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Tributary Use and Large-Scale Movements of Grass Carp in Lake Erie

Cleyo Harris[1,2], Travis O. Brenden[1], Chris S. Vandergoot[1],
Matthew D. Faust[3], Seth J. Herbst[4], and Charles C. Krueger[1]

[1]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824
[2]Lake Erie Management Unit, Fisheries Division, Michigan Department of Natural Resources, Waterford, MI 48327
[3]Sandusky Fisheries Research Station, Division of Wildlife, Ohio Department of Natural Resources, Sandusky, OH 44870
[4]Fisheries Division, Michigan Department of Natural Resources, Lansing, MI 48909

Running title: Lake Erie Grass Carp Movement

Abstract

Infrequent captures of invasive, non-native grass carp (*Ctenopharyngodon idella*) have occurred in Lake Erie over the last 30+ years, with recent evidence suggesting that wild reproduction in the lake's western basin (WB) is occurring and that abundance is increasing. Information on grass carp movements in the Laurentian Great Lakes is lacking, but an improved understanding of large-scale movements and potential aggregation areas could inform control strategies and risk assessment of grass carp spread to other parts of Lake Erie and other Great Lakes. Twenty-three grass carp captured in Lake Erie's WB were implanted with acoustic transmitters and released. Movements were monitored with acoustic receivers deployed throughout Lake Erie and elsewhere in the Great Lakes. Grass carp dispersed up to 236 km, with approximately 25% of fish dispersing greater than 100 km from their release location. Mean daily movements ranged from 0.004 to 2.49 km/day, with the highest daily averages occurring in the spring and summer. The Sandusky River, Detroit River, Maumee River, and Plum Creek were the most heavily used WB tributaries. Seventeen percent of grass carp moved into Lake Erie's central or eastern basins, although all fish eventually returned to the WB. One fish emigrated from Lake Erie through the Huron-Erie Corridor and into Lake Huron. Based on these results, past assessments may have underestimated the risk of grass carp spread. We recommend focusing grass carp control efforts on Sandusky River and Plum Creek and secondarily on Maumee and Detroit Rivers given their high use by tagged fish.

Keywords: Laurentian Great Lakes, acoustic telemetry, invasive species, movement, risk assessment, control strategies

Introduction

Grass carp (*Ctenopharyngodon idella*) is a large herbivorous cyprinid species native to eastern Asia (Lee et al., 1980; Shireman and Smith, 1983) and first imported to the United States in the early 1960s for biocontrol of aquatic vegetation. Initial introductions in Arkansas and Alabama were for research purposes (Mitchell and Kelly, 2006). The stocking of grass carp in public and private impoundments for vegetation biocontrol began in 1969 and was prevalent throughout the 1970s. Initial stocking efforts were considered beneficial because vegetation was successfully controlled in systems where fish were stocked; however, concerns quickly arose regarding unintended expansion and establishment of grass carp populations into other systems (Bailey, 1978; Chilton and Muoneke, 1992; Mitchell and Kelley, 2006; Dibble and Kovalenko, 2009). This led to methodologies for producing monosex grass carp and eventually for producing triploid grass carp that functionally were sterile (Mitchell and Kelly, 2006). In the early 1980s, a procedure for inducing triploidy in grass carp using temperature or pressure shocking was developed (Cassani and Caton, 1985). Subsequently, many U.S. states and Canadian provinces required that grass carp stocking be limited to triploid fish, although several other U.S. states continued to allow the stocking of diploid (i.e., reproductively viable) grass carp (Mitchell and Kelly, 2006; MICRA, 2015).

Widespread stocking and subsequent escapement and spread led to establishment of grass carp populations throughout much of the Mississippi River basin and other areas of the United States (Courtenay, 1993; USGS, 2018). In some systems, grass carp populations were found to be comprised of a mixture of triploid and diploid individuals (Schulz et al., 2001), which is suggestive of multiple invasion sources. The presence of diploid grass carp in populations is of particular concern to managers because of the possibility of their continued spread and expansion into new waters and escalating deleterious effects in systems where they have become naturalized.

In the Laurentian Great Lakes of North America, captures of grass carp have occurred since the 1980s. The first documented captures of grass carp in the Great Lakes were in Ohio and Ontario waters of Lake Erie in 1985 (USGS, 2018). Since then, grass carp have been captured in all the Great Lakes with the exception of Lake Superior (USGS, 2018). Captures of grass carp in the Great Lakes were infrequent or were unreported from the 1980s to 2000s (USGS, 2018); however, in the 2010s, capture and reporting rates of grass carp, primarily by commercial fishers, began increasing in Lake Erie's western basin (WB) (Cudmore at al., 2017). The risk of natural reproduction in the Sandusky River was elevated in 2012 when juvenile grass carp were captured and determined to be reproductively viable (i.e., diploid) (Chapman et al. 2013). Subsequently, grass carp eggs were collected in the Sandusky River, which was the first confirmed evidence of grass carp spawning in the Great Lakes (Embke et al. 2016). More recently, grass carp eggs and larvae were collected from the Maumee River (P. Kocovsky, U.S. Geological Survey, personal communication). Although to date, grass carp spawning has only been detected in the Sandusky and Maumee rivers, Kocovsky et al. (2012) identified a total of 7 Lake Erie tributaries that may be conducive to grass carp spawning.

The confirmation of grass carp spawning in Lake Erie tributaries prompted a study by Wieringa et al. (2017) evaluating ploidy of a large sample of grass carp captured from the WB of Lake Erie. Ploidy was determined for 60 grass carp, mostly captured by commercial fishing operations. Approximately 87% of tested fish were diploid (i.e., reproductively viable) (Wieringa et al. 2017).

The combined findings of Embke et al. (2016) and Wieringa et al. (2017) elevated concerns among fishery biologists in the region that grass carp either had or soon could become established in Lake Erie, which in turn could contribute to grass carp spread elsewhere in the Great Lakes region. The greatest concern about grass carp establishment centers around their potential to reduce and/or modify aquatic vegetation densities and composition (Bain et al., 1993; Cudmore et al., 2017). Through bioenergetics modeling, van der Lee (2017) estimated that a population of grass carp under average temperature conditions could consume 27.6 kg of vegetation per kg of fish per year depending on the energy density of the vegetation. van der Lee (2017) additionally conducted simulations to determine the effect that grass carp populations at various biomass densities could have on an invaded wetland and found that within one year grass carp could reduce vegetation densities by more than 50%. Gertzen et al. (2017) identified 33 fish and 18 bird species that were expected to experience high negative effects from grass carp establishment in the Great Lakes.

One information gap that has made it difficult to evaluate risk to the Great Lakes from grass carp establishment in Lake Erie or elsewhere in the Great Lakes is the lack of information on grass carp movement in a system like the Great Lakes (Cudmore et al., 2017). Additionally, the Lake Erie Committee, a binational committee comprised of fishery agency representatives from states and provinces with management authority over the lake, issued a position statement regarding Asian carp, which is a group term that includes grass carp (Chapman and Hoff, 2011). The committee recommended research be conducted to better understand fish behavior and space use to assist with development of future control strategies (http://www.glfc.org/pubs/lake_committees/erie/LEC_docs/position_statements/LEC_Asian_Carp_Position%20Statement.pdf). Grass carp can be an elusive species to capture through standard assessment methods (Mitchell, 1980; Maceina et al., 1999); therefore, any information about grass carp space use would allow better target control efforts and ostensibly improve capture efficiency.

The purpose of this study was to improve understanding of grass carp spatio-temporal movement behavior in Lake Erie and to identify areas of high use to inform the development of control strategies. The study was accomplished by implanting grass carp with acoustic transmitters and monitoring movements using widely dispersed passive acoustic receivers. Specifically, we deployed receivers in tributaries to the WB of Lake Erie and relied on detections from an extensive network of acoustic receivers deployed throughout Lake Erie and other areas of the Great Lakes as part of the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al., 2018) to monitor broader movements of tagged fish. Specific objectives for this study were to quantify 1) dispersal (i.e., furthest distance that grass carp moved from their tagging location), 2) total movement (the summation of interpolated path movements) and average daily movements of grass carp, 3) tributary use within the WB of Lake Erie, 4) intra-Lake Erie spread, and 5) emigration from Lake Erie to other areas of the Great Lakes region (e.g., Lake St. Clair, Lake Huron, Lake Ontario).

Methods

Study site

Lake Erie is the shallowest and most productive of the Laurentian Great Lakes. The lake consists of three distinct basins (Figure 1; Ryan et al., 2003). The western basin (WB) is the shallowest (mean depth = 7.4 m) followed by the central (mean depth = 18.5 m) and eastern basins (mean depth = 24.5 m). For this study, the WB of Lake Erie was defined as the area from the confluence with the Detroit River to Point Pelee in Leamington, ON on the northern shoreline and Sandusky, OH on the southern shoreline (Figure 1). Lake Erie receives outflow from lakes Huron and St. Clair via the St. Clair and Detroit rivers and empties into Lake Ontario via the Welland Canal and Niagara River. Most of the lake is classified seasonally during the summer as coolwater (20–28°C), with coldwater (<20°C) habitat limited to the eastern basin and portions of the central basin (Hokanson, 1977).

