GRASS CARP MOVEMENT AND SPACE USE IN LAKE ERIE: IMPLICATIONS FOR MANAGEMENT EFFORTS

By

Cleyo Harris

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ABSTRACT

GRASS CARP MOVEMENT AND SPACE USE IN LAKE ERIE: IMPLICATIONS FOR MANAGEMENT EFFORTS

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Grass Carp (*Ctenopharyngodon idella*) is an invasive species to the Laurentian Great Lakes that was first detected in the 1980s. The current invasion front for the Great Lakes is believed to be the western basin (WB) of Lake Erie, with spawning occurring in at least two WB tributaries. Targeted control is being used to reduce population densities in Lake Erie and lessen the risk of spread to other lakes. The effectiveness of this control strategy is hindered by two significant information gaps: the extent of intra- and inter-lake movements of Grass Carp and knowledge as to where in Lake Erie fish might aggregate. I used acoustic telemetry technology to quantify broad-scale movements of Grass Carp in Lake Erie, including movement to other Lake Erie basins and other Great Lakes. I additionally quantified movement and identified aggregation areas in the Sandusky River, which is a prime area for control due to it being the tributary with the most consistent annual spawning. Grass Carp dispersed up to 236 km from release locations, with approximately 25% of fish dispersing more than 100 km. Mean daily movement was as high as 2.49 km/day, with the highest movement occurring in the spring and summer. The Sandusky, Detroit, and Maumee rivers and Plum Creek were the most heavily used WB tributaries. In the Sandusky River, Grass Carp aggregated between river kilometers (RKMs) 34 and 36, and at RKM 45. During spawning conditions, fish also aggregated near RKM 48.6, close to the suspected spawning location for Grass Carp in the river. Based on my results, I believe past assessments have underestimated the risk of inter-basin and inter-lake spread of Grass Carp. I recommend focusing Grass Carp control efforts on Sandusky River and Plum Creek, and secondarily on Maumee and Detroit Rivers. Control efforts in the Sandusky River should be targeted for 20 RKMs below the former location of Ballville Dam; control policies should consider the use of passive capture gear during spring and summer months when movement in the Sandusky River is the greatest.

ACKNOWLEDGEMENTS

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PREFACE

The chapters in this thesis were drafted as standalone papers to be submitted for publication in peer-reviewed journals. For this reason, both chapters are written in the first person plural narrative, even though the thesis has one author. Chapter 1 was submitted and accepted for publication in *Journal of Great Lakes Research*. Chapter 2 has been formatted for eventual submission to *North American Journal of Fisheries Management*. All references in the thesis have been formatted in a style consistent with *North American Journal of Fisheries Management*.

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INTRODUCTION

Grass Carp (*Ctenopharyngodon idella*) is an herbivorous xenocyprinid species (Tan and Armbruster 2018) native to eastern Asia (Lee et al. 1980; Shireman and Smith 1983) that was first introduced to the United States in the early 1960s for biocontrol of aquatic vegetation. Initial introductions were in Arkansas and Alabama for research purposes (Mitchell and Kelly 2006). In 1970, commercial fishers operating near one of the Arkansas research stations where Grass Carp were being studied caught free-ranging fish. Escapement had occurred, which was later confirmed through interviews of biologists working at the station (Mitchell and Kelly 2006). Stocking of Grass Carp in public and private waters for vegetation biocontrol first occurred in 1969 and was prevalent through the 1970s. Although initially these introductions were considered beneficial due to successful control of vegetation, concerns quickly arose regarding expansion to other systems (Bailey 1978; Chilton and Muoneke 1992; Mitchell and Kelley 2006; Dibble and Kovalenko 2009).

Concerns over expansion and establishment of Grass Carp populations led to the development of methodologies for producing monosex fish and eventually to producing triploid fish that functionally were sterile (Cassani and Caton 1985; Mitchell and Kelly 2006). Subsequently, many U.S. states began limiting Grass Carp stocking to triploid fish, although other states continued to permit the stocking of diploid Grass Carp (Mitchell and Kelly 2006; MICRA 2015). The U.S. Fish and Wildlife service (USFWS) operates an inspection service for natural resource agencies to test the ploidy status of Grass Carp shipments. The inspection process requires randomly testing 120 fish for ploidy status. If a single diploid individual is found in the sample, the shipment fails inspection and no stocking can occur (https://www.fws.gov/warmsprings/FishHealth/frgrscrp.html). The 120 fish sample size was established because with a 95% confidence interval the probability of not detecting a diploid in a shipment of 500 fish would be no greater than 2.1% (Papoulias et al. 2010). Thus, even with the USFWS certification program, there remains a small chance that certified triploid Grass Carp shipments can contain reproductively fertile fish.

Widespread stocking and subsequent escapement 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). A species is considered established when individuals that have been naturally produced in a system spawn and produce their own offspring that recruit to the population (Cudmore et al. 2017). In some systems, Grass Carp populations have been found to comprise a mixture of triploid and diploid individuals (Schulz et al. 2001), possibly suggesting multiple invasion sources.

In North America's Laurentian Great Lakes, 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. To date, Grass Carp have been captured in each of the Great Lakes except for Lake Superior (USGS 2018). Captures of Grass Carp in the Great Lakes were infrequent or unreported from the 1980s to 2000s (USGS 2018); however, in the 2010s, capture and/or reporting of Grass Carp, primarily by commercial fishers, began increasing in Lake Erie's western basin (WB) (Cudmore et al. 2017). The prevailing belief by fishery management biologists initially was that captured Grass Carp were triploid and consequently there was no risk of establishment (J. Tyson, Great Lakes Fishery Commission, *personal communication*). Concerns about possible establishment were elevated in 2012 when juvenile Grass Carp were caught in the Sandusky River, a tributary to Lake Erie's WB, 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 were collected from the Maumee River (P. Kočovský, U.S. Geological Survey, *personal communication*). To date, Grass Carp spawning has only been detected in the Sandusky and Maumee rivers, although Kočovský et al. (2012) identified seven Lake Erie tributaries that may be conducive to Grass Carp spawning.

