


Spawning site fidelity and apparent annual survival of walleye (*Sander vitreus*) differ between a Lake Huron and Lake Erie tributary

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Abstract

Fidelity to spawning habitats can maximise reproductive success of fish by synchronising movements to sites of previous recruitment. To determine the role of reproductive fidelity in structuring walleye *Sander vitreus* populations in the Laurentian Great Lakes, we used acoustic telemetry combined with Cormack–Jolly–Seber capture–recapture models to estimate spawning site fidelity and apparent annual survival for the Tittabawassee River in Lake Huron and Maumee River in Lake Erie. Walleye in spawning condition were tagged from the Tittabawassee River in Lake Huron and Maumee River in Lake Erie in 2011–2012. Site fidelity and apparent annual survival were estimated from return of individuals to the stream where tagged. Site fidelity estimates were higher in the Tittabawassee River (95%) than the Maumee River (70%) and were not related to sex or fish length at tagging. Apparent annual survival of walleye tagged in the Tittabawassee did not differ among spawning seasons but was higher for female than male walleye and decreased linearly as fish length increased. Apparent annual survival of walleye tagged in the Maumee River did not differ among spawning seasons but was higher for female walleye than male walleye and increased linearly as fish length increased. Greater fidelity of walleye tagged in the Tittabawassee River than walleye tagged in the Maumee River may be related to the close proximity to the Maumee River of other spawning aggregations and multiple spawning sites in Lake Erie. As spawning site fidelity increases, management actions to conserve population structure require an increasing focus on individual stocks.

KEYWORDS

acoustic telemetry, capture–recapture, Cormack–Jolly–Seber model, Great Lakes

1 | INTRODUCTION

Reproductive fidelity is the propensity of an iteroparous organism to return to the same spawning site over subsequent spawning seasons

and is an important component in the life history of many marine and freshwater fishes (Binder et al., 2016; Block et al., 2005; Green & Wroblewski, 2000; Hendry, Castric, Kinnison, & Quinn, 2004). Reproductive fidelity includes two types of behaviours distinguished

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by the relationship between natal source and spawning location as an adult. Spawning site fidelity is a behaviour where individuals spawn at a site of previous spawning experience that may or may not be their natal site. Natal homing (philopatry) can be thought of as a subcategory of spawning site fidelity where adult individuals return to their natal site for spawning. The mechanisms associated with homing of individuals to natal spawning sites have received substantial attention in anadromous salmonids (Dittman & Quinn, 1996; Putman, Jenkins, Michielsens, & Noakes, 2014), but mechanisms associated with spawning site fidelity have been less studied in freshwater fish species that reside in large lakes. Reproductive fidelity may synchronise animal movements to known spawning grounds, limit the number of individuals at spawning grounds and facilitate accumulation of genetically based local adaptations (Leggett, 1977). Understanding reproductive fidelity of fish is important for development of management strategies to conserve locally adapted populations. Mounting evidence suggests conservation of populations serves to stabilise system processes and increase the resilience of species to withstand environmental perturbations and exploitation (Schindler et al., 2010; Thériault, Moyer, Jackson, Blouin, & Banks, 2011).

Lake Huron and Lake Erie support the two largest walleye (*Sander vitreus*) populations in the Laurentian Great Lakes (Roseman, Kocovsky, & Vandergoot, 2010). Historically, Lake Huron and Lake Erie walleye populations were impacted by overfishing, pollution, habitat degradation and establishment of invasive species (Schneider & Leach, 1977). Stocking programs, initiated in the 1970s, led to expansion of Saginaw Bay, Lake Huron walleye populations and development of a sport fishery in Saginaw Bay (Johnson, He, & Fielder, 2015). Natural reproduction of Saginaw Bay walleye expanded during the early 2000s and led to cessation of stocking programs in 2006 and attainment of management rehabilitation goals in 2009 (Johnson et al., 2015). The Saginaw Bay walleye population was estimated to number 2–3 million in 2012 (Fielder & Bence, 2014). In Lake Erie, declining catch rates and high mercury levels resulted in closure of walleye fisheries in 1970 (Schneider & Leach, 1977). The recreational walleye fishery in Lake Erie was reopened in 1973, and walleye populations slowly recovered (Hatch, Nepszy, Muth, & Baker, 1987). In contrast to recovery plans in Lake Huron, walleye rehabilitation efforts for Lake Erie walleye did not include stocking of hatchery-reared fish but relied on natural spawning in tributaries and on abundant in-lake reefs and shoals in the western basin. Lake-wide abundance was estimated as more than 25 million adult individuals during 2010–2015 (Walleye Task Group, 2016).

Survival and mortality rates are key demographic parameters that influence population dynamics and necessary for development of management strategies to maintain sustainable walleye populations in Lake Erie and Lake Huron. Survival rates are routinely estimated by capture of marked individuals by the fisheries in lakes Huron and Erie. However, fishery-dependent estimates of survival rates are constrained by spatially and temporally uneven fishing pressure and may fail to detect variation in survival rates owing to movement of fish. Telemetry-based methods for estimating apparent survival rates can be estimated along migration routes or shorter time steps than from traditional tagging studies (Melnychuk, 2012).