Transmitter implantation

Fifty grass carp collected from Michigan and Ohio waters of Lake Erie by commercial fishing operations (n=48 fish) and state agency sampling efforts (n=2 fish) were implanted with acoustic transmitters between 2014 and 2017. Total lengths of tagged fish ranged from 50.5 to 128.0 cm ($\bar{x}$ =90.9 cm) and body mass ranged from 5.3 to 28.2 kg ($\bar{x}$ =11.7 kg). Age of fish estimated using sectioned pectoral fin rays ranged from 3 to 14 years ($\bar{x}$ =6.7 years). Ploidy was determined for 39 of the 50 fish through blood samples using methodologies described in Krynak et al. (2015). Approximately 95% (n=37 fish) of the fish for which ploidy could be determined were diploid. Ploidy was indeterminable for 11 of the tagged fish because either blood was not collected at time of capture, samples coagulated before testing, or ploidy results were inconclusive.

Following capture, grass carp were held until a surgery crew was able to get onsite to perform surgery to implant a transmitter, which included sedating the fish, performing the surgery, and allowing recovery time prior to release. The time span between capture and transmitter implantation was as little as a few hours but in some cases was up to two days. When necessary, captured fish were held in large (railcar size) storage containers placed directly in

Lake Erie filled with lake water, occasionally along with the rest of the commercial catch. Before transmitter implantation, fish were transferred to a 379-L aerated holding tank. Each grass carp was anesthetized using a portable electroanesthesia system (Smith-Root, Vancouver, Washington) using pulsed-direct current, 30 V, 100 Hz, and 25% duty cycle for 3 seconds. After achieving stage-4 anesthesia (Bowzer et al., 2012), transmitters were surgically implanted intracoelom. Surgical procedures followed methods described by Hayden et al (2014) and guidelines described by Cooke et al. (2011). During the study, surgeries were performed by three different surgeons given the logistical challenges of where and when grass carp were captured. Acoustic transmitters (Model V16-4H, Vemco, Halifax, Nova Scotia) were inserted through a small ventral incision located along the midline of the fish, posterior to the pelvic girdle. Incisions were closed with 2 to 3 absorbable monofilament sutures (PDS-II, 3-0, Ethicon, Somerville, NJ). Transmitters were configured to emit a tag-specific code (69 kHz) at random intervals between 60-180 seconds to reduce probability of code collisions. After surgery, fish were returned to the aerated tank and tagged with uniquely numbered external lock-on loop tags (Model FT-4; Floy Tag & Manufacturing Inc., Seattle, Washington) just below the anterior portion of the dorsal rays. The lock-on tags provided a phone number to call if tagged grass carp were harvested. Fish remained in the aerated tank until regaining equilibrium and then were returned to the lake nearby their capture site (< 1.5 km away). Tagged grass carp were released in the following locations: Sandusky River (n=18), Plum Creek (n=10), nearshore area of Marblehead and Catawba Islands (n=8), Sandusky Bay (n=5), Raisin River (n=5), north Maumee Bay (n=3), and Huron River (n=1).

Acoustic receivers

Tagged grass carp were detected using acoustic receivers, hereafter referred to simply as receivers, deployed in select tributaries of the WB of Lake Erie for this study and by a large set of GLATOS receivers deployed throughout Lake Erie and other parts of the Great Lakes (Krueger et al., 2018). Receivers recorded date, time, and unique transmitter ID code when a tagged grass carp was detected. For this study, receivers (Model VR2W, Vemco, Nova Scotia) were deployed in 13 tributaries located in either Michigan or Ohio (Table 1). Ontario tributaries were not monitored because consultation with provincial fishery agency biologists did not identify tributaries that grass carp were likely to spawn or use. Criteria for selecting tributaries in which to deploy receivers were: 1) tributaries from which grass carp had previously been collected based on review of records from the U.S. Geological Survey Nonindigenous Aquatic Species database (USGS, 2018), and 2) WB tributaries with a watershed size greater than 100 km^2 based on the Great Lakes Hydrography Dataset (Forsyth et al., 2016). Although Stony Creek (Michigan) and Cedar Creek (Ohio) met the criteria for deploying receivers, site visits suggested that these two tributaries were too shallow for receivers to function effectively; consequently, receivers were not deployed in either of these systems. Actual deployment of receivers in the Maumee, Sandusky, and Detroit rivers was not necessary as receivers were already deployed in desired locations by other GLATOS projects. Tributaries with receiver deployments had watershed sizes ranging from 89 km^2 (Plum Creek) to 16,972 km^2 (Maumee River).

Receiver deployments in the tributaries varied each year from 2015 through 2017, with increased monitoring each year. Only tributaries identified with potential for grass carp spawning (Kocovsky et al., 2012) and/or historic capture locations (USGS, 2018) were monitored in 2015 because of the low number of tagged fish. In 2016 and 2017, all 13 tributaries were monitored with up to 2 receivers located near the mouth of the tributaries to detect grass carp use. In 2017, more intensive monitoring of the Raisin River, Plum Creek, Sandusky River, and Maumee River was conducted to measure upstream movement of grass carp in these tributaries. The number of additional receivers deployed in these tributaries ranged from 2 (Plum Creek) to 8 (Sandusky River). The additional upstream receivers were placed proximal to locations of anticipated high turbulence sections of river or dams where fish passage was obstructed and were generally deployed in the spring and retrieved in the fall to avoid ice-related loss or damage in the winter. One exception was Plum Creek where ice-related loss or damage was low risk because this system receives warmwater discharge from a coal-fired power plant. Range testing of acoustic receivers deployed in tributaries specifically for this study suggested that at distances within 100 m the probability of detecting a transmitter was greater than 50%, with most tributaries have having detection probabilities greater than 60 or 70% (Appendix A).

Receivers deployed as part of other GLATOS projects provided potential detection information from more than 2500 receivers located throughout Lakes Erie and Huron from 2015 to 2017. Some of these receivers were deployed year-round whereas others were seasonal deployments (Figure 2). The spatial configuration of receivers deployed as part of GLATOS was not temporally consistent because of shifting objectives of other projects. Most notably, beginning in 2016, a change from using receiver lines or gates in Lake Erie to a grid pattern occurred. The modified Lake Erie receiver deployment strategy was intended to increase the frequency of detections and better assess movements of some of the more commonly tagged species in Lake Erie (e.g., walleye, lake trout; Kraus et al. 2018).

Data Analysis

Detection data from all receivers were used to construct a georeferenced detection history for each tagged grass carp. Analyses herein were based primarily on detections collected through 31 December 2017, although in some cases we mention movements that occurred during 2018. To eliminate the effects of false positive detections (Simpfendorfer et al., 2015), single detections more than 60 minutes apart from another detection with the same unique, tag-specific code were removed from the dataset; this resulted in filtering out 0.2% of 739,774 total detections. To reduce possible post-surgery behavioral effects, only fish detected on acoustic receivers more than 60 days after initial tagging were included in analyses. This criterion was met by 23 tagged grass carp with total lengths ranging from 75.2 to 115.1 cm and body mass ranging from 5.3 to 22.4 kg. Of the 23 fish that met criteria for inclusion, ploidy could be determined for 19 fish, 89% (n=17) were diploid and 11% (n=2) were triploid. Of those 23 fish, the average time span between date of surgery and last detection was approximately 580 days and ranged from 90 to 1350 days.

During the study, no tagged grass carp was reported as harvested. Additionally, no tagged grass carp was ever repeatedly detected near one receiver without subsequent detections elsewhere, which might be considered indicative of a natural mortality event. In August 2018, one grass carp that was implanted with an acoustic transmitter in March 2017 based on its external lock-on loop tag number was recaptured by Ohio DNR biologists during routine electrofishing surveys on the Sandusky River and sacrificed. Upon dissection, the acoustic transmitter could not be located, suggesting that the fish had shed the transmitter. The duration between surgery and last detection for this fish was 153 days. External and internal examination of the fish showed no obvious point of transmitter expulsion.

Movements between subsequent receiver detections for tagged grass carp was estimated in R (R Core Team, 2018) through interpolated paths generated with the interpolate_path function from the GLATOS package (https://gitlab.oceantrack.org/GreatLakes/glatos). Descriptors of movement included maximum dispersals (the furthest distance from release location to a detection location), total movement distances (the summation of interpolated path movements), and mean daily movement distances. Daily movements for fish located multiple times during a day were calculated by summing distances of the interpolated movement paths during that day. If during a day a fish was only detected on a single receiver, its daily movement was assumed to be 0. When fish were undetected for a period of several days and then detected on a different receiver from their last prior location, daily movements were calculated as the distance between receiver locations divided by the number of days that elapsed between detections. Seasonal movements were grouped into the four astronomical seasons: autumn, spring, summer, and winter. We acknowledge that our descriptors of movement are likely negatively biased as we are unable to account for movements that occur outside the detection range of receivers. Such bias is not unique to this study but rather is a feature of telemetry studies that rely on passive acoustic detections. Fish use of WB tributaries in Lake Erie were based on number of tagged fish that entered tributaries and length of time fish were located in tributaries. Migration from the WB of Lake Erie into the central and eastern basins was also based on number of tagged fish that moved into these other basins and length of time until fish were detected moving back to western Lake Erie. Emigration from Lake Erie into Lake St. Clair or Lake Huron was based on number of tagged fish detected on receivers in these other systems without returning to Lake Erie.

Results

Maximum dispersal

Maximum dispersal (i.e., furthest distance from release location to a detection location) of tagged grass carp ranged from 1 to 236 km ($\bar{x}$ = 60.7 km; standard error of the mean [SE] =14.4 km). Twenty-six percent of tagged grass carp had maximum dispersals greater than 100 km. Large maximum dispersals were not unique to fish released in specific locations, but instead was a feature of fish released in the River Raisin (1 triploid fish), Plum Creek (2 diploid fish), North Maumee Bay (1 diploid fish), and Sandusky River (2 diploid fish). Conversely, 39% of tagged grass carp (6 diploid and 3 unknown ploidy) had maximum dispersals of less than 15 km. With the exception of two individuals, grass carp with the shortest maximum dispersals were released in the Sandusky River and never left the river. In addition, two other fish that were tagged and released in Plum Creek exhibited limited spatial movements and were last detected nearby at the confluence of Plum Creek and Lake Erie.

Total movement distance

Total movement distance (i.e., the summation of interpolated path movements) ranged from 1 to 615 km ($\bar{x}$ = 263.2 km; SE = 42.1 km). Thirty percent of the tagged grass carp (6 diploid and 1 triploid) had total movement distances greater than 400 km. Two diploid fish with total movement distances greater than 400 km did not leave the Sandusky system, but made multiple movements throughout the Sandusky River and Sandusky Bay. Conversely, 30% of tagged grass carp (5 diploid and 2 unknown ploidy) had total movement distances of less than 100 km.

With respect to seasonality, average total movement (averaged across fish) was similar during spring ($\overline{x}$ = 95.6 km; SE = 16.9 km) and summer ($\overline{x}$ = 93.9 km; SE = 23.3 km) and greater than during autumn and winter. Thirty percent of fish accumulated more than 50% of their total movement distances during spring, whereas 22% accumulated more than 50% of the movement during summer. Average total movement was approximately 40 to 55% less during autumn and winter than during spring and summer. Average total movement during the autumn was 56.7 km (SE = 13.7 km); only 13% of fish accumulated more than 50% of the movement during autumn. Average total movement during the winter was 42.5 km (SE = 1.8 km), and no fish accumulated more than 50% of the movement during winter.

Mean daily movement

Mean daily movement of tagged grass carp ranged from 0.004 to 2.49 km/day ($\overline{x}$ = 0.76 km; SE = 0.12 km). Only twenty-five percent of tagged grass carp had mean daily movements greater than 0.88 km/day. Four of six fish with the longest mean daily movements also were those that had the largest maximum dispersals. However, the other two fish with the largest mean daily movements had relatively low maximum dispersals (15 km and 21 km). These two fish spent long periods of time in the Sandusky River and moved extensively throughout the river but ultimately never left the river. The average (averaged across fish) of mean daily movements was highest during summer ($\overline{x}$ = 1.08 km; SE = 0.61 km) and spring ($\overline{x}$ = 0.61 km; SE = 0.15). During autumn, the average of mean daily movements was 0.54 km (SE = 0.11 km). The lowest average of mean daily movements was observed during winter (0.22 km; SE = 0.06 km).

Tributary Use

Over the course of the study, 10 of 13 Lake Erie WB tributaries monitored were used by tagged grass carp: Crane Creek, Detroit River, Huron River, Maumee River, Ottawa River, Portage River, Plum Creek, Sandusky River, River Raisin, and Toussaint River. Of these tributaries, the Sandusky River was used most. Tributary use varied between years. In 2016, seven tributaries were used by 10 of 11 grass carp with three fish ultimately being detected in more than one tributary. In 2017, nine tributaries were used by 21 of 23 grass carp with eight fish ultimately being detected in more than one tributary. The number of tributaries used by individual grass carp during 2016 and 2017 ranged from one to six tributaries.

The Sandusky River, the second largest watershed included in this study (Table 1), was used by the largest number of grass carp overall with fish remaining in the river for multiple seasons and using the full available river reach. A total of 18 fish (78% of 23 fish) were detected in the Sandusky River at least once during the study (Figure 3), which was not surprising given that 11 of the 23 tagged fish were originally tagged and released in the river. In 2016, three fish were detected in the river for a range of one to 366 days ($\bar{x} = 158.3$ days; SE = 39.1 days). Typically, fish that were detected in 2016 resided in the lower 8 km of the river although a single fish moved further upstream to Freemont, OH, about 24 km upstream from Muddy Creek Bay during late May and early June. The area between Ballville Dam and Fremont, Ohio was identified by Embke et al. (2019) as one of the most probable spawning locations for grass carp in the Sandusky River. In 2017, 17 fish (74% of 23 fish) were detected in the river for a range of 1 to 300 days ($\bar{x} = 175.5$ days; SE =19.8 days). Grass carp were detected in the Sandusky River throughout 2017, though the highest number of fish (13 fish) were detected in the river during May, close to the spawning season for grass carp. The fewest number of fish (7 fish) were detected during August. In early March, 11 of 17 grass carp (65%) detected in the Sandusky

River in 2017 were captured, tagged, and released in Sandusky River so neither their original time of entry into the river could be determined nor if the fish simply resided in the river. Fish detected entering the river in 2017 did so in spring and autumn. The largest number of grass carp (13 fish) moved upstream to the Fremont, OH area during May and July. Movement to the Fremont, OH area occurred during each season, though fewer fish ($\leq$ 3 fish) exhibited this movement pattern outside the months of May and July. Fish were generally detected in the lower eight km of the Sandusky River. Eight (47%) of the 17 grass carp did not exit the river in 2017; rather they resided throughout the winter. Fish exiting the Sandusky River without returning in 2017 did so from mid-May through mid-October with most (75%; 6 of 8 fish) doing so mid-May through early July. Between March and November 2017, five grass carp moved from the Sandusky River into Sandusky Bay, but subsequently returned to the Sandusky River in 2017. Seasonal movement distance, the cumulative distance moved in the Sandusky River through the duration of a season, was similar in the spring ($\bar{x}$ = 61.1 km; SE = 12.2 km), autumn ($\bar{x}$ = 60.9 km; SE = 13.6 km) and summer ($\bar{x}$ = 58.6 km; SE = 6.4 km), but lowest during the winter season ($\bar{x}$ = 7.4 km; SE = 1.2 km).

Plum Creek was used by a total of eight grass carp (35% of 23 fish) during the study (Figure 4), of which four fish were captured and released in the tributary. Fish typically entered the tributary in September or October and overwintered until spring the following year. A single fish was detected in Plum Creek in 2015 spending 115 days after entering the tributary in September and remaining there through winter and exiting in early May 2016. In 2016, 7 fish were detected in the tributary for a range of 85 to133 days ($\bar{x} = 110.1$ days; SE = 3.6 days). One fish was captured, tagged, and released in Plum Creek during February so it is uncertain when this fish entered the tributary but it exited mid-June. The other five fish entered Plum Creek in early September through early October and then remained in the tributary through the winter. All five fish exited Plum Creek during spring 2017: three fish in April and two fish in early June. During summer 2016 and 2017, fish occasionally entered Plum Creek but generally exited the same day or within three days. Seven fish (30% of 23 fish) used Plum Creek in 2017 with use ranging from three to 261 days ($\bar{x} = 120.7$ days; SE =16.5 days) with two fish continuing the pattern of entering in September and October to overwinter. Grass carp remained in the lower three kilometers of Plum Creek with 99.9% of the detections occurring in the lower one kilometer of the tributary.

The Maumee River is the largest watershed monitored in this study (Table 1) and though identified as suitable for spawning (Kocovsky et al. 2012), only four grass carp (17% of 23 fish) used the river during spring and summer. Three grass carp used the Maumee River at varying times between April and August, with number of days spent in the river ranging from 1 to 72 days ($\bar{x} = 32.7$ days; SE =10.9 days) annually. All fish were largely found in the lowest 21 km of the river, although one fish moved approximately 51 km upstream from the mouth of the Maumee River to an area just below the Grand Rapid Dam.