The confirmation of Grass Carp spawning in Lake Erie tributaries prompted a ploidy evaluation of 60 Grass Carp caught mostly by commercial fishing operations from the WB of Lake Erie (Wieringa et al. 2017). Approximately 87% of tested fish were diploid (i.e., reproductively viable) (Wieringa et al. 2017). How or when diploid Grass Carp first entered Lake Erie is unknown, although possible pathways include escapement from inland waters and human-mediated releases, such as bait fish sales, intentional stocking prior to implementation of existing state and provincial prohibitions, illegal stocking after the activity was banned, or unintentional stocking (e.g., diploid contamination in a triploid batch of Grass Carp) (Cudmore et al. 2017).

The combination of elevated catch reports, confirmation of Grass Carp spawning in at least two WB tributaries, and the prevalence of spawning-capable individuals raised concerns about possible negative effects in Lake Erie as populations increased. The greatest concerns about elevated Grass Carp densities center on their potential to reduce aquatic vegetation densities and/or modify aquatic vegetation composition (Bain 1993; Cudmore et al. 2017). Through bioenergetics modeling, van der Lee (2017) estimated that under average temperature conditions Grass Carp 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; they found that within one year, Grass Carp could reduce vegetation densities by more than 50%. Further, 33 fish and 18 bird species were identified that were expected to experience high negative effects from Grass Carp establishment in the Great Lakes (Gertzen et al. 2017).

Concerns about population expansion and negative effects on aquatic and terrestrial communities stemming from elevated Grass Carp densities led state, provincial, and federal fishery agencies in the Lake Erie basin to develop a coordinated strategy to control Grass Carp. Robinson et al. (in press) conducted a multi-party, collaborative decision analysis to determine objectives and control actions for Grass Carp in Lake Erie. The decision analysis project led to the establishment of a goal of annually removing 390 spawning-capable Grass Carp to reduce the risk of spread and negative effects on aquatic and terrestrial communities (DuFour et al. in review). Based on expert elicitation, the most effective control strategy for achieving this suppression goal was targeted removal efforts concentrated in areas of high catchability combined with techniques to disrupt spawning in the Sandusky River (Robinson et al. in press).

Although targeted removal was identified as a preferred control policy by Robinson et al. (in press), enactment of this policy is challenged by Grass Carp being notoriously difficult to capture with traditional fishing methods (Mitchell 1980; Maceina et al. 1999). In 2014, an exercise involving 10 state, provincial, and federal fishery agencies was conducted on Lake Erie to practice a coordinated response if one of the major Chinese carps [i.e., Silver Carp (*Hypophthalmichthys molitrix*), Bighead Carp (*Hypophthalmichthys nobilis*), or Black Carp (*Mylopharyngodon piceus*)] was detected in the lake. Although it was intended to be a practice response, the agencies targeted Grass Carp during the exercise as a secondary objective to reduce population abundance. Control efforts consisted of boat electrofishing (219 electrofishing runs = 96 hours of electrofishing time) and gillnetting (53 gillnet lifts = 58.8 hours of soak time); locations where control efforts were implemented were informed by positive eDNA detections of Grass Carp in Lake Erie over the previous few week (S.J. Herbst, Michigan DNR, *unpublished data*). Despite this large amount of effort, only two Grass Carp were captured during the exercise (S.J. Herbst, Michigan DNR, *unpublished data*).

For targeted sampling in Lake Erie to be a feasible method of control, knowledge as to areas where Grass Carp aggregate and how these aggregation areas change temporally is needed. Additionally, control policies for Grass Carp could be informed by knowledge as to what environmental conditions prompt high levels of fish movement because some capture methods are more efficient when fish are moving. In terms of assessing the risk of inter-basin or inter-lake spread of Grass Carp from the WB of Lake Erie, improved understanding of the extent of fish movement in the region would be beneficial. Based on previous research conducted primarily in southern U.S. reservoirs, inter-basin movements of Grass Carp in Lake Erie would be expected to be limited. Although Grass Carp sometimes have home ranges in excess of 1,000 ha, generally once areas with appropriate vegetation are encountered fish become quiescent, although behavior can vary annually (Bain et al. 1990; Clapp et al. 1993; Chilton and Poarch 1997). How transferrable results from southern U.S. reservoirs are to the Great Lakes is unclear given cooler water temperatures and uncertainty as to the availability of preferred food resources for Grass Carp in Lake Erie. Previous modeling suggested that once Grass Carp invaded a system, they could spread to other systems within 5 to 10 years (Currie et al. 2017). However, the modeling acknowledged that little is known about Grass Carp movement and as a result, risk of spread to other Great Lakes may be higher than what their results indicated.

The goals of this research was to 1) quantify broad-scale movements of Grass Carp in Lake Erie, including movement to other Lake Erie basins and other Great Lakes, and 2) quantify movements and identify areas of possible Grass Carp aggregation in the Sandusky River. The main purpose was to provide information that could improve efforts to control Grass Carp in Lake Erie and lessen the risk of population spread and expansion to the other Great Lakes.

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CHAPTER 1

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

Introduction

Grass Carp (*Ctenopharyngodon idella*) is a large herbivorous xenocyprinid species (Order: Cypriniformes; Family: Xenocyprinidae) (Tan and Armbruster 2018) 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). Grass Carp stocking 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 spread and establishment of Grass Carp populations into other systems (Bailey 1978; Chilton and Muoneke 1992; Mitchell and Kelley 2006; Dibble and Kovalenko 2009). This concern led to methods for producing monosex Grass Carp and eventually producing triploid Grass Carp that functionally were sterile (Cassani and Caton 1985; Mitchell and Kelly 2006). 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). A species is considered established when individuals that are naturally produced in a system spawn and produce their own offspring that recruit to the population (Cudmore et al. 2017). In some systems, Grass Carp populations were comprised 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 a concern to managers because fish may continue to spread into new waters, increase in abundance, and cause escalating deleterious effects.

In North America's Laurentian Great Lakes, 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, and since, have been captured in each of the Great Lakes except for Lake Superior (USGS 2018). Captures of Grass Carp in the Great Lakes were infrequent or unreported from the 1980s to 2000s (USGS 2018); however, in the 2010s, capture and/or reporting of Grass Carp, primarily by commercial fishers, began increasing in Lake Erie's western basin (WB) (Cudmore et al. 2017). The prevailing belief by resource agencies initially was that captured Grass Carp were triploid and therefore there was no risk of establishment (J. Tyson, Great Lakes Fishery Commission, *personal communication*). Concerns about possible establishment were elevated in 2012 when juvenile Grass Carp were caught in the Sandusky River, a tributary to Lake Erie's WB, 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. Kočovský, U.S. Geological Survey, *personal communication*). To date, Grass Carp spawning has only been detected in the Sandusky and Maumee rivers, although Kočovský et al. (2012) identified seven Lake Erie tributaries that may be conducive to Grass Carp spawning.

The confirmation of Grass Carp spawning in Lake Erie tributaries prompted a ploidy evaluation of 60 Grass Carp caught mostly by commercial fishing operations from the WB of Lake Erie (Wieringa et al. 2017). Approximately 87% of tested fish were diploid (i.e., reproductively viable) (Wieringa et al. 2017). How or when diploid Grass Carp first entered Lake Erie is unknown, although possible pathways include escapement from inland waters and human-mediated releases, such as bait fish sales, intentional stocking prior to existing state and provincial prohibitions being implemented, illegal stocking after the activity was banned, or unintentional stocking (e.g., diploid contamination in a triploid batch of Grass Carp) (Cudmore et al. 2017).

The combined findings of Embke et al. (2016) and Wieringa et al. (2017) elevated concerns that Grass Carp either had or soon could become established in Lake Erie, which could contribute to their spread and establishment elsewhere in the Great Lakes. The greatest concern about Grass Carp establishment centers around their potential to reduce aquatic vegetation densities and/or modify aquatic vegetation composition (Bain 1993; Cudmore et al. 2017). Through bioenergetics modeling, van der Lee (2017) estimated that 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%. Further, 33 fish and 18 bird species were identified that were expected to experience high negative effects from Grass Carp establishment in the Great Lakes (Gertzen et al. 2017).

A critical 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 behavior, including movement (Cudmore et al. 2017). The Lake Erie Committee, a binational committee comprised of state and provincial fishery agency representatives with management authority on Lake Erie, issued a position statement regarding Asian carp, which is a group term that includes Grass Carp (Chapman and Hoff 2011), recommending 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 are difficult to capture with standard assessment methods (Mitchell 1980; Maceina et al. 1999); therefore, information about Grass Carp space use, including areas where Grass Carp aggregate, would allow control efforts to be more spatially targeted and ostensibly improve capture efficiency.

The purpose of this study was to improve understanding of Grass Carp movement in Lake Erie and to identify areas of high use to inform 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. Study objectives 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 1.1; Ryan et al. 2003). The 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 west from the line extending from Point Pelee in Leamington, ONT to Sandusky, OH (Figure 1.1). 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 (including the WB) 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).

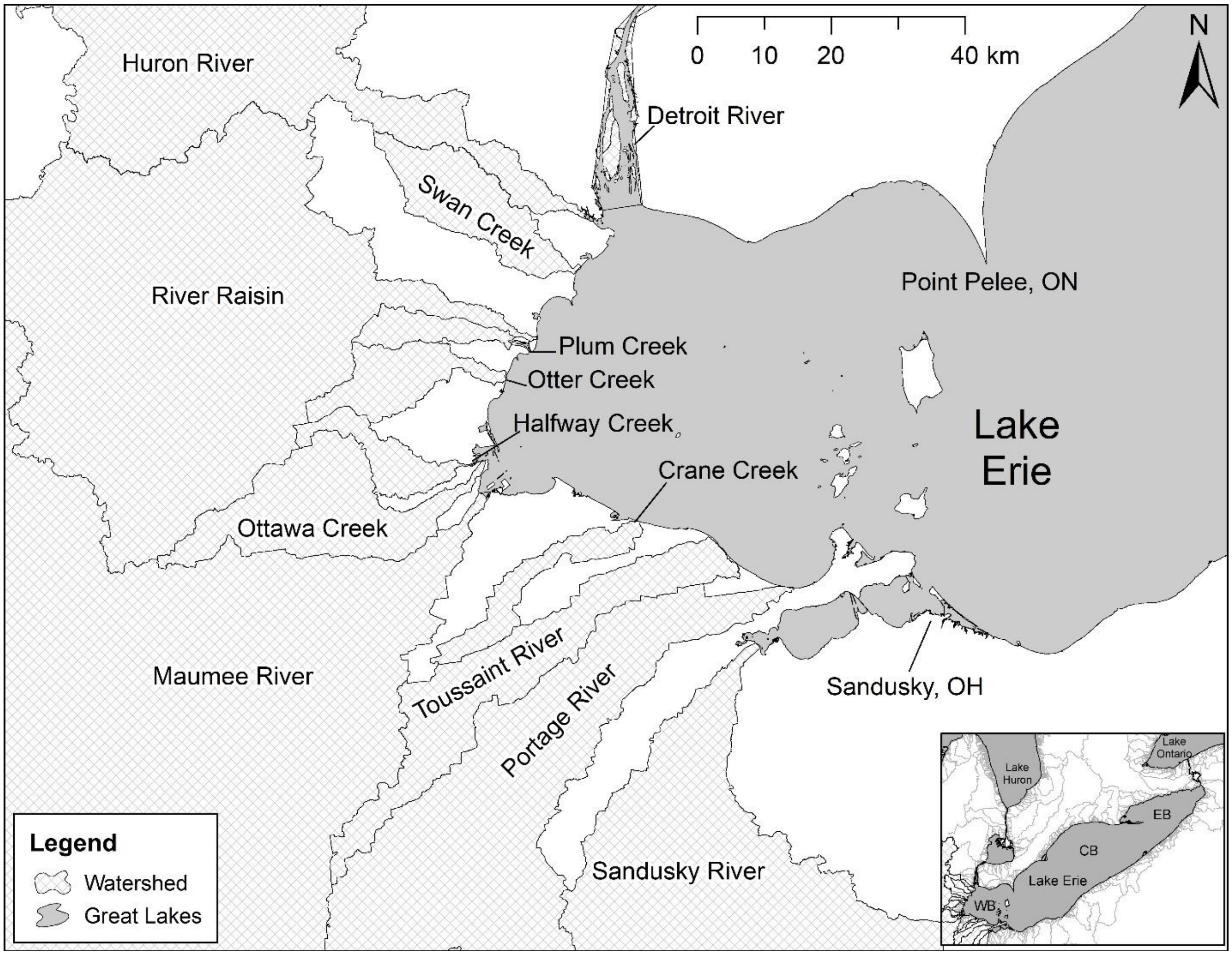

Figure 1.1. Watersheds of the western Lake Erie tributaries meeting at least one of two selection criteria; 1) tributaries from which Grass Carp had previously been collected based on review of records from the U.S. Geological Survey Nonindigenous Aquatic Species database (USGS 2018), and 2) tributaries with a watershed size greater than 100 km^2 based on the Great Lakes Hydrography Dataset (Forsyth et al. 2016).

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 dorsal 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 methods 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.

After capture, Grass Carp were held until transmitters could be implanted. Time between capture and transmitter implantation was as short as a few hours but in some cases was up to two days. When necessary, fish captured by commercial fishing operations were held in large [≈12 m (L) × 3 m (W) × 0.9 m (D)] storage containers placed directly in Lake Erie filled with lake water, sometimes with the rest of the commercial catch. Prior to transmitter implantation, fish were retrieved from storage containers via dip nets and placed into 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 (Vandergoot et al. 2011). After achieving stage-4 anesthesia (Bowzer et al. 2012), transmitters were surgically implanted into the coelom. Surgical procedures followed established guidelines and methods (Cooke et al. 2011; Hayden et al. 2014). During the study, surgeries were performed by three different surgeons given the logistical challenges of where and when Grass Carp were captured; 92% of surgeries were performed by two surgeons. 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). All transmitters were configured to emit a tag-specific code (69 kHz) at random intervals between 60-180 seconds to reduce probability of code collisions. Estimated transmitter lifespan was approximately 6.7 years. 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 caught. Fish remained in the aerated tank until regaining equilibrium and then were returned to the lake near their capture site (< 1.5 km away). Post-surgery holding time ranged from 30 minutes to one hour. Tagged Grass Carp were released in the 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. Because insufficient receivers were available to monitor all WB tributaries, the following set of criteria was used to select tributaries where receivers were deployed: 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); or 2) WB tributaries with a watershed size greater than 100 km^2 based on the Great Lakes Hydrography Dataset (Forsyth et al. 2016). Based on these criteria, receivers (Model VR2W, Vemco, Nova Scotia) were deployed in 13 tributaries located in either Michigan or Ohio (Table 1.1). 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 (A. Cook, Ontario Ministry of Natural Resources and Forestry, *personal communication*). 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. Deployment of new 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).

Table 1.1. 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 Kočovský 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

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 (Kočovský et al. 2012) or historic capture locations (USGS 2018) were monitored in 2015 because of the low number of tagged fish (*n* = 12). In 2016 and 2017, all 13 tributaries were monitored with up to 2 receivers located in the tributary but near Lake Erie proper 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 gear loss or damage in the winter. One exception was Plum Creek where ice-related gear loss or damage was low 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 the probability of detecting a transmitter was greater than 50% at distances within 100 m, with most tributaries having detection probabilities greater than 60 or 70% within 100 m (Appendix A).

Receivers deployed as part of other GLATOS projects provided potential detection information from more than 2500 additional 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 2.2). 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 lines of receivers 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 the more commonly tagged species in Lake Erie (e.g., Walleye, *Sander vitreus*; Kraus et al. 2018).

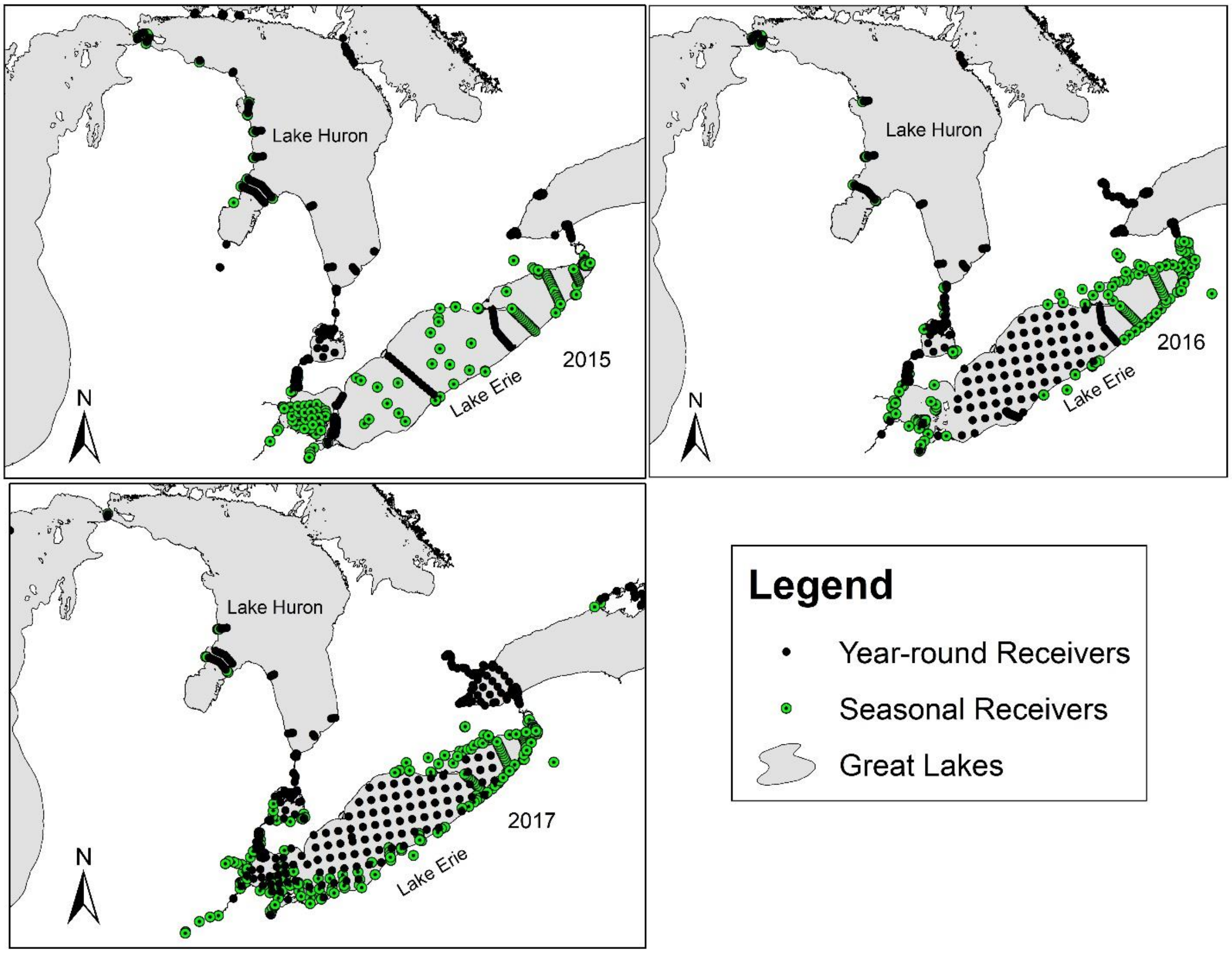

Figure 1.2. Placement of acoustic telemetry receivers in Lake Huron, Lake Erie, Lake St. Clair, Detroit River, and St. Clair River from 2015 to 2017.

Data analysis

Detection data from all receivers were used to construct georeferenced detection histories 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.

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 dispersal (the furthest distance from release location to a detection location), total distance moved (the summation of interpolated path movements), and mean daily distance moved. 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 km. When fish were undetected for a period of several days and subsequently detected on a different receiver from their 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 (Crossin et al. 2017). Fish use of WB tributaries in Lake Erie were based on number of tagged fish that entered tributaries and length of time fish were 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 into the WB of 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

Twenty-three Grass Carp met our criteria of having detections beyond 60 days for inclusion in analyses. Total lengths of these Grass Carp ranged from 75.2 to 115.1 cm and body mass ranged from 5.3

to 22.4 kg. Ploidy was determinable for 19 individuals; 89% (*n*=17) were diploid and 11% (*n*=2) were triploid. The average time span between date of surgery and last detection was approximately 580 days and ranged from 90 to 1350 days. Thirteen of the 23 fish that met our criteria for inclusion were tagged at water temperatures less than 10°C (17 of the total 50 fish were tagged at these temperatures); the other 10 fish were tagged at water temperatures greater than 10°C (33 of the total 50 fish were tagged at these temperatures).

During the study, no tagged Grass Carp were reported as harvested. Additionally, no tagged Grass Carp was ever repeatedly detected near one receiver without subsequent detections elsewhere, which would be indicative of a natural mortality event or expelled tag. 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 during routine electrofishing surveys on the Sandusky River and sacrificed. Upon dissection, the acoustic transmitter could not be located, indicating 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.

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 at specific locations, but instead was a behavior shown by 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. Except for two individuals, Grass Carp with the shortest maximum dispersals were released in the Sandusky River and never left the river.

Additionally, two other fish tagged and released in Plum Creek showed 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.

Seasonally, average total movement (averaged across fish) was similar during spring ($\bar{x}$ = 95.6 km; SE = 16.9 km) and summer ($\bar{x}$ = 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 <0.01 to 2.49 km/day ($\bar{x}$ = 0.76 km/day; SE = 0.12 km). Only 25% 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 were only detected in the river, suggesting they never left the river. The average (averaged across fish) of mean daily movements was highest during summer ($\bar{x}$ = 1.08 km; SE = 0.61 km) and spring ($\bar{x}$ = 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

During 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 heavily. Further, 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. Grass Carp using multiple tributaries often did so in spring and summer, traveling to another tributary days after the last detection in the previous tributary. Some transitions to other tributaries did occur in the fall as well, taking one or more months.

The Sandusky River, the second largest watershed included in this study (Table 1.1), 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 1.3); 11 of the tagged fish that were detected in the Sandusky River were originally tagged and released in the river, whereas the other seven fish were tagged and released in other areas of the lake. 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 eight km of the river although a single fish moved further upstream to Fremont, OH, about 24 km upstream from Muddy Creek Bay during late May and early June. The area between the Ballville Dam and Fremont, OH was identified by Embke et al. (2019) as a highly probable spawning location for Grass Carp in the

Sandusky River. In 2017, 17 fish (74% of 23 fish) were detected in the river for a range of one to 300 days ($\bar{x} =$ 175.5 days; SE =19.8 days). Grass Carp were detected in the Sandusky River throughout 2017, though the largest 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 later 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 (3 fish) and autumn (1 fish). 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 throughout the year. 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). Seasonal movement distance was lowest during the winter season ($\bar{x}$ = 7.4 km; SE = 1.2 km).

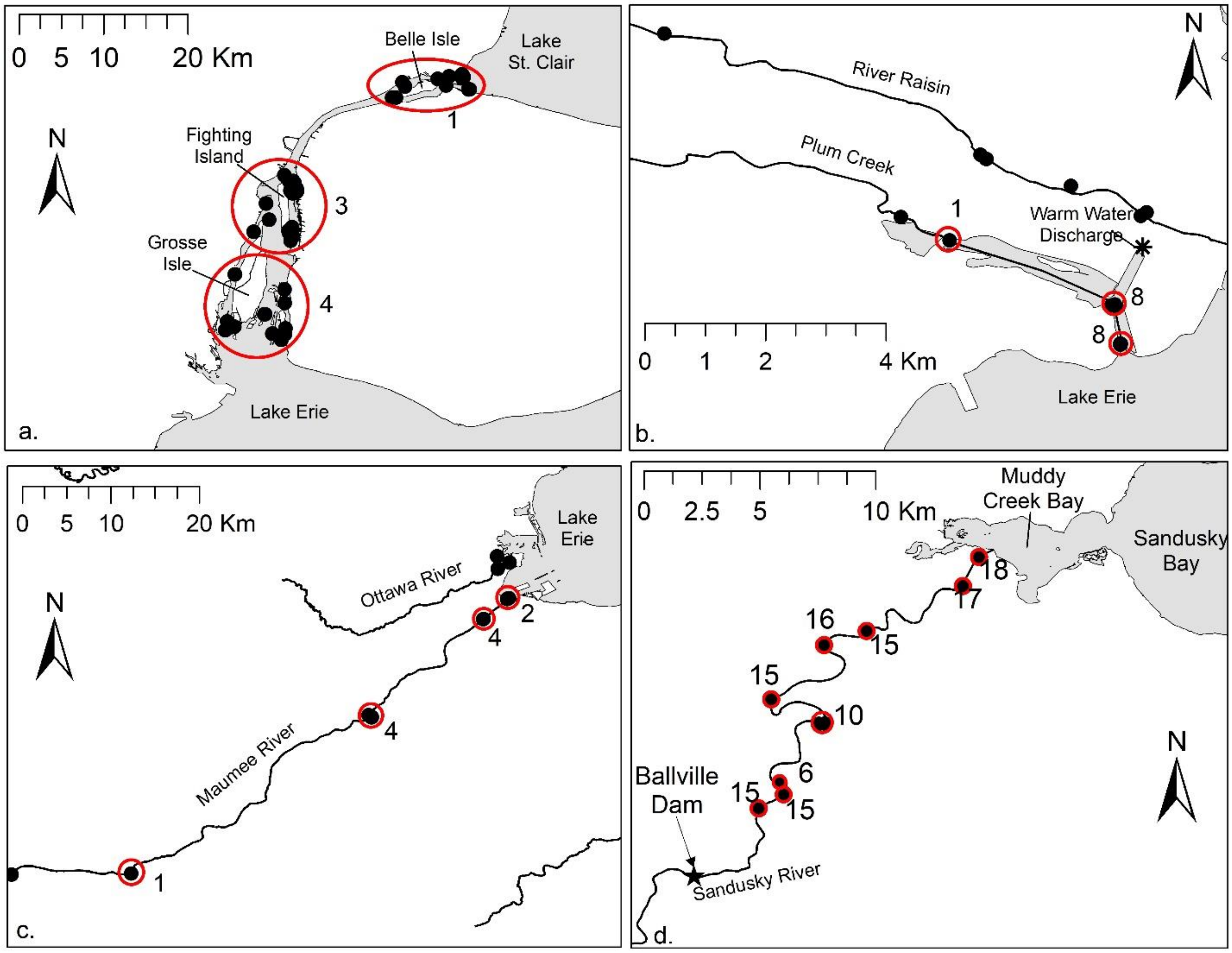

Figure 1.3. Locations of acoustic telemetry receivers in the Detroit River (a.), Plum Creek (b.), Maumee River (c.), Sandusky River, (d.) with the total number of tagged Grass Carp detected on each receiver, from January 1, 2015 through December 31, 2017.

Plum Creek was used by a total of eight Grass Carp (35% of 23 fish) during the study (Figure 1.3), 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, seven fish were detected in the tributary for a range of 85 to 133 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, 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 1.1) and was used by four Grass Carp (17% of 23 fish). 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 (MI), Ottawa River, Portage River, River Raisin, and Toussaint River were used by 1 to 4 fish that typically spent 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. These four fish moved into Lake Erie's central basin and one was detected in the eastern basin. Fish seemed to move to the central basin during summer given they were first detected in the central basin in June, August, or September. Two fish moved at least as far into the central basin 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 eastern basin (approximately 240 km east of Sandusky, OH) in early fall. All four fish returned to the WB after their 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 1.4). That individual was a diploid fish tagged in September 2016 in Plum Creek and detected later at 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 five 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. No evidence occurred that the fish returned to Lake Erie. No Grass Carp were detected downstream of Lake Erie in the Niagara River, Welland Canal, or Lake Ontario.

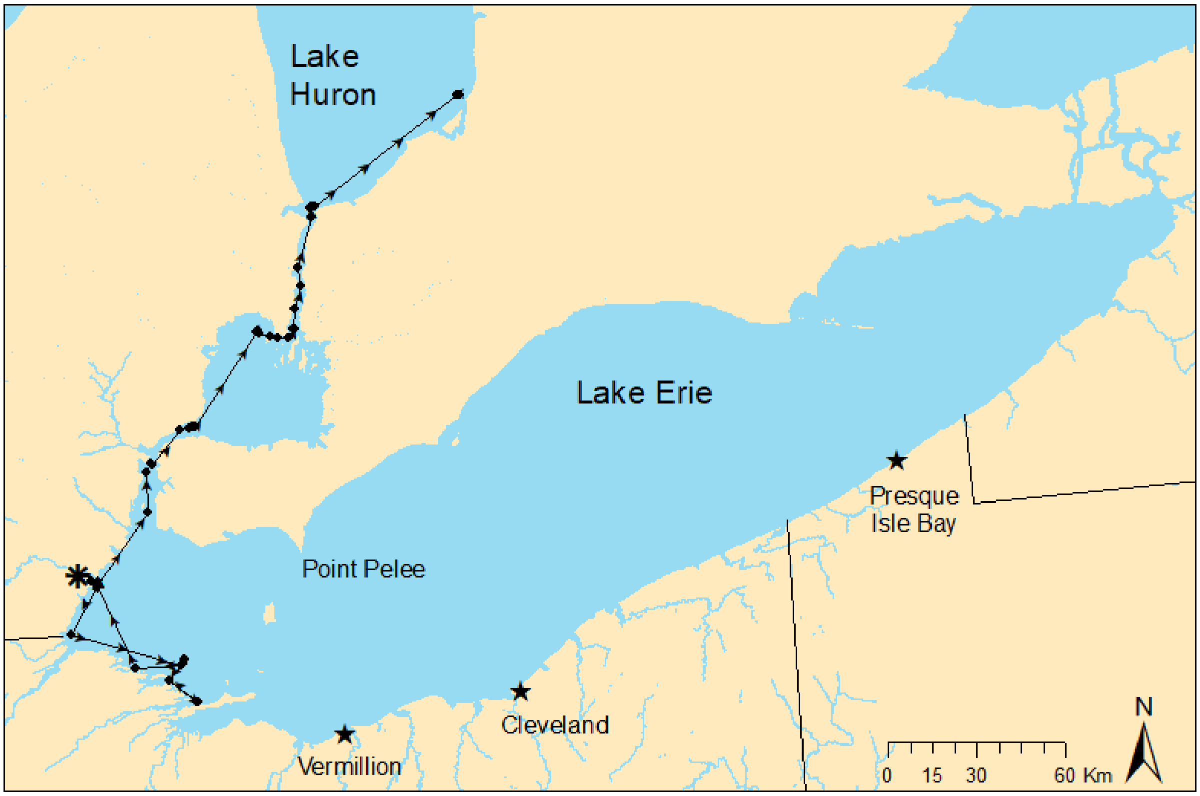

Figure 1.4. Receiver detections (circles) through the end of 2017 and movement directions (lines with arrows) of a tagged diploid Grass Carp, measuring 77 cm total length and weighing 6.3 kg, that emigrated from Lake Erie to Lake Huron. The asterisk indicates the approximate location where the fish was released after transmitter implantation.

Discussion

This study represents the first documentation of Grass Carp movement in the Great Lakes. Tagged Grass Carp tended to remain in the WB of Lake Erie and although multiple tributaries were used, the Sandusky River was most heavily used by telemetered fish. While many of the tagged Grass Carp in this study were originally tagged in the Sandusky River, almost 40% of the fish that used the Sandusky River were originally tagged in other areas of the lake suggesting Grass Carp were broadly attracted to this tributary. Use of the Sandusky River generally peaked during the spring and early summer presumably in preparation for and during Grass Carp spawning events, which are believed to be triggered by increased discharges (Shireman and Smith 1983; Cudmore and Mandrak 2004; Kočovský et al. 2012). Except for migrations to Fremont, OH, presumably for spawning, Grass Carp in the Sandusky River spent most of their time in the lower 8 km of the river.

Our observation that tagged Grass Carp resided in the Sandusky River for long periods throughout the year was unexpected. Descriptions of Grass Carp behavior have indicated that after spawning, fish tend 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) found that movement of Grass Carp declined during winter 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, fish were occasionally observed moving considerable distances in the river, including movement upstream near the identified Grass Carp spawning area.

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; before the findings of Embke et al. (2016), no confirmed evidence of Grass Carp spawning had occurred in the Laurentian Great Lakes. Of the tributaries used by Grass Carp, the most likely systems where Grass Carp may have spawned based on collections during the presumed spawning season (Embke et al. 2016; Kočovský et al. 2012) 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; USGS 2019: https://www.usgs.gov/news/newly-hatched-invasive-grass-carp-found-maumee-river-ohio) and our data showed movement and use of the projected spawning area in the Sandusky River at the time of egg collection (Embke et al. 2019), suggesting movement and use were for spawning activities. The Detroit River was not identified by Kočovský et al. (2012) as being suitable for Grass Carp spawning, and it has been hypothesized that 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). Some survival was found when eggs were buried in sand (George et al. 2015); 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. According to Cudmore et al. (2017), Grass Carp typically require > 50 km of river for successful reproduction. Embke et al. (2017) collected fertilized eggs in the lower portion of the Sandusky River, yet the magnitude of successful recruitment of fertilized eggs to the adult stage is unknown. Plum Creek is somewhat unique among WB tributaries because it receives warmwater discharge from a coal-fired power plant, and likely provides Grass Carp with a thermal refuge during cold winter 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), though that is not a measurement of individual movement. In their native range, Grass Carp in the Amur River along the border of Russia and China, 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 when accessible water distances were greater than 120 km (Bain et al. 1990; Maceina et al. 1999). 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). Others have observed Grass Carp dispersing up to 71 to 99 km from release locations (Bain et al. 1990; Maceina et al. 1999), sometimes in short time periods (e.g., one fish moved 53 km in nine days; Bain et al. 1990). Additionally, Bain et al. (1990) observed a large difference in annual movements of tagged Grass Carp in their study with movement averaging around 2 km and then the following year fish moved nearly 33 km on average. Bain et al. (1990) theorized that the difference in movement was a result of tagged Grass Carp reaching sexual maturity during the second year of the study. In contrast, others have found stocked Grass Carp to move extensively (5 to 10 km) immediately after stocking; however, after acclimation fish showed little movement (Chilton and Poarch 1997). 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 made it difficult to identify variables (e.g., sex, ploidy) that potentially influenced movement of individual Grass Carp. Movement across seasons is likely driven by 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 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.

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, nor are 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, we have recorded instances of tagged Grass Carp being recaptured nearly 3 years after implantation with the transmitter and external tag retained. Separating tag shedding from mortality events is difficult; 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 shedding declined to 15% when implanting large 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. Water temperature that fish were returned to also may have affected the survival of fish, given that we were able to conduct analyses on more than 75% of fish released into water temperatures less than 10° C, but on only around 30% of those released into water temperature greater than 10° C. Future investigation into the survival of Grass Carp after surgical implantation of acoustic transmitters would be useful for maximizing the amount of information to be learned from telemetry studies.

Various other explanations exist 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. Moving receivers in Lake Erie from lines to grids in 2016 was expected 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, increased detections did not occur for Grass Carp. 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, Common Carp (*Cyprinus carpio*), and Channel Catfish (*Ictalurus punctatus*). Grass Carp movement appears to be quite different than the conditions simulated by Kraus et al. (2018) such that expected detections did not occur.

The primary motivation to study Grass Carp movement behavior in Lake Erie and to identify areas of high use was to inform control efforts for Grass Carp. Tagged fish heavily used 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 (Herbst et al. in review). Success of initial control efforts was low due to the difficulty of locating and capturing Grass Carp. Since 2018, Grass Carp captures by fishery management agencies have increased and biologists are using summaries of detections from passive receivers, detections from real-time receivers, and active tracking to inform response effort locations (L. Nathan, Michigan Department of Natural Resources, *personal communication*). Using tagged conspecifics to improve control efforts for invasive species has been referred to as the "Judas fish" technique and 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 Grass Carp control. Although Plum Creek was not as heavily used as the Sandusky River, tagged Grass Carp were observed making repeated visits to this area, which 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 having been originally caught in these tributaries, 11 fish and 4 fish respectively. However, we did observe fish tagged and released elsewhere in Lake Erie and then moving into Sandusky River (seven tagged Grass Carp) or Plum Creek (four tagged Grass Carp) on occasion suggesting some characteristic occurs at these tributaries that attracts fish. Other tributaries that are candidates for control efforts are the Maumee and Detroit rivers. Both rivers were used by four tagged Grass Carp, although fish generally spent more time in the Detroit River than the Maumee River.

This study provides critical insight not only into areas where Grass Carp control efforts could be directed, but also the seasonal timing to deploy those efforts. Further, our results provide empirical information about Grass Carp movement in 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.

APPENDICES

APPENDIX A

Detection Probabilities of Select Tributaries to Western Lake Erie

Average detection probability for WB Lake Erie tributaries in which acoustic telemetry receivers were deployed for this study to monitor tributary use by Grass Carp, 2015-2017. Range testing was conducted at each receiver location using the same basic design. Acoustic telemetry transmitters were buoyed within 1 m of the bottom of the given tributary at the following distances from the receiver: 50 m, 100 m, 200 m, 300 m, and 400 m. Duration of range tests ranged from 1 to 2 weeks at each receiver location. Detection probabilities were calculated using Vemco Range Test software (Version 1.9.22.0; AMIRIX Systems Inc. 2014) and represent the probability of the receiver detecting a single transmission from a transmitter (Model V16-4x; Vemco).

Table 1.2. Average detection probability for WB Lake Erie tributaries in which acoustic telemetry receivers were deployed for this study to monitor tributary use by Grass Carp, 2015-2017.

Tributary	50m	100m	200m	300m	400m
Crane Creek	68.3%	66.7%	63.9%	60.7%	51.2%
Halfway Creek	99.8%	52.6%	0%	0%	0%
Huron River	80.2%	80.2%	79.8%	76.4%	NA
Maumee River	82.3%	79.7%	77.6%	77.1%	13.2%
Ottawa River	65.6%	66.4%	44.4%	61.8%	49.2%
Otter Creek	91.8%	84.8%	86.0%	0.4%	0.3%
Plum Creek	68.4%	66.0%	66.5%	62.8%	55.4%
Portage River	74.7%	73.1%	42.4%	68.0%	67.3%
River Raisin	75.3%	74.1%	63.7%	64.8%	55.6%
Swan Creek	65.2%	57.5%	52.4%	51.8%	21.6%
Toussaint River	74.9%	74.5%	73.4%	68.7%	68.7%

APPENDIX B

Detailed Account of Intra-Basin Movements

Of the fish that moved into the central basin, one fish (diploid) that was originally tagged in the Maumee River moved to the central basin of Lake Erie just north of Vermillion, OH, which is approximately 30 km east of Sandusky, OH, during September 2016 but within approximately one week it had returned to Plum Creek approximately 93 km away (Figure 1.5). In September 2017, the fish moved even further into the central basin to an area just north of Cleveland, OH, approximately 83 km east of Sandusky, OH (Figure 1.5). Within approximately three weeks, that fish was once again detected on the receiver just north of Vermillion, OH and a week after that it had moved into Sandusky Bay (Figure 1.5). Another Grass Carp (diploid) also was detected on a receiver just north of Cleveland, OH in June 2017 (Figure 1.6). That fish moved to this area from the Sandusky River and Bay. Detections of this fish on receivers north of Vermillion, OH occurred intermittently in 2018 with the fish returning to the Sandusky River/Bay in June 2018. The third fish (triploid) that moved into the central basin was detected in early August 2017 on a receiver approