850571
12	Psi O to M	0.109687	0.041256	0.051078	0.219958

(b) Males

	Parameter	Estimate	Standard error	95% Confidence Interval	
				Lower	Upper
1	S F:Fox	1.000000	2.04E-09	1.000000	1.000000
2	S M:Menominee	1.000000	2.00E-09	1.000000	1.000000
3	S O:Peshtigo-Oconto	1.000000	1.20E-09	1.000000	1.000000
4	P F:Fox	0.120108	0.02037	0.085552	0.166087
5	P M:Menominee	0.387164	0.050787	0.293430	0.490072
6	P O:Peshtigo-Oconto	1.000000	7.75E-08	1.000000	1.000000
7	Psi F to M	0.015183	0.010359	0.003950	0.056552
8	Psi F to O	0.244587	0.027721	0.194385	0.302879
9	Psi M to F	0.000000	0.000000	0.000000	0.000000
10	Psi M to O	0.050694	0.024703	0.019151	0.127438
11	Psi O to F	0.755760	0.050161	0.644957	0.840533
12	Psi O to M	0.095725	0.039314	0.041653	0.204978

(c) Females

	Parameter	Estimate	Standard error	95% Confidence interval	
				Lower	Upper
1	S F:Fox	1.000000	0.000000	1.000000	1.000000
2	S M:Menominee	1.000000	0.000000	1.000000	1.000000
3	S O:Peshtigo-Oconto	1.000000	0.000000	1.000000	1.000000
4	P F:Fox	0.064822	0.021187	0.033761	0.120885
5	P M:Menominee	0.253133	0.060115	0.153788	0.387283
6	P O:Peshtigo-Oconto	1.000000	3.31E-07	0.999999	1.000001
7	Psi F to M	0.000000	0.000000	0.000000	0.000000
8	Psi F to O	0.151947	0.033389	0.097328	0.229426
9	Psi M to F	0.039626	0.039138	0.005467	0.236476
10	Psi M to O	0.103708	0.040458	0.046986	0.213560
11	Psi O to F	0.840325	0.095296	0.566754	0.954898
12	Psi O to M	0.129372	0.091807	0.029196	0.423368

for lake sturgeon spawning in the four tributaries to Green Bay, Lake Michigan. Detailed information pertaining to spawning periodicity, spawning site fidelity and inter-tributary movements during the non-breeding season are presented. Lake sturgeon historically spawned in many Great Lakes tributaries. Lake Sturgeon using the Green Bay Rivers represents a metapopulation. The rivers are relatively close together (72 km is the maximum distance from the Menominee to the Fox River, with the Peshtigo and Oconto rivers lying between them) and that proximity may collectively be necessary to satisfy the year round requirements for lake sturgeon residents of all Green Bay Rivers. Generally, there was a high degree of fidelity to natal rivers, but heterogeneity was documented. Spawning site fidelity appears to be less for lake sturgeon originating from the Oconto and Peshtigo rivers relative to fish from the Menominee and Fox rivers. High levels of natal fidelity are likely one of the reasons that previous research has documented high levels of spatial genetic structure (DeHaan et al., 2006; Homola et al., 2012).

4.2 | General aspects of breeding ecology

Post-surgery duration of occupancy in the spawning river of capture days was highly variable among rivers (0-149 days). Duration of occupancy for males and females was significantly different. Post-surgery river residence time in the Menominee River was significantly longer than residence times for sturgeon following surgery in the other three rivers. The long post-surgery residence time for sturgeon in the Menominee River is likely unrelated to discharge or river watershed area since the Fox River is larger. However, the Menominee River supports the largest population in Green Bay (approx. 1,000 sturgeon > 127 cm) of the four rivers (Elliott & Gunderman, 2008). Adult sturgeon post-spawning migration has also been documented as being highly variable in other systems. For example, Auer (1999) found that the period of occupancy varied from 1 to 54 days in the Sturgeon River, Lake Superior. In our study, male sturgeon remained at spawning sites longer than females, possibly related to staging prior to spawning and the increase in potential to spawn with multiple females (Baker, Crossman, Duong, Forsythe, & Scribner, 2013). We based spawning periodicity estimates on spring detections on receivers at known spawning sites and dates on each river. Our estimates of spawning periodicity (1.9-3.4 years) are comparable to those reported for other populations of lake sturgeon (Bruch et al., 2009; Forsythe, Crossman, Bello, Baker, & Scribner, 2012a;). Our small sample size did not allow us to quantify spawning periodicity as a function of body size/age. Spawning periodicity differences between male and female lake sturgeon are important in this long lived, iteroparous species, particularly for small populations (Sugg, Chesser, Dobson, & Hoogland, 1996); males may modify when they spawn to increase mating numbers based on the timing of spawning by females (Forsythe et al., 2012).

Spawning time is associated with environmental and genetic factors of migrating fish (Cushing, 1990; Rogers, Allen, & Porak, 2006). Lake sturgeon entered Green Bay Rivers in early to mid-April. Sturgeon were detected at spawning site receivers for periods of 13-25 days. The Peshtigo River (2013-16) provides the most complete data set for sturgeon spawning activity of the four rivers. Sturgeon presence at the spawning site occurred approx. for a 3-week period each spring. Daily discharge and temperature seemed to be factors associated with initiation of spawning, as has been described previously in the Black Lake (Michigan) lake sturgeon population (Forsythe et al., 2012). Lower daily discharge was linked to earlier arrival at the spawning site and was not preceded by higher flows. Spawning activity was observed when temperatures exceeded 12°C. In 2006, sturgeon spawning on the Peshtigo River was described over three events with temperatures from 13.9 to 14.5°C (Caroffino et al., 2010).

Detections during non-spawning periods were common at all eighteen receivers (overall average of 41%; 47 fish detected by receivers), although detections during non-spawning periods varied greatly across rivers (91%; 21 of 23 fish in the Menominee River to 22%; 7 of 32 fish in the Peshtigo River). Male Sturgeon was more than twice as likely to be detected than females during the non-spawning period. Our acoustic telemetry data demonstrated high sturgeon activity on the lower Menominee River, as supported by previous, targeted Michigan and Wisconsin DNR lake sturgeon assessments conducted periodically from April through November (Wisconsin and Michigan DNR, unpublished data). Non-targeted assessments by Wisconsin DNR on the other three rivers in the fall of the year rarely detect lake sturgeon (Wisconsin DNR, unpublished data). Year-long use of the lower Menominee River may be a factor of the overall sturgeon population sizes in that river and possibly also the potential origin of a number of these fish from the upper Menominee River, above the two lowest dams.

Genetic analyses have shown that movement patterns among the lake sturgeon populations in Lake Michigan tributaries varied following the most recent glacial retreat (Bernatchez & Wilson, 1998). In general, genetic assignments indicated that the proportion of lake sturgeon captured in their river of origin varied among the four rivers but the assignments for each river were dominated by the population associated with that river. Site fidelity was evident for each river as determined by high concordance between captured river and genetically assigned river, but straying or lack of strong fidelity for some fish is evident. Analysis of the greater Lake Michigan populations indicates that historic Lake Michigan gene flow and contemporary straying rates were nonrandom (Homola et al., 2012).

Transition probabilities of individuals tagged in the Peshtigo-Oconto and Fox-Wolf rivers and detected elsewhere were higher than transition probabilities of fish tagged in the Menominee River. Transition probabilities characterizing movements of lake sturgeon from rivers of origin into other rivers are consistent with straying rates and with the degree of genetic differentiation among rivers, suggesting individuals that stray successfully reproduce (Homola et al., 2012). However, it is interesting to note that transition probabilities were asymmetrical. Data are consistent with basin-wide straying estimates (Homola et al., 2012) that showed certain populations characterized by high net rates of immigration or emigration. It is possible that olfactory cues are less distinct between the Wolf and Peshtigo-Oconto rivers due to the close geographic proximity of the Wolf River spawning grounds to the headwaters of the Peshtigo and Oconto rivers (Homola et al., 2012), possibly explaining the high movement probability between these two sets of rivers. In addition, the distance between the spawning grounds on the lower Fox River compared to the Wolf River may explain the increased apparent straying of fish collected and sampled in the lower Fox, Oconto and Peshtigo rivers. Many of the lower Fox River fish are likely from the upper Fox River and of Fox or Wolf River origin, but this cannot be confirmed through PIT tag recaptures since less than one percent of all recaptured sturgeon in Green Bay were tagged in the upper Fox and Wolf rivers (R. Koenigs, D. N. R. Wisconsin (personal communication, March 1, 2016).

The anomalies in this data set include one female assigned to the Manistee River (eastern Lake Michigan) population with high confidence (96%), which was detected below the Menominee dam not only in May 2012 but also during the 2015 spawning period (30 April-13 May). In addition, a 2nd fish (male, 142 cm total length) captured in the Fox River in this study was originally captured and PIT-tagged during an approximate spawning time (13 May 1999) in the Manistee River. That fish was genetically assigned with high confidence (95%) to the Fox-Wolf population. These fish provide important examples of what has been identified as higher observations of strays between the Manistee River and the Fox, Oconto, Peshtigo and Menominee rivers (Homola et al., 2012).

Lake sturgeon straying rates are difficult to quantify over a large area like Lake Michigan, particularly for a long-lived fish species characterized by delayed sexual maturity and long inter-spawning intervals. Previous studies noted that contemporary straying rates were high (mean = 0.105), asymmetrical, and highly variable across populations (Homola et al., 2012). We also observed high straying rates, although they were more predictable in the relatively smaller populations in Green Bay. Lake sturgeon initially captured in the Peshtigo and Oconto rivers and fish genetically assigned to these rivers tended to be encountered in the Fox River but not in the Menominee River. Our results demonstrated by far the largest movement probabilities were from the Peshtigo-Oconto Rivers to the Fox River.

The transmitters associated with this project will expire between 2019 and 2025. The receivers will be maintained through 2025. Data collected from these transmitters over the next several years will yield valuable additional information regarding the sturgeon populations in Green Bay.

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