The Detroit River, the main tributary to the WB and the upstream connecting waterway to the upper Great Lakes, was used by four grass carp (17% of 23 fish), during summer and fall of 2016 and 2017. Fish entered the river during summer (June – August) but the amount of time spent in river varied, ranging annually from two to 120 days ($\bar{x} = 49.0$ days; SE =26.1 days). Fish generally stayed in the lowest 22 km section of the Detroit River, although one grass carp moved all the way through the Detroit River and into Lake St. Clair.

The other monitored tributaries to the WB were used by relatively few fish and duration of use was limited. Crane Creek, Huron River, Ottawa River, Portage River, River Raisin, and

Toussaint River were used by 1 to 4 fish typically spending 1 or 2 days in the tributary through 2016 and 2017. Halfway Creek, Otter Creek, and Swan Creek had no detections of tagged grass carp during the study.

Inter-Basin Movement within Lake Erie

Although most tagged grass carp were only detected in Lake Erie's WB or its tributaries, four grass carp (17% of 23 fish) were detected moving into other Lake Erie basins. The four fish moved into Lake Erie's central basin and one continued through to the eastern basin. Fish that moved to the central basin appeared to so during the summer given they were first detected in the central basin in June, August, or September. Two fish moved into the central basin as far as Cleveland, OH (approximately 83 km east of Sandusky, OH), midway along the southern shoreline. The third fish moved just into the western edge of the central basin (approximately 16.5 km southeast of Point Pelee). The single fish that moved into the eastern basin was detected at the east end of the central basin (approximately 192 km east of Sandusky, OH) in summer and then was detected in the east basin (approximately 240 km east of Sandusky, OH) in early fall. All four fish returned to the WB following the inter-basin movements. Detailed descriptions of fish movements into the central or eastern basins and their returns to the WB can be found in Appendix B.

Emigration from Lake Erie

A single grass carp (4% of 23 fish) emigrated from Lake Erie during this study (Figure 7). That individual was tagged in September 2016 in Plum Creek and detected later at the Ottawa River, Toussaint Reef, Toussaint River, Portage River, and Crane Creek in early June 2017, before returning to Plum Creek. It remained in Plum Creek for approximately two weeks before it moved to the lower end of the Detroit River. Over the course of 5 days the fish was detected on numerous receivers that indicated upstream movement through the Detroit River, Lake St. Clair, and St. Clair River. The final detection of this individual was on 3 July 2017 approximately 60 km northwest of the St. Clair River, near Grand Bend, ONT in Lake Huron, and no evidence the fish returned to Lake Erie. No grass carp were detected downstream of Lake Erie in the Niagara River, Welland Canal, or Lake Ontario.

Discussion

This study represents the first documentation of grass carp habitat use and movement of grass carp in the Great Lakes. Tagged grass carp tended to remain in the WB of Lake Erie and, though multiple tributaries were used, the Sandusky River received the most use by telemetered fish. While many of the tagged grass carp in this study were originally tagged in the Sandusky River, we also found that 7 fish (30% of 23 fish) tagged elsewhere in Lake Erie occasionally moved into the Sandusky River. Use of the Sandusky River generally peaked during the spring and early summer presumably in preparation and during grass carp spawning events, which are believed to be triggered by increased discharges (Shireman and Smith, 1983; Cudmore and Mandrak, 2004; Kocovsky et al., 2012). Prior to and following migrating upstream to Fremont, OH, presumably for spawning, when grass carp were in the Sandusky River, they spent most of their time in the lower eight km of the Sandusky River upstream from Sandusky Bay.

Grass carp were expected to move into tributaries during the spring spawning season and then return to Lake Erie to feed. However, our observation that tagged grass carp resided in the Sandusky River for long periods throughout the year was unexpected. Descriptions of grass carp biology have indicated that after spawning, fish tended to leave rivers and enter floodplains, lakes, and backwaters to feed, before returning to rivers to overwinter in deep holes in lower parts of rivers during which time fish do not feed (Shireman and Smith, 1983). Research in a 27, 479 ha Tennessee reservoir (Bain et al., 1990) and 2,025 ha Florida impoundment (Nixon and Miller, 1978) indicated that movement of grass carp declines during colder months. Generally, our results supported this notion, with total movement and average daily movement being lower in winter than during other seasons; however, movement still occurred and fish were not sedentary during the winter season. Although grass carp spent most of their time during the winter in the lower eight km of the Sandusky River upstream from Sandusky Bay, some tagged grass carp moved upstream to suspected spawning areas.

Part of our motivation for monitoring use of tributaries to Lake Erie's WB was to help identify systems in which grass carp might spawn; prior to the findings of Embke et al. (2016), there had been no empirical evidence of grass carp spawning in the Laurentian Great Lakes. Of the tributaries used by grass carp, the most likely systems where grass carp may have spawned based on detections during the spawning season were the Sandusky, Maumee, and Detroit rivers. Of these three systems, spawning in the Sandusky and Maumee Rivers has already been confirmed (Embke et al., 2016; P. Kocovsky, U.S. Geological Survey, unpublished data) and our data show movement and use of the projected spawning area in the Sandusky River at the time of egg collection, suggesting the movement and use could have been for spawning activities. The Detroit River was not identified by Kocovsky et al. (2012) as being suitable for grass carp spawning and it has been hypothesized that the length of the river is not of sufficient length given its discharge for eggs to hatch prior to being deposited in Lake Erie (Cudmore et al., 2017. Whether deposition prior to hatching indeed prevents egg survival has yet to be confirmed

(Cudmore et al., 2017); consequently, it is not known with certainty whether successful grass carp recruitment could occur in the Detroit River. Although Plum Creek was a heavily used tributary, grass carp generally only used this stream between fall and late winter, not coinciding with suitable grass carp spawning conditions. As well, Plum Creek is unlikely to be of sufficient length for grass carp spawning, which typically require > 50 km of river for successful reproduction (Cudmore et al. 2017). Plum Creek is somewhat unique among WB tributaries because it receives warmwater discharge from a coal-fired power plant. As a result, we speculate that grass carp used this tributary as a thermal refuge during the coldwater months.

Other studies of grass carp movement in reservoirs and rivers have yielded wide ranging movement patterns and while the movements we observed were not as large as seen in river systems, our observations were typically greater than that reported from reservoirs. Stocked grass carp spread more than 1,700 km up the Mississippi River from initial stocking sites (Guillory and Gasaway, 1978). Similarly, in the Amur River, forming the border between Russia and China and within the native range of grass carp, movements in excess of 500 km have been noted (Gorbach and Krykhtin, 1988). Within large reservoirs in the U.S., studies evaluating grass carp movement using radio or acoustic telemetry have generally shown maximum movements of 100 km. Clapp et al. (1993) observed a maximum movement distance of triploid grass carp from their stocking site of 17.1 km and a median distance of 10.4 km. Median home range size was approximately 5,300 ha (Clapp et al., 1993). Bain et al. (1990) observed grass carp dispersing up to 71 km from release locations with one fish moving 53 km in 9 days. Maceina et al. (1999) found grass carp dispersing upwards of 99 km. Additionally, Bain et al. (1990) observed a large difference in annual movements of tagged grass in their study. In the initial year of the Bain et al. (1990) study, grass carp movement averaged only around 2 km; the following year, grass carp movement averaged nearly 33 km. Bain et al. (1990) theorized that the temporal difference in movement was as a result of tagged grass carp reaching sexual maturity during the second year of the study. Chilton and Poarch (1997) found stocked grass carp to move extensively (5 to 10 km) immediately after stocking; however, after acclimation fish showed little movement. With respect to daily movements, Maceina et al. (1999) reported grass carp swimming a minimum of 0.52 km/day, whereas Bain et al. (1990) reported a maximum daily movement rate of 6 km/day, which illustrates the wide range of movement behaviors that have been reported previously.

Small sample sizes in the present study makes it difficult to identify variables that potentially influence movement behavior of individual grass carp and to evaluate potential differences between diploid and triploid grass carp. Movement behavior of grass carp is believed to be related to spawning, feeding, and selection of overwintering habitats (Cudmore and Mandrak, 2004). Many of the upstream movements we observed in Lake Erie tributaries occurred during late spring and early summer and were likely related to spawning behavior. However, some of the largest movements involving tagged grass carp moving into the central and eastern Basins of Lake Erie and Lake Huron were likely not related to spawning given they occurred from June to October in the open water, possibly in search of foraging opportunities.

A shortcoming of this study was not being able to conclusively determine the fates of tagged fish. We were able to make use of detection information from slightly less than 50% of the tagged grass carp given our criteria for analyzing detection results. The fates of those other fish are not known, as is the fates of fish for which we collected sufficient detection data to include in analyses but that then went missing. One instance of tag shedding was observed after a fish was at liberty for more than 150 days, and we cannot rule the possibility that other instances of tag shedding occurred. Alternatively, there was one instance a tagged grass carp was recaptured more than a year following implantation with the transmitter and external tag remaining in place. Separating tag shedding from mortality events is difficult to do; consequently, composite estimates of these events are frequently reported (Stich et al., 2015). Grass carp mortality or transmitter shedding rates as high as 65% were observed in confined areas but improvements up to 15% were observed when implanting larger fish and using improved surgical procedures (Maceina et al., 1999). Likewise, Clapp et al. (1993) reported transmitter shedding or mortality rates of 47%. We suspect that many of the fish that provided few or no detections and were not included in analyses ultimately died shortly after transmitter implantation. The capture and storage of fish were likely stressful events based on observed external conditions of fish when transmitter implantation occurred. For instance, fish frequently had epidermal abrasions and broken fins ostensibly due to either initial capture or subsequent storage.

There are various other explanations regarding the potential fates of tagged fish with few or no detections. Tagged grass carp may have been harvested either by commercial fishers or recreational anglers and not reported. Electronic tags such as those used here may also fail prematurely (e.g., Holbrook et al. 2016). Fish may also be alive with functional transmitters and be located somewhere outside the detection range of a receiver. In moving receivers in Lake Erie from a gated to a gridded array in 2016, it was expected based on the simulation study of Kraus et al. (2018) to improve spatial and temporal information about a tagged individual's fate across a range of conditions (e.g., detection probability, tag power; Kraus et al., 2018). However, the simulations conducted by Kraus et al. (2018) made explicit assumptions about speed and turning angles of movement tracks, and was based on pilot telemetry studies involving walleye (*Sander vitreus*), common carp (*Cyprinus carpio*), and channel catfish (*Ictalurus punctatus*). Grass carp movement behavior may be quite different than the conditions simulated by Kraus et al. (2018) such that expected detections may be less frequent than what was suggested based on the results of that study.

The primary motivation to study grass carp spatio-temporal movement behavior in Lake Erie and to identify areas of high use was to inform control efforts for grass carp. Tagged fish heavily utilized the Sandusky River and Plum Creek, and future actions within these systems may improve the effectiveness of removal efforts. Lake Erie fishery management agencies have begun coordinated control efforts in Lake Erie's WB to reduce grass carp densities. Success of initial control efforts was low due to the difficulty of locating and capturing grass carp. Capture rates increased in 2018, however, as a result of using real-time receiver detections to inform the location of response efforts (ODNR unpublished data). These efforts were isolated and should be more thoroughly evaluated. Using tagged conspecifics to improve control efforts for invasive species has been referred to as the "Judas fish" technique. This technique has been used with reproductively viable individuals to inform control efforts for species including common carp, (Bajer et al., 2011; Taylor et al., 2012), northern snakehead (*Channa argus*; Lapointe et al., 2010), silver carp (*Hypophthalmichthys molitrix*; Coulter et al., 2016), and lake trout (*Salvelinus namaycush*; Dux et al., 2011). Use of the Sandusky River was twice as high as the next most used tributary, with grass carp spending much of their time in the lower Sandusky River. Thus, targeting control efforts in the lower section of the Sandusky River and then moving control efforts upstream when discharge increases during the spawning season may be an effective approach for catching grass carp. Although Plum Creek was not as heavily used as the Sandusky River, we did observe tagged grass carp making repeat visits to this area and this stream could serve as a focal point for control efforts as well. Our results for Sandusky River and Plum Creek may have been biased somewhat as a result of some of our tagged fish originally being caught in each tributary, 11 fish and 4 fish respectively. However, we did observe fish tagged and released elsewhere in Lake Erie and then moving into Sandusky River (7 tagged grass carp) or Plum Creek (4 tagged grass carp) on occasion suggesting some characteristic occurs there that attracts fish to the specific tributaries. Other tributaries that are candidates for control efforts are the Maumee and Detroit Rivers. Both rivers were used by 4 tagged grass carp, although fish generally spent more time in the Detroit River than the Maumee River.

This study provides critical insight into areas where grass carp control efforts could be directed and seasonal timing to deploy those efforts. The insights into grass carp movement provide empirical information for Lake Erie that can be used to inform the risk of spread and areas to strategically allocate control efforts. The sample of tagged fish in this study was 91% diploid, suggesting that recommended actions be directed towards the highest risk individuals with the ability to reproduce. Further investigation into grass carp movements in the Sandusky and Maumee rivers could identify proximal cues for upstream movements that may be related to spawning activities and further improve control efforts. More fine-scale position information in Lake Erie as well could provide information on habitat use and help pinpoint control efforts. With the transmitter life extending longer than this study, the tagged fish could be used to investigate catchability in an open system which would inform the level of removal effort needed to achieve population reduction or suppression. The high level of grass carp detection in the Sandusky River and coverage with receivers could be used to model movement in the river and provide more detailed information for control efforts.

Acknowledgments

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Table 1. Western Lake Erie tributaries meeting at least one of two selection criteria; 1) tributaries from which grass carp had previously been collected based on review of records from the U.S. Geological Survey Nonindigenous Aquatic Species database (USGS, 2018), and 2) tributaries with a watershed size greater than 100 km^2 based on the Great Lakes Hydrography Dataset (Forsyth et al., 2016). Length available is the estimated tributary length to either the first barrier or was estimated to the first barrier or to where the stream width was less than 5-7 m, like a criterion used by Kocovsky et al. (2012).

Tributary	State/Province Jurisdiction	Watershed size (km^2)	Length available (km)
Crane Creek	Ohio	133	18.7
Detroit River	Michigan/Ontario	1,813	44.0
Halfway Creek	Michigan	116	4.2
Huron River	Michigan	2305	43.9
Maumee River	Ohio	16,972	54.1
Ottawa River	Michigan/Ohio	446	26.2
Otter Creek	Michigan	175	5.5
Plum Creek	Michigan	89	5.4
Portage River	Ohio	1,365	102.0
River Raisin	Michigan	2,736	37.0
Sandusky River	Ohio	3,462	26.2
Swan Creek	Michigan	255	7.1
Toussaint River	Ohio	524	32.8

Figure Captions

Figure 1. Watersheds of the western Lake Erie tributaries meeting at least one of two selection criteria; 1) tributaries from which grass carp had previously been collected based on review of records from the U.S. Geological Survey Nonindigenous Aquatic Species database (USGS, 2018), and 2) tributaries with a watershed size greater than 100 km^2 based on the Great Lakes Hydrography Dataset (Forsyth et al., 2016).

Figure 2. Placement of acoustic telemetry receivers in Lake Huron, Lake Erie, Lake St. Clair, Detroit River, and St. Clair River from 2015 to 2017. Different color combinations indicate seasons that individual receivers were deployed.

Figure 3. Locations of acoustic telemetry receivers in the Sandusky River and the total number of tagged grass carp detected on each receiver, from January 1, 2015 through December 31, 2017.

Figure 4. Locations of acoustic telemetry receivers in Plum Creek and the total number of tagged grass carp detected on each receiver, from January 1, 2015 through December 31, 2017.

Figure 5. Locations of acoustic telemetry receivers in the Maumee River and the total number of tagged grass carp detected on each receiver, from January 1, 2015 through December 31, 2017.

Figure 6. Locations of acoustic telemetry receivers in the Detroit River and the total number of tagged grass carp detected on a group of receivers as identified by the red circles, from January 1, 2015 through December 31, 2017.

Figure 7. Receiver detections (circles) through the end of 2017 and movement directions (lines with arrows) of a tagged diploid grass carp, measuring 77 cm total length and weighing 6.3 kg, which emigrated from Lake Erie to Lake Huron. The asterisk indicates the approximate location where the fish was released after transmitter implantation.

Figure 1

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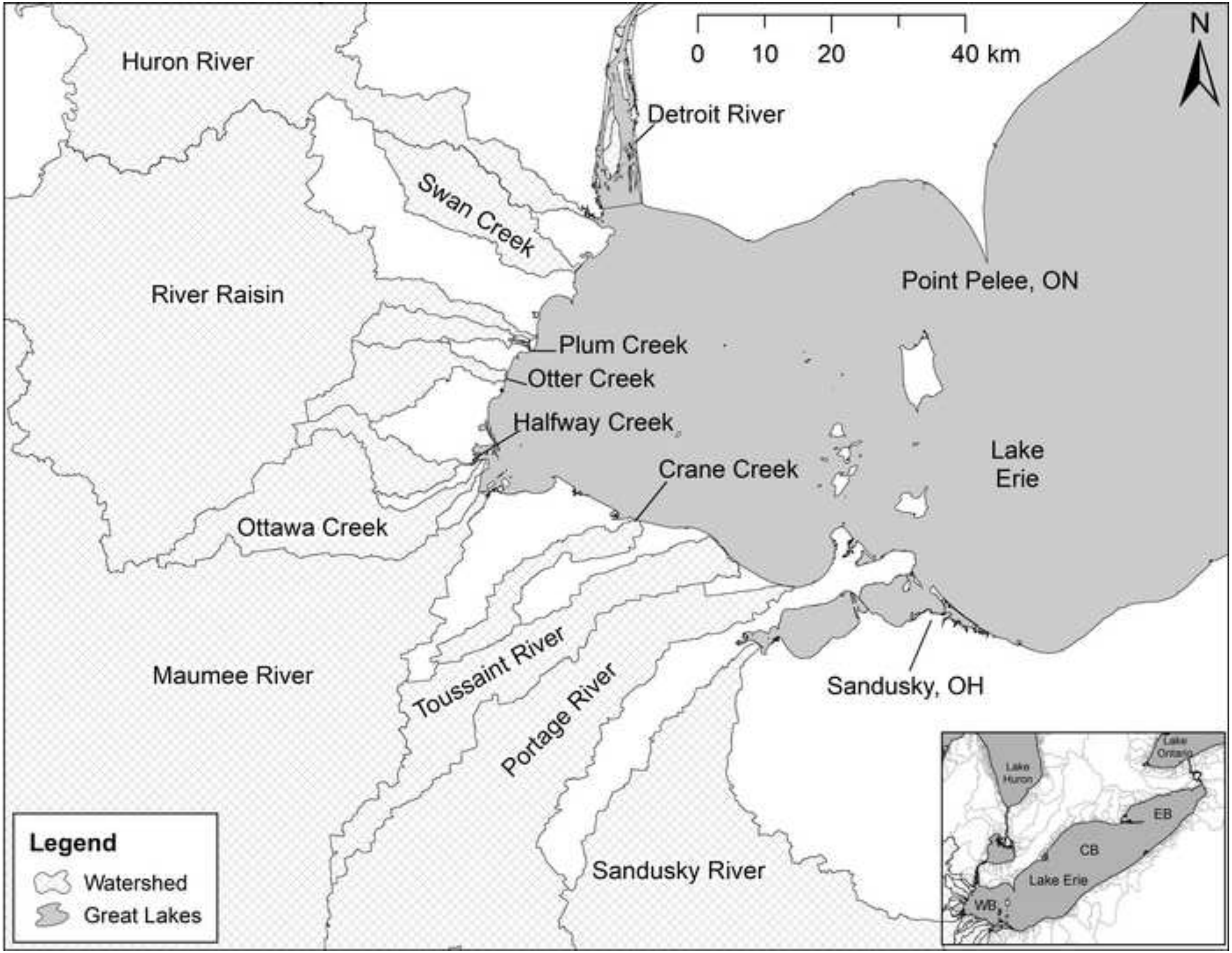
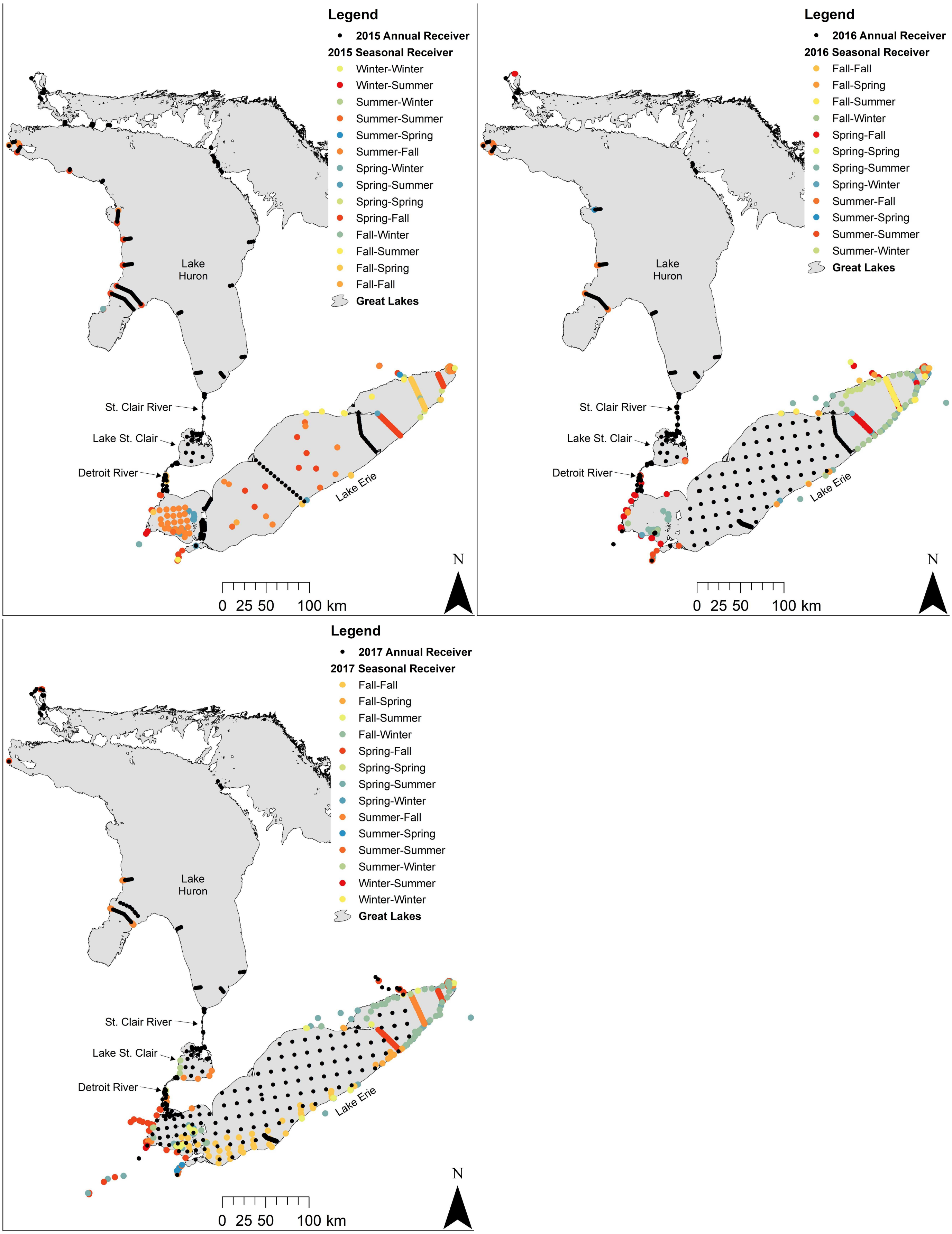


Figure 2


Legend
2015 Annual Receiver
2015 Seasonal Receiver
Winter-Winter
Winter-Summer
Summer-Winter
Summer-Summer
Summer-Spring
Summer-Fall
Spring-Winter
Spring-Summer
Spring-Spring
Spring-Fall
Fall-Winter
Fall-Summer
Fall-Spring
Fall-Fall
Great Lakes
Lake Huron
St. Clair River
Lake St. Clair
Detroit River
Lake Erie
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Legend
2016 Annual Receiver
2016 Seasonal Receiver
Fall-Fall
Fall-Spring
Fall-Summer
Fall-Winter
Spring-Fall
Spring-Spring
Spring-Summer
Spring-Winter
Summer-Fall
Summer-Spring
Summer-Summer
Summer-Winter
Great Lakes
Lake Huron
St. Clair River
Lake St. Clair
Detroit River
Lake Erie
0 25 50 100 km
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Legend
2017 Annual Receiver
2017 Seasonal Receiver
Fall-Fall
Fall-Spring
Fall-Summer
Fall-Winter
Spring-Fall
Spring-Spring
Spring-Summer
Spring-Winter
Summer-Fall
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Figure 3
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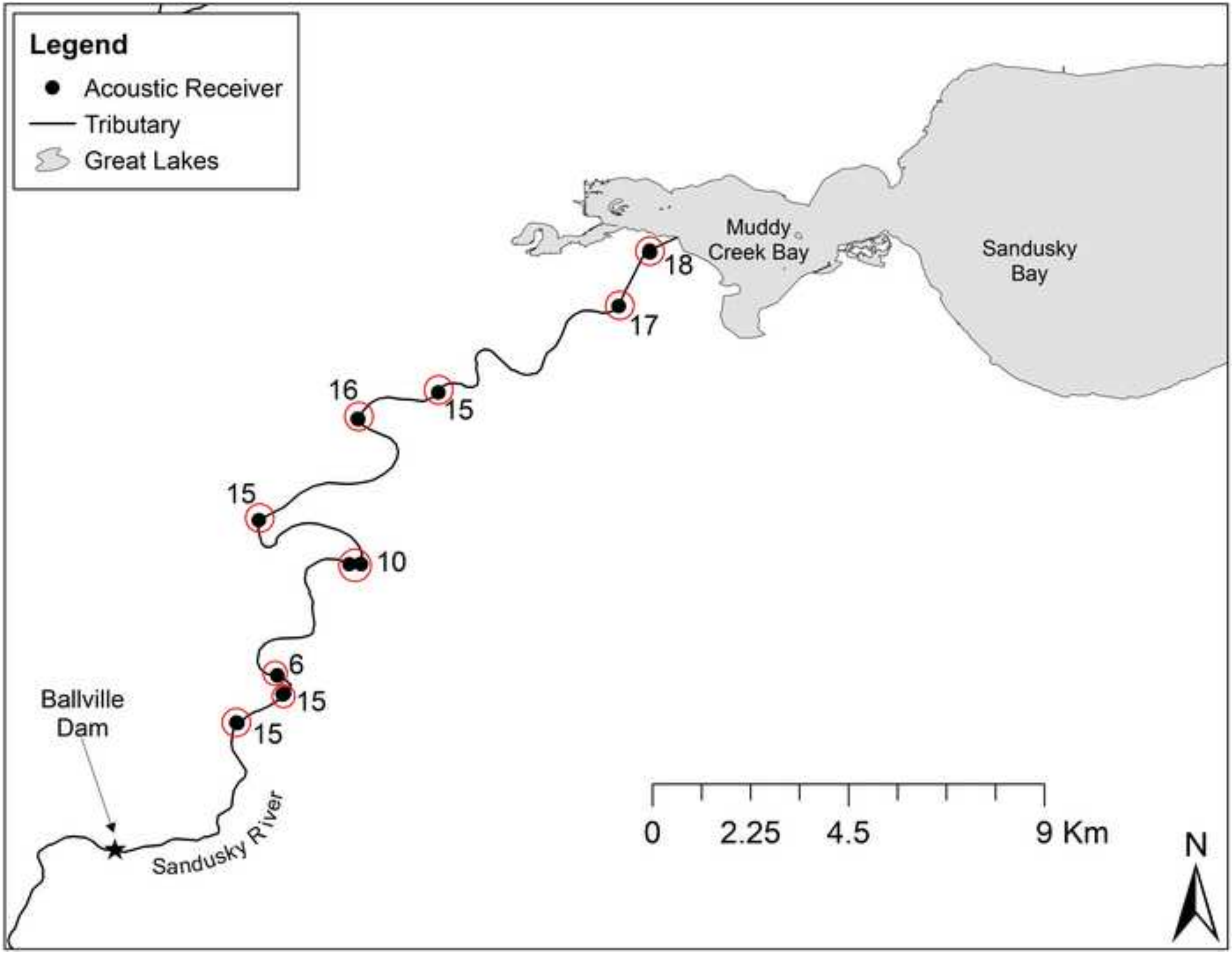

Figure 4
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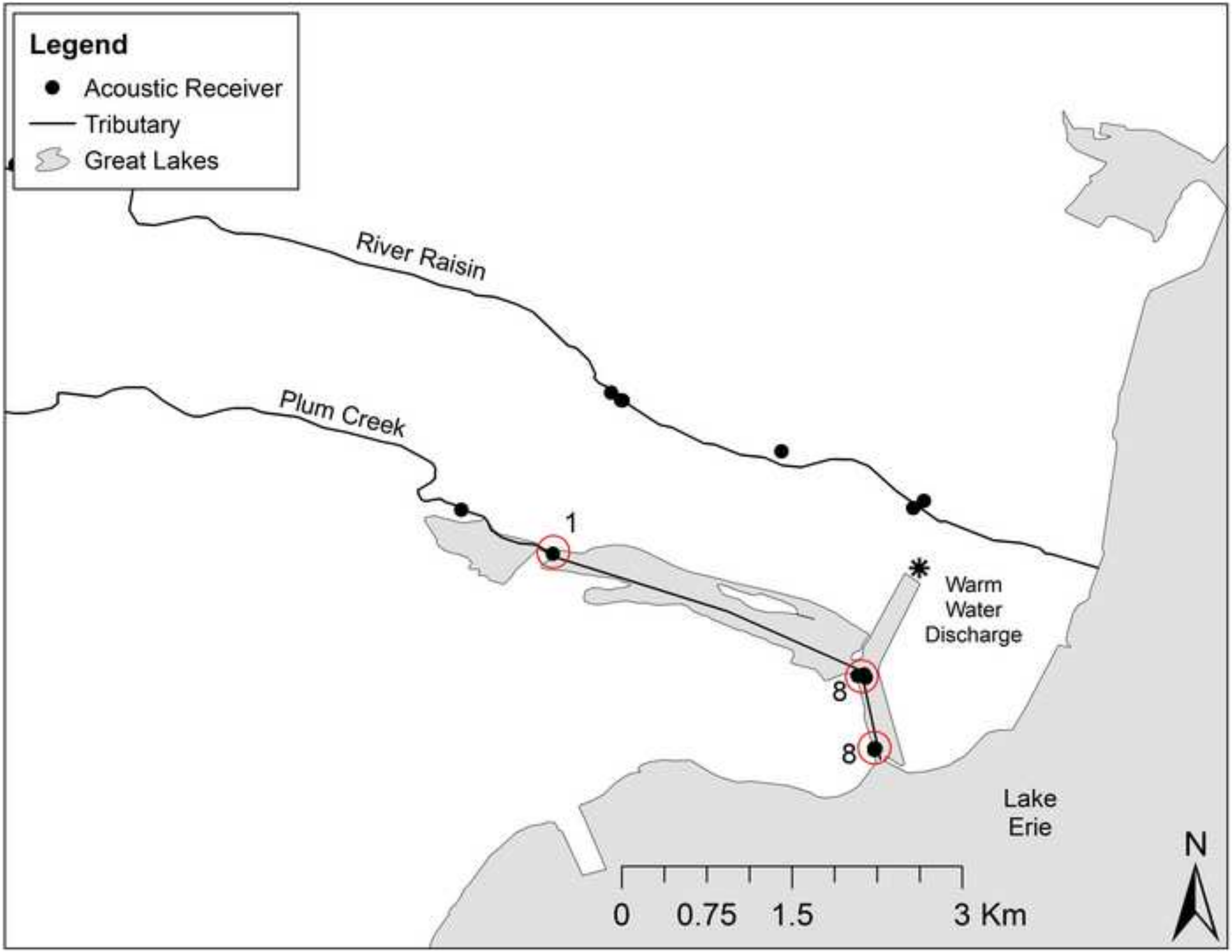

Figure 5
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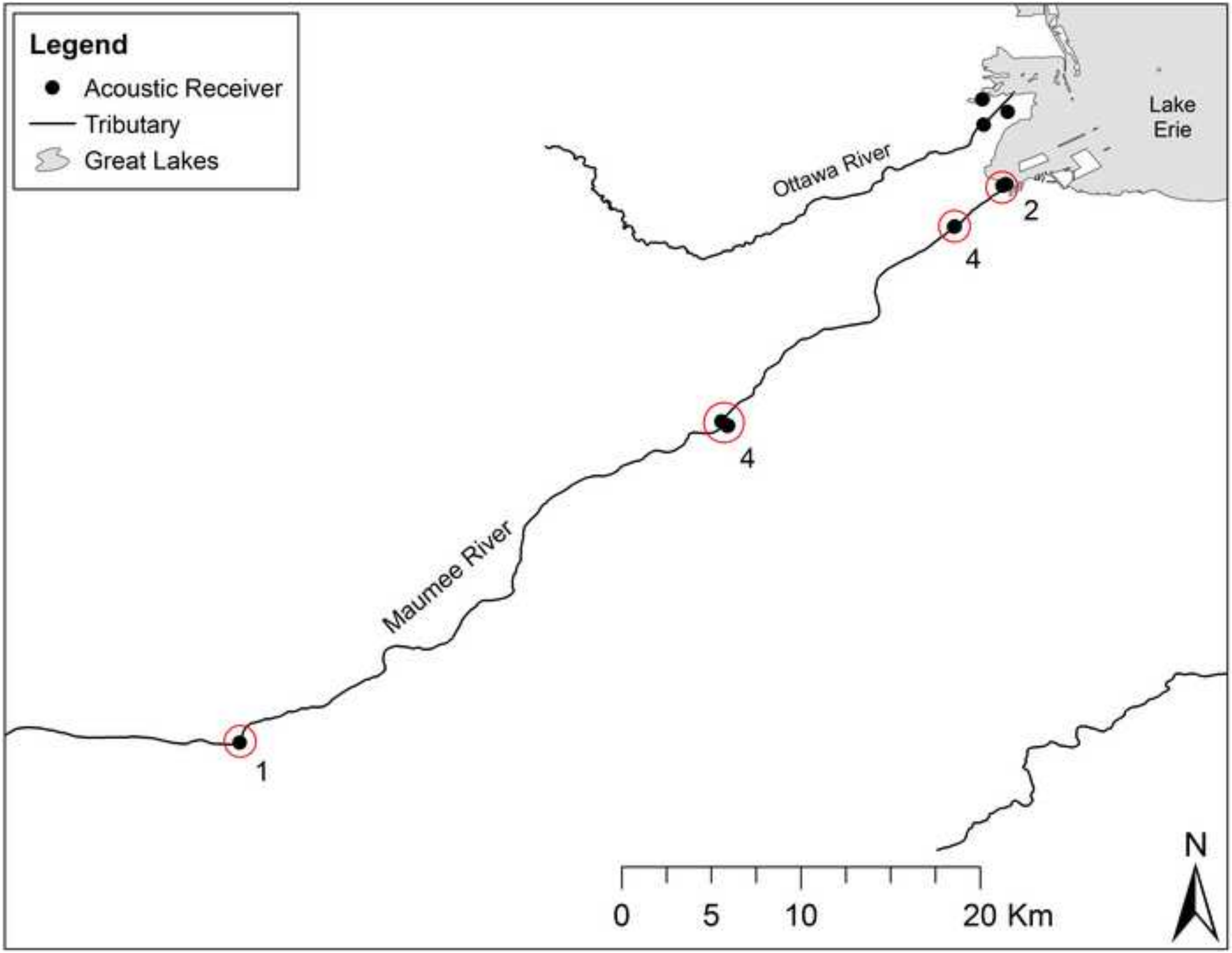

Figure 6
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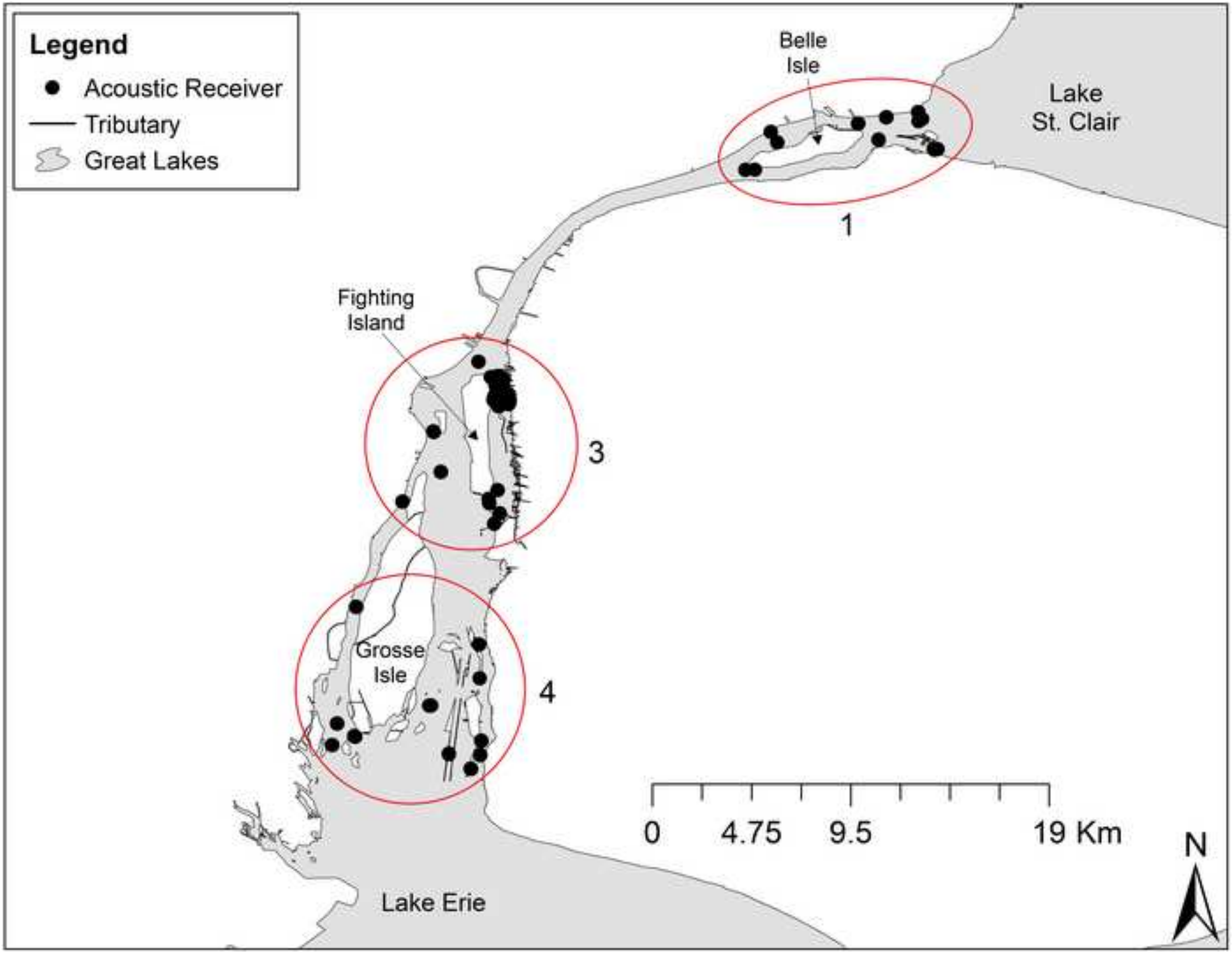
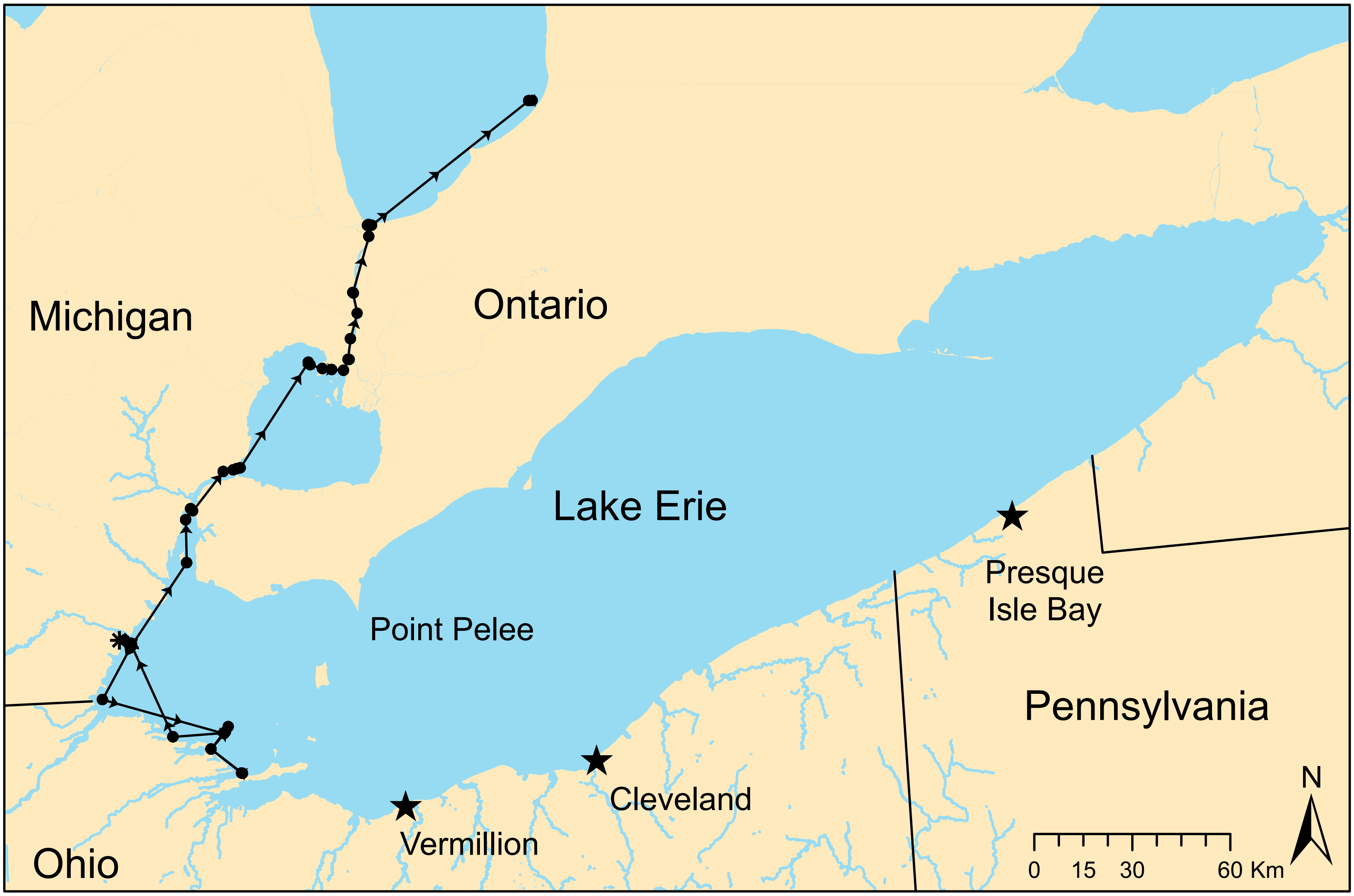


Figure 7



Michigan
Ontario
Lake Erie
Point Pelee
Presque
Isle Bay
Pennsylvania
Cleveland
Vermillion
Ohio
N
0
15
30
60 Km