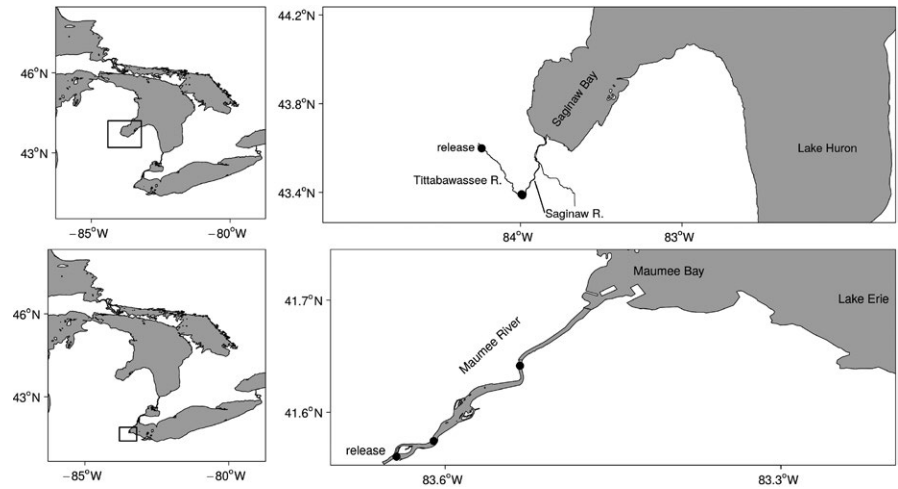
The mechanisms, role and biological significance of walleye spawning site fidelity are not well understood in the Laurentian Great Lakes. Walleye undergo seasonal spawning movements and form spawning aggregations in Saginaw Bay tributaries, but no spawning is known to occur on reef complexes in open-water regions of Lake Huron (Fielder, 2002). Walleye populations in Lake Erie are supported by large spawning aggregations in the Sandusky, Detroit and Maumee rivers and nearshore reef complexes (Goodyear, Edsall, Ormsby Dempsey, Moss, & Polanski, 1982; Pritt et al., 2013; Roseman et al., 1996). Past investigations into walleye spawning site fidelity in the Great Lakes were limited to repeated observation of individuals tagged and recovered at the same spawning site in subsequent years, or inferred from the levels of genetic differentiation among populations (Crowe, 1962; Fielder, 2014; Stepien, Murphy, Lohner, Haponski, & Sepulveda-Villet, 2010; Wang et al., 2007; Wolfert, 1963; Zhao, Einhouse, & MacDougall, 2011). However, whether walleye in the Great Lakes return to natal spawning sites or more generally return to the site of first or previous spawning experience is unknown. Estimates of site fidelity derived from recapture of marked individuals by commercial or recreational fisheries do not account for mortality of tagged fish or biases associated with heterogeneous spatial and temporal tag recovery.

Our objective was to determine whether the degree of site fidelity differed between walleye spawning aggregations in the Tittabawassee (Lake Huron) and Maumee (Lake Erie) rivers. We used acoustic telemetry combined with Cormack–Jolly–Seber capture–recapture models to compare estimates of spawning site fidelity and apparent annual survival between the two rivers. Apparent annual survival was defined as the probability that an individual was alive and available for detection in the following year. The presence or absence of walleye in the Tittabawassee or Maumee rivers was quantified during four consecutive spawning seasons and the proportion of individuals that returned to the river where tagged was estimated during subsequent spawning seasons. Information-theoretic model selection was used to test for differences in spawning site fidelity across annual spawning seasons, fish length and sex for walleye tagged in the Tittabawassee and Maumee rivers.

2 | METHODS

Movements of two adfluvial walleye populations in the Great Lakes were monitored using acoustic transmitters (hereafter referred to as “tags”) within the Great Lakes Acoustic Telemetry Observation System receiver network (Figure 1). The Tittabawassee River supports the largest known spawning aggregation of walleye in Lake Huron, estimated at 173,000 fish in 2011 (MDNR, Unpublished data) and drains approximately 6400 km² of agricultural lands in the central lower peninsula of Michigan. Most walleye spawning habitat in the Tittabawassee River is located within 2–3 km of the Dow Dam, a barrier to upstream fish movement, in Midland, MI, approximately 47 km upstream of the Tittabawassee river mouth. The Tittabawassee River joins with Shiawassee and Cass rivers to form the Saginaw River approximately 50 km upstream of the mouth of the Saginaw River to

FIGURE 1 Map of study sites. Walleye in spawning condition were implanted with acoustic tags and released in the Tittabawassee River (top right) and Maumee River in 2011 and 2012 (bottom right pane). Release locations were upstream of one acoustic receiver line in the Tittabawassee River (black circle, top right pane) and two acoustic receiver lines in the Maumee River (black circle, bottom left pane). Black squares in top left and bottom left panes depict extent of study area in Lake Huron and Lake Erie



Saginaw Bay, Lake Huron. Movement between Saginaw Bay and the Tittabawassee River spawning areas represents a one-way distance of approximately 100 km. The Saginaw River flows through large urban areas and is highly modified and industrialised.

The Maumee River, located in the Lake Erie watershed, supports a walleye population of approximately 600,000 fish (Pritt et al., 2013). The Maumee River watershed is the largest in the Great Lakes and drains more than 21,500 km² in Ohio, Indiana and Michigan. The Maumee River empties into Lake Erie at Maumee Bay, located in the south-west corner of Lake Erie. Known walleye spawning grounds start approximately 25–30 km upstream of the Maumee River mouth to Lake Erie, and extend upstream approximately 25 km to the first dam, which serves as a barrier to further upstream movement. The lower 12 km of the Maumee River flows through Toledo, Ohio, and is heavily modified and industrialised, similar to the Saginaw River.

In total, 492 walleye in spawning condition were captured and tagged from the Tittabawassee and Maumee rivers in March–April 2011 and 2012 (Table 1). Walleye were captured using boat-mounted electrofishing equipment immediately downstream of Dow Dam (Midland, MI) in the Tittabawassee River and near Orleans Park (Perrysburg, OH) in the Maumee River. Captured fish were transferred to stream-side holding tanks until tags were implanted and biological characteristics recorded. In 2011, walleye selected for tagging were chosen to represent the size distribution of the respective adult walleye populations in Saginaw Bay or Maumee Bay. Male and female walleye were tagged in nearly equal numbers in the Maumee and Tittabawassee rivers in 2011 (Table 1). In 2012, nearly equal numbers

of male and female walleye were tagged in the Tittabawassee River; however, only female walleye were chosen for tagging from the Maumee River in 2012 (Table 1).

Before implantation of acoustic tags, biological characteristics (total length, sex) and dorsal fin clips were collected from each walleye. Age of tagged walleye was determined by counting annual growth increments on dorsal fin segments by at least two experienced readers. Paired t-bar anchor tags (Floy Tag Inc.) were inserted between the pterygiophores below the base of the second dorsal fin to allow individuals to be identified during and after tagging and to alert anglers to the presence of an internal tag. Walleye were anaesthetised using a portable electroanaesthesia unit (Smith-Root, pulsed DC, 35 volts, 3 s treatment period; Vandergoot et al., 2011). Anaesthetised fish were placed in a cushioned foam cradle and acoustic tags (Vemco V16-4H tags, average nominal delay 120 s, 152 dB output, 24 g in air, 68 mm × 16 mm dia or V16-6H tags, 95 mm × 16 mm dia, 36 g in air, 152 dB output, average nominal delay 90 s) were inserted into the coelomic cavity through a small incision located on the centre line of the ventral surface of the fish. Fish gills were continuously irrigated with river water during surgery. After the tag was inserted, incisions were closed using two to three interrupted sutures (Ethicon PDS-II size 2-0, monofilament). Walleye were transferred immediately to recovery tanks containing river water after tagging. Once each fish regained equilibrium, it was released into the river near the capture location. On average, each surgery took 2.5 min and fish were released 30 min after completion of surgery. All surgical tools and tags were sterilised before surgery.

TABLE 1 Total length (TL, mm ± standard deviation, SD), number of female (F) and male (M) and mean age (year) of walleye tagged in the Tittabawassee River in Lake Huron and in the Maumee River in Lake Erie in 2011–2012

River	Sex	2011			2012		
		No. tagged	Mean ± SD TL (mm)	Mean age (year)	No. tagged	Mean ± SD TL (mm)	Mean age (year)
Tittabawassee	M	98	519 ± 40	8	29	492 ± 41	8
	F	101	584 ± 63	8	31	547 ± 46	7
Maumee	M	103	515 ± 44	7	1	584	13
	F	97	624 ± 59	8	32	620 ± 67	8

Omnidirectional acoustic receivers (VR2W, 69 kHz, Vemco, Halifax, NS) deployed as part of the Great Lakes Acoustic Telemetry Observation System network (<http://data.glos.us/glatos>) detected fish movements in and out of the Tittabawassee and Maumee rivers. Multiple receivers were deployed in each river to improve detection of tagged walleye and provide full spatial coverage of the river. Two acoustic receivers were deployed near the mouth of the Tittabawassee River during the annual walleye spawning period with the exception of 2014 when only one acoustic receiver was deployed (Figure 2). In Lake Erie, acoustic receivers were deployed 7–19 km upstream of the mouth of the Maumee River. At least two acoustic receivers were deployed annually in the Maumee River during March–April 2011–2014 (Figure 2). For our analysis of site fidelity, detections on all receivers in the Maumee River were considered one location and all receivers in the Tittabawassee River were considered one location. All detection data were screened for false positives caused by environmental noise and signal collisions using the short-interval criteria described by Pincock (2012). False detections were considered detections that were not accompanied by at least one other detection from the same tag on the same receiver within 1 hr and were removed from the data set. More than 99% of detections passed the filter for our data sets.

Cormack–Jolly–Seber (CJS) open-population models have been used to estimate survival rates from imperfect sampling of a marked population (Burnham, Andersen, White, Brownie, & Pollock, 1987; Lebreton, Burnham, Clobert, & Anderson, 1992). CJS models incorporate presence and absence information from successive sampling occasions to estimate the probability of encountering an individual at the sample site, given that the individual was alive and available to be sampled, and the probability of surviving to the next sampling interval (Lebreton et al., 1992). If all tagged individuals available for detection are detected during a sampling occasion, the probability of

encountering an individual at the sampling site, given that the fish is alive and does not emigrate, is an estimate of site fidelity (p) (Binder et al., 2016). CJS models cannot distinguish between emigration of an individual out of the study area and death of an individual; therefore, survival rate estimates from CJS models represent “apparent survival” (ϕ) or the probability that an individual survives to the next year and does not emigrate from the population ($\phi = 1 - \text{mortality} - \text{emigration}$). Apparent survival and survival are equal when emigration is zero and ϕ can be thought of as a minimum estimate of survival if emigration from the population occurs. We could not determine whether walleye spawned after entering the Tittabawassee or Maumee rivers, although inferring spawning after travelling many kilometres upstream seemed reasonable. Our data provided a unique opportunity to unequivocally determine whether an individual returned to the same river during successive spawning seasons. In this study, we used CJS models to estimate site fidelity (p) as the annual proportion of walleye that subsequently returned to the river in which they were tagged during the 2011 or 2012 spawning season.

Before fitting CJS models, we created a compact “encounter history” for each tagged fish that summarised presence (1) or absence (0) at each spawning season from 2011 to 2014 (Table 2; Lebreton et al., 1992; Binder et al., 2016). For example, an encounter history of “1010” represented a walleye that was tagged in 2011 and was detected in 2013 but was not detected in 2012 or 2014. Similarly, a detection history of “0101” represented a walleye tagged in 2012 that was not detected in 2013 but was detected in 2014. The spawning season for each year was identified as time when walleye were detected on receivers in the Tittabawassee and Maumee rivers and extended from February 1 to June 1 of each year. For both rivers across all years, less than three walleye were detected on receivers between June 1 and

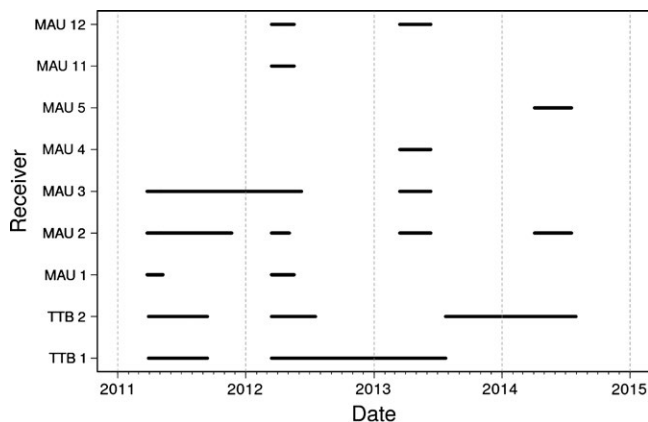


FIGURE 2 Acoustic receiver deployment and recovery schedule for the Tittabawassee (TTB) and Maumee (MAU) rivers. Lines represent periods of time when receivers were deployed in river for each receiver. Receivers in Maumee River were deployed at two locations. Stations MAU 11 and MAU 12 were located 19 km upstream of Maumee River mouth and MAU 1–5 were located 7 km upstream of river mouth. Two acoustic receivers were deployed approximately 1 km of each other near the mouth of the Tittabawassee River (TTB 1, TTB 2)

TABLE 2 Encounter histories of walleye in the Maumee and Tittabawassee rivers during spawning seasons (February – June), 2011–2014. Encounter history reflects the presence (1) or absence (0) of each individual in the Tittabawassee and Maumee rivers. Encounter histories for walleye tagged in 2012 begin with “0”. Count is the number of walleye observed with each capture history. Encounter histories represent all fish tagged in 2011 and 2012

Encounter History	Tittabawassee R Count	Maumee R. Count
1000	87	138
1100	43	24
1111	39	17
1110	25	9
1101	0	1
1001	1	4
1010	2	5
1011	2	2
0100	22	24
0110	16	2
0111	21	5
0101	1	2

February 1 of the next year. CJS models were specified and fit using the RMark interface for Program Mark using maximum likelihood methods (Laake, 2013; White & Burnham, 1999). A suite of candidate models were used to test whether p or ϕ differed among spawning seasons ("year"), sex or fish length at tagging (Table 3). Fish length at tagging was used as a surrogate for age in CJS models because all ages did not include both male and female walleye. The unbalanced nature of our data required walleye of different ages to be combined for inclusion in models. Instead of subjectively combining walleye of different ages in groups for CJS modelling, we modelled length as a continuous individual covariate. To test whether p or ϕ differed among spawning seasons, sex or fish length at tagging, we compared models in which p or ϕ was allowed to differ among years, sex or fish length at tagging to models in which p or ϕ was assumed equal among all years, sex or length at tagging. p and ϕ are not independently estimable in the last time interval in these models (i.e., 2013–2014), so λ was estimated as the joint probability of surviving and returning to the spawning river during the last time interval (Binder et al., 2016; Lebreton et al., 1992). To test whether λ differed among sex or by fish length at tagging, we compared models that allowed sex and length at tagging to differ with models in which λ was equal for males and females and did not vary with fish length at tagging.

Akaike's information criterion (AIC) was used to evaluate which model fit the data "best" among those evaluated (Burnham & Anderson, 2002). Optimal models were identified as the model with the lowest AIC value and the highest model weights (w_i). Candidate models with $\Delta QAIC_c$ values < 2 have similar explanatory power (Burnham & Anderson, 2002). Prior to model selection, we used the median \hat{c} goodness-of-fit test to assess the degree of overdispersion (\hat{c}) in the data. The global model used for median \hat{c} analysis included

TABLE 3 Variables used to construct models to test for time and length effects on apparent annual survival (ϕ), site fidelity (p) and the joint probability of surviving and returning to the spawning river during the last time interval (λ) for walleye spawning in the Tittabawassee River in Lake Huron and the Maumee River in Lake Erie during 2011–2014

Parameter	Variable	Description
p	year	Site fidelity different among all years
	sex	Site fidelity different by male and female
	length	Site fidelity different by length of fish at tagging ^a
ϕ	year	Apparent annual survival different among all years
	sex	Apparent annual survival different among male and female
	length	Apparent annual survival different by length of fish at tagging ^a
λ	sex	Lambda different by sex
	length	Lambda different by length

^aFish length at tagging was modelled as a continuous individual covariate.

"sex" and "year" variables but not length at tagging. Estimates of \hat{c} calculated from the global model for the Tittabawassee and Maumee rivers were used to correct for overdispersion in AIC values (QAIC), model weights and confidence limits of parameter estimates (Burnham & Anderson, 2002). Sequential model selection limited the number of candidate models and simplified interpretation. First, to test whether λ differed between sex and fish length at tagging, all combinations of sex and length variables were tested with the global model for p and ϕ (Table 3). The model with the lowest QAIC for λ was carried through to the next step. In the second step, the most parsimonious model for p was identified by comparing all combinations of "year", "sex", "length" variables and their interactions while retaining the best model for λ and the global model for ϕ (Table 3). The final model selection step retained the best λ and p models identified in the previous steps and tested all combinations of "year", "sex", and "length" variables to identify the most parsimonious model for ϕ as identified with the lowest QAIC value (Table 3). The most parsimonious model, defined as the model containing the "best" variables from each step of the sequential selection process for λ , p and ϕ , was used to calculate parameter estimates and 95% confidence intervals for λ , p and ϕ .

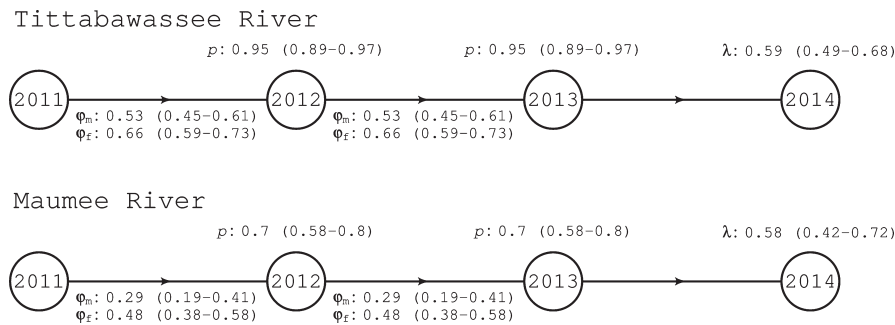
3 | RESULTS

Mean length of walleye tagged in the Tittabawassee and Maumee rivers during the 2011 and 2012 spawning season ranged from 491 mm to 623 mm (Table 1). Within each river and tagging year, mean length of female walleye was greater than male walleye (Table 1). Walleye tagged in 2012 were slightly smaller than individuals tagged in 2011 for both rivers. Median age (based on dorsal spine annuli) of walleye tagged during the 2011 and 2012 spawning seasons in the Tittabawassee River was 7 years (range – 3–18 years) with most (50%) fish between 6 and 8 years of age. Male and female walleye tagged in the Tittabawassee River had the same median age, but spread of ages was slightly higher for males (interquartile range- 3 years) compared to females (interquartile range- 2 years). The age distribution of walleye tagged in the Maumee River differed little from the Tittabawassee River. Median age of all walleye tagged in the Maumee River was 8 years, with 50% of tagged fish between 5 and 8 years old. Median age of male walleye tagged in the Maumee River was 7 years (interquartile range- 3 years). Median age of female walleye tagged in the Maumee River was 8 years (interquartile range- 3 years).

In total, 311,180 acoustic detections from walleye were recorded on receivers in the Tittabawassee and Maumee rivers during the 2011 – 2014 spawning seasons. More than 87% of all detections were recorded on receivers in the Maumee River and 13% of detections were recorded on acoustic receivers in the Tittabawassee River. Walleye tagged in the Tittabawassee River were only detected on acoustic receivers in the Tittabawassee River and no walleye tagged in the Maumee River were detected in the Tittabawassee River during the study. In the Tittabawassee River, 58% of tagged walleye were detected during at least one spawning season after tagging and 23% were detected during all subsequent spawning seasons (Table 2).

TABLE 4 QAIC_c results for comparison of Cormack–Jolly–Seber models testing for sex and length effects on the joint probability of surviving and returning to the spawning river during the last time interval (λ)

River	Model	Param	QAIC _c	Δ QAIC _c	w_i	QDeviance	\hat{c}
Tittabawassee	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda(\text{length})$	9	549.11	0.00	0.39	530.72	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda$	9	549.46	0.35	0.32	531.07	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda(\text{length} + \text{sex})$	10	550.94	1.83	0.16	530.46	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda(\text{sex})$	10	551.25	2.14	0.13	530.77	1.3
Maumee	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda$	9	303.99	0.00	0.38	285.41	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda(\text{length})$	9	304.15	0.16	0.35	285.57	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda(\text{sex})$	10	306.03	2.04	0.14	285.32	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}),$ $p(\text{year} + \text{sex} + \text{length}), \lambda(\text{length} + \text{sex})$	10	306.13	2.14	0.13	285.43	1.7

**FIGURE 3** Model estimates of site fidelity (p), mean annual apparent survival for male (φ_m) and female (φ_f) walleye and lambda (λ) from the most parsimonious Cormack–Jolly–Seber models for the Tittabawassee and Maumee rivers, 2011–2014. λ is the joint probability of surviving to the last time interval and returning to the Tittabawassee or Maumee rivers during 2014 spawning year. Circles represent spawning year, and arrows represent time. Walleye were tagged in 2011 and 2012 and the most parsimonious model for each river included constant site fidelity for male and female walleye and year. Lambda (λ) was constant for male and female walleye in both rivers

Thirty per cent of walleye tagged in the Maumee River in 2011 and 2012 were detected at least once during subsequent spawning seasons and 9.4% were detected during all subsequent spawning seasons after tagging (Table 2).

Goodness of fit estimated by the median \hat{c} overdispersion test for CJS models containing all variables except fish length at tagging for λ , p , and φ (i.e., $\lambda[\text{sex}]$, $p[\text{sex} + \text{year}]$, $\varphi[\text{sex} + \text{year}]$) was 1.3 ($SE = 0.050$) for fish tagged in the Tittabawassee River and 1.7 ($SE = 0.064$) for fish tagged in the Maumee River. These estimates of \hat{c} were used to adjust model AIC_c values and variance estimates for overdispersion in all CJS models (White & Burnham, 1999).

The joint probability of surviving and returning to the spawning site during the last time interval (λ) did not differ by sex or by length at tagging in either Tittabawassee or Maumee rivers (Table 4). The largest Δ QAIC_c value for candidate models fit to λ was 2.14 for both rivers (Table 4). For each river, including length at tagging and sex covariates did not substantially improve model fit over the null model (i.e., λ); these covariates did not contribute substantially to the explanatory ability of the models.

Constant λ was retained as the “best” model for λ and retained in subsequent models to identify the most parsimonious models for p and φ .

Estimates of site fidelity (p) from the highest ranked (i.e., model with lowest AIC value) CJS model were relatively high in both rivers, but was greater in the Tittabawassee River (95%) than in the Maumee River (70%) (Figure 3). Uncertainties (95% confidence intervals) around point estimates of walleye site fidelity were non-overlapping; however, in the Tittabawassee River, intervals were smaller than the Maumee River (Figure 3). Explanatory power of models that included spawning year, sex or fish length at tagging as covariates was similar for estimates of p for the Tittabawassee or Maumee rivers. Δ QAIC_c values of the three top-ranked models for p to the Tittabawassee River were less than 2 and Δ QAIC_c value of the fourth-ranked model was marginally greater than 2 (Δ QAIC_c = 2.04) (Table 5). Furthermore, the set of top-ranked models for the Tittabawassee River included the null model of constant p among spawning years, sex or fish length at tagging (Table 5). None of the five top-ranked models for the Tittabawassee River included additive

TABLE 5 QAIC_c results for comparison of Cormack–Jolly–Seber models used for determining the most parsimonious model for estimating site fidelity (p) of Walleye detected in the Tittabawassee and Maumee rivers during the spawning period 2011–2014

River	Model	Param	QAIC _c	Δ QAIC _c	w_i	QDeviance	\hat{c}
Tittabawassee	$\varphi(\text{year} + \text{sex} + \text{length}), p, \lambda$	6	544.23	0.00	0.31	532.05	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{length}), \lambda$	6	545.09	0.86	0.20	532.91	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year}), \lambda$	7	545.41	1.18	0.17	531.17	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{sex}), \lambda$	7	546.28	2.04	0.11	532.03	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year} + \text{length}), \lambda$	8	547.41	3.18	0.06	531.10	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year} + \text{sex}), \lambda$	8	547.48	3.25	0.06	531.17	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{sex} + \text{length}), \lambda$	8	548.17	3.94	0.04	531.86	1.3
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year} + \text{sex} + \text{length}), \lambda$	9	549.46	5.23	0.02	531.07	1.3
Maumee	$\varphi(\text{year} + \text{sex} + \text{length}), p, \lambda$	6	298.39	0.00	0.30	286.12	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{length}), \lambda$	6	298.45	0.06	0.29	286.18	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year}), \lambda$	7	299.90	1.51	0.14	285.55	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{sex}), \lambda$	7	300.40	2.01	0.11	286.05	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year} + \text{sex}), \lambda$	8	301.88	3.49	0.05	285.42	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year} + \text{length}), \lambda$	8	301.99	3.60	0.05	285.53	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{sex} + \text{length}), \lambda$	8	302.49	4.10	0.04	286.04	1.7
	$\varphi(\text{year} + \text{sex} + \text{length}), p(\text{year} + \text{sex} + \text{length}), \lambda$	9	303.99	5.60	0.02	285.41	1.7

effects of two or more covariates (Table 5). For the Maumee River, the four top-ranked models had Δ QAIC_c values ≤ 2 , indicating these models had similar explanatory power (Table 5). Similar to the Tittabawassee River, Maumee River candidate models with year, sex and length at tagging as covariates were not more highly ranked than models with constant p (Table 5). For both the Maumee and Tittabawassee rivers, constant p was retained in models to identify the best supported model for φ .

Apparent annual survival (φ) differed by sex and length at tagging in the Tittabawassee and Maumee rivers. Estimates of mean apparent annual survival for female walleye (0.66 Tittabawassee, 0.48 Maumee) were higher than male walleye in each river (0.53 Tittabawassee, 0.29 Maumee; Figure 3). For male and female walleye combined, mean φ was higher in the Tittabawassee River than the Maumee River (Figure 3). Estimates of φ decreased linearly with length at tagging in the Tittabawassee River and increased linearly with length in the Maumee River (Figure 4). Within either river, φ of female walleye was higher than male walleye for all lengths and the slope of the relationship between fish length at tagging and φ was similar for male and female fish (Figure 4). Based on Δ QAIC_c, the three highest ranked models for φ in the Tittabawassee and Maumee rivers had similar explanatory power (Table 6). Sex and length at tagging covariates were included in two of the top three models for the Tittabawassee River, suggesting apparent annual survival differed by length of fish and by sex. Spawning year was included in one of the three top-ranked models for the Tittabawassee River, but inclusion of the variable in only one of the top three ranked models indicated that spawning year may have minimally influenced apparent annual survival in the Tittabawassee River. Spawning year was not included in the three highest ranked models for the Maumee River (Table 6). The top-ranked models for the Tittabawassee and Maumee rivers were

highly favoured over the null model of constant φ , suggesting sex and length at tagging influenced φ .

4 | DISCUSSION

Spawning site fidelity differed between the Tittabawassee (0.95) and Maumee (0.7) rivers in our study. Moreover, our findings suggested biotic or abiotic variables operating at the stock level influenced spawning site fidelity. The western basin of Lake Erie supports multiple large walleye spawning aggregations on open-water reef complexes and tributaries located along the southern shore near the Maumee River (Fraker et al., 2015; Goodyear et al., 1982; Pritt et al., 2013). Multiple spawning aggregations and sites in close proximity to the Maumee River may increase the probability that some individuals will locate suitable spawning habitat different from areas used in previous years. Walleye that were tagged in the Maumee River have a high probability in subsequent spawning seasons of encountering other walleye spawning aggregations in western Lake Erie and may choose to spawn in these locales rather than the Maumee River. In contrast, the Tittabawassee River in Lake Huron is the primary source of walleye recruits to Saginaw Bay and supports the largest known spawning aggregation in Saginaw Bay (Johnson et al., 2015). Walleye that previously spawned in the Tittabawassee River probably returned to the Tittabawassee River in successive years because the probability of encountering other spawning aggregations in Saginaw Bay or Lake Huron was low. Interestingly, spawning site fidelity of walleye tagged in Van Buren Bay in eastern Lake Erie was estimated at 92% based on an analysis of a long-term capture–recapture data set of 13,900 jaw-tagged walleye spanning 16 years (Zhao et al., 2011). This estimate was higher than our estimate for the Maumee

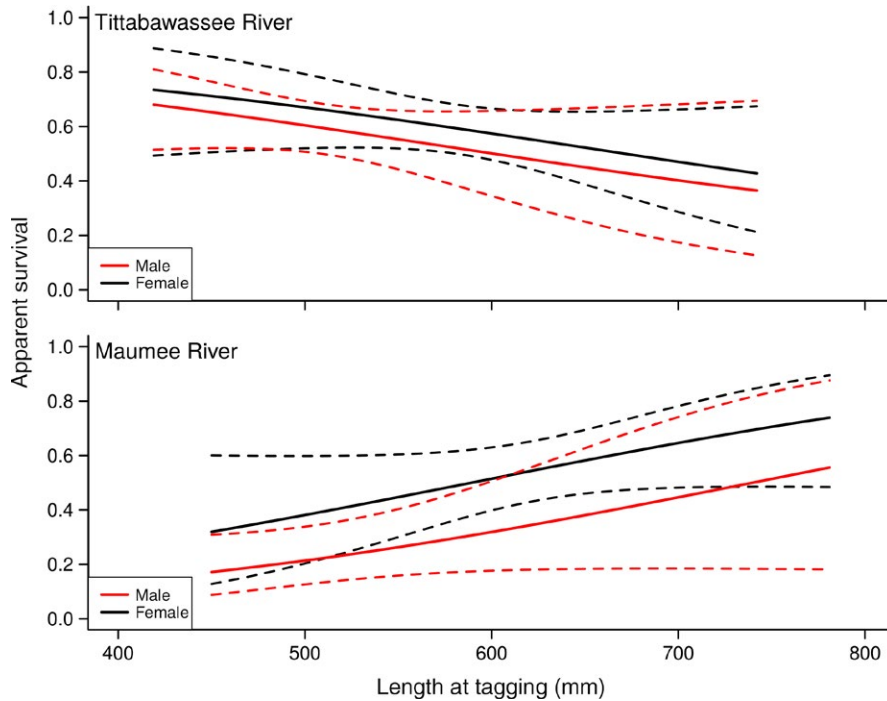


FIGURE 4 Apparent annual survival of walleye implanted with acoustic tags in 2011 and 2012 from the Tittabawassee and Maumee rivers as a function of fish length at tagging and sex. Apparent annual survival was estimated using the most parsimonious model for each river. See Figure 2 for mean annual estimates of apparent annual survival. Dashed lines are 95% confidence intervals

TABLE 6 QAIC_c results for comparison of Cormack–Jolly–Seber models used for determining the most parsimonious model for estimating apparent annual survival (ϕ) of walleye detected in the Maumee and Tittabawassee rivers during the spawning period 2011–2014

River	Model	Param	QAIC _c	Δ QAIC _c	w_i	QDeviance	\hat{c}
Tittabawassee	$\phi(\text{sex} + \text{length}), p, \lambda$	5	542.42	0.00	0.42	532.29	1.3
	$\phi(\text{length}), p, \lambda$	4	543.87	1.45	0.20	535.78	1.3
	$\phi(\text{year} + \text{sex} + \text{length}), p, \lambda$	6	544.23	1.82	0.17	532.05	1.3
	ϕ, p, λ	3	545.22	2.81	0.09	15.05	1.3
	$\phi(\text{year} + \text{length}), p, \lambda$	5	545.47	3.05	0.08	535.34	1.3
	$\phi(\text{year}), p, \lambda$	4	546.50	4.08	0.05	14.29	1.3
	$\phi(\text{sex}), p, \lambda$	4	546.83	4.41	0.04	14.62	1.3
	$\phi(\text{year} + \text{sex}), p, \lambda$	5	548.14	5.73	0.02	13.89	1.3
Maumee	$\phi(\text{sex} + \text{length}), p, \lambda$	5	296.39	0.00	0.31	286.20	1.7
	$\phi(\text{length}), p, \lambda$	4	297.18	0.78	0.21	289.05	1.7
	$\phi(\text{sex}), p, \lambda$	4	297.31	0.91	0.20	17.06	1.7
	$\phi(\text{year} + \text{sex} + \text{length}), p, \lambda$	6	298.39	2.00	0.12	286.12	1.7
	$\phi(\text{year} + \text{length}), p, \lambda$	5	298.91	2.51	0.09	288.72	1.7
	$\phi(\text{year} + \text{sex}), p, \lambda$	5	299.26	2.87	0.07	16.95	1.7
	ϕ, p, λ	3	310.51	14.12	0.00	32.32	1.7
	$\phi(\text{year}), p, \lambda$	4	310.89	14.50	0.00	30.65	1.7

River in western Lake Erie but similar to estimates of spawning site fidelity in the Tittabawassee River. The Van Buren Bay walleye population is the largest source of walleye to the eastern basin of Lake Erie (Goodyear et al., 1982; MacDougall, Wilson, Richardson, Lavender, & Ryan, 2007; Schneider & Leach, 1979; Zhao et al., 2011). Similar to the Tittabawassee River, few other spawning aggregations and habitats are nearby to the Van Buren Bay site and possibly high spawning site fidelity may confer an evolutionary advantage in systems with few spawning aggregations (Zhao et al., 2011). Variable spawning site

fidelity may provide an advantage such that high fidelity is advantageous when spawning habitat is scarce and reduced fidelity is advantageous to colonise and use all available sites when spawning habitat is abundant.

Our estimates of spawning site fidelity were consistent with other studies. In a study of walleye movements in a chain of lakes in northern Wisconsin, walleye were tagged on spawning grounds and movements were tracked using radio telemetry at weekly intervals over two successive spawning seasons (Weeks & Hansen, 2009). In that study,

82% of walleye were estimated to have returned to the lake where originally tagged. This estimate was comparable to 70% site fidelity to Maumee River and 95% site fidelity to the Tittabawassee River estimated by our study. Although walleye returned to the same lake during the spawning season in multiple years, the study did not determine whether walleye returned to the same location within a lake (Weeks & Hansen, 2009). Similarly, we estimated site fidelity at the spatial scale of the river and did not determine whether walleye returned to the same area of the Tittabawassee or Maumee rivers in successive spawning seasons. The similarity between our estimates and other studies suggests high spawning site fidelity may be a general characteristic of walleye populations in all systems and an important component of the species life history.

Estimates of apparent annual survival in our study were similar to annual survival estimated from fishery-dependent tag-recovery studies for the Tittabawassee River walleye (Figure 3). Estimates of annual survival calculated using a Brownie-structured tag-recovery model for the Saginaw Bay walleye fishery varied by year and averaged 58% (range 33%–76%) during 2005–2010 (Fielder, 2014). Using a statistical catch-at-age model, total age-specific annual mortality for walleye during 2005–2011 ranged from 30% to 40% for age 4 and older walleye in Saginaw Bay, corresponding to a total annual survival of 60%–70% (Fielder & Bence, 2014). In comparison, mean apparent annual survival estimated from our CJS models was 66% (59%–73%; 95% CI) for females and 53% (45%–61%; 95% CI) for males. Our study focused only on the Tittabawassee River walleye population, but the other studies cited above used data from Saginaw Bay waters in general. Estimates of apparent annual survival for the Tittabawassee River walleye population should be similar to published estimates of annual survival for Saginaw Bay walleye because the Tittabawassee River spawning population is considered the primary source of the Saginaw Bay walleye stock, if walleye emigration from the Tittabawassee River population is negligible (Johnson et al., 2015). Estimates of age-specific total annual mortality for walleye increased from approximately 30% at age 6 to a maximum of approximately 35% for ages 10–13 calculated for the 2005–2011 time period (Fielder & Bence, 2014). If annual mortality is converted to annual survival (annual survival = 1–mortality), the negative relationship between length and apparent annual survival observed in our study is consistent with the negative relationship observed for age and annual survival during 2011–2014 in statistical catch-at-age models (Fielder & Bence, 2014). Apparent annual survival decreased nearly linearly with increasing length in our study in contrast to the asymptotic relationship between age and annual survival observed in statistical catch-at-age models (Fielder & Bence, 2014). Differences between size-specific apparent annual survival from telemetry and age-specific annual survival from catch-at-age models may reflect differences in walleye size structure included in analysis, real differing rates between the two time periods, differences in the method of calculation or emigration of walleye from the Tittabawassee River population.

Stock-specific estimates of annual survival were not available for Maumee River walleye; however, apparent annual survival estimated in our study was lower than annual survival rates reported for walleye

in the western basin of Lake Erie. Using a statistical catch-at-age modelling approach, annual survival for walleye at least 2 years old in western Lake Erie ranged from 60% to 70% (Walleye Task Group, 2016). Similarly, annual survival of age 5 and older walleye in western Lake Erie was estimated to range from 64% to 77% using a Brownie tag-recovery model (Vandergoot & Brenden, 2014). In contrast, mean estimates of apparent annual survival for walleye of the same age from the Maumee River ranged from 29% to 48% in our study. The difference between apparent annual survival and annual survival may reflect bias in estimates of apparent annual survival owing to emigration of walleye from the Maumee River spawning stock to other spawning areas. The magnitude of the effect of emigration on apparent annual survival may be substantial and depends on the number of emigrants and spatial constraints of sampling (Cilimburg, Lindberg, Tewksbury, & Hejl, 2002). To qualitatively determine whether walleye emigrated from the Maumee River, we estimated how many of the 162 tagged walleye that were not detected in the Maumee River the year after tagging but were detected on the large number of acoustic receivers deployed in the Great Lakes basin during the summers of 2012 and 2013 (Hayden et al., 2014). If a walleye was not detected on Maumee River receivers during the spawning season but was detected on receivers other than the Maumee River, then the fish was alive and had not used the Maumee River in subsequent spawning years. Twelve walleye tagged but not detected later in the Maumee River in 2011 or 2012 were detected on other receivers in the Great Lakes basin and were at large through summer 2013. Clearly some walleye in our sample did not return to the Maumee River during the spawning season in subsequent years. Of the fish that did not return to the Maumee River during our study, acoustic receiver coverage in Lake Erie was insufficient to separate walleye that died and individuals that avoided detection. However, our estimates of site fidelity could be considered unbiased if the failure to return was permanent (Schaub & Royle, 2014).

The positive relationship between fish length and apparent annual survival in our study may be linked to differential emigration of young and small (i.e., <530 mm TL, age 6) walleye from the Maumee River spawning stock. Estimates of apparent annual survival will be biased low for small individuals if small walleye (<530 mm TL, age 6) show lower site fidelity to the Maumee River in higher proportion than large individuals (>530 mm TL). The mechanisms walleye use for repeatedly navigating to the same spawning site are unknown but spawning site fidelity appears to develop as adults and strengthens over multiple spawning seasons (Olson, Schupp, & Macins, 1978). Emigration of small walleye from the Maumee River is consistent with individuals that have not developed strong spawning site fidelity from repeated spawning seasons. Alternatively, small walleye may have been disproportionately affected by the tagging process, which resulted in small walleye abandoning the Maumee River as a spawning site. Repeated return of individuals to the natal site for spawning is a specific type of spawning site fidelity required for accrual of genetic differences and development of local adaptations. Some spawning populations of walleye in the Great Lakes have been shown to be genetically distinct (Brenden et al., 2015; Stepien et al., 2010); however, weak levels of genetic differentiation among walleye populations have been reported from Lake Erie (Stepien

et al., 2010). The lack of population genetic structure in most Great Lakes walleye spawning stocks may be explained by small walleye having weak natal site fidelity, especially in systems where multiple spawning aggregations and habitats are in close proximity.

CJS models provide mortality-independent estimates of site fidelity using the frequency of marked individuals recaptured over repeated sampling events when the probability of encountering an individual equals one. In scenarios where few marked individuals are encountered and few spawning locations are sampled, populations then must be sampled over multiple spawning seasons for unbiased estimates of spawning site fidelity. Studies employing electronic tags provide mortality-independent estimates of spawning site fidelity when a sufficient number of detections may be obtained to identify dead fish from nonhoming individuals (Binder et al., 2016; Weeks & Hansen, 2009). Few studies have used this approach to estimate spawning site fidelity because the assumption of perfect detection probabilities is seldom met with traditional external tags and recapture methods. Although the probability of detecting a single tag transmission from a tagged fish using acoustic telemetry varies dramatically over time and space (Hayden et al., 2016; Heupel, Semmens, & Hobday, 2006), deployment of multiple acoustic receivers in the study area increases the probability of detecting all tagged individuals to near 1 (Hayden et al., 2016). In our study, multiple acoustic receivers recording tag transmissions 24 hr per day were deployed near the mouths and upstream in the Tittabawassee and Maumee rivers nearly continuously during the study period. Walleye tags transmitting approximately every two minutes provided multiple opportunities during upstream and downstream spawning movements to be detected by receivers (Hayden et al., 2014).

Our observation of spawning site fidelity greater than 70% to the Tittabawassee and Maumee rivers suggested spawning site fidelity may be an important component of walleye life history. The large differences between the Tittabawassee and Maumee rivers in spawning site fidelity proportions showed that the propensity of walleye to return to the same spawning site varied among populations and may be influenced by abiotic and biotic variables. Walleye that did not return to the Maumee or Tittabawassee rivers in subsequent years after tagging either spawned at different spawning sites or did not spawn every year. Limited evidence suggests female walleye from Lake Erie may skip reproductive seasons (i.e., reproductive holidays) in years when they lack sufficient lipid reserves (Henderson & Nepszy, 1994; Henderson, Wong, & Nepszy, 1996). Therefore, differences in spawning site fidelity may be influenced by the prevalence of skipped spawning. Based on these findings, the current management paradigm of managing the western Lake Erie walleye stock as a single population may be justified given that approximately 30% of walleye we tagged did not return to the Maumee River but likely spawned at different locations in Lake Erie or did not spawn every year. As spawning site fidelity increases, management actions to conserve population structure will need to increasingly focus on individual populations. Due to the high spawning site fidelity, managers may need to consider managing the Tittabawassee River as an individual population to conserve potential accumulated genetic adaptations. Given the differences in spawning site fidelity between the Maumee and Tittabawassee rivers,

a better understanding of populations-specific mechanisms that influence spawning site fidelity of walleye are needed to develop effective management plans.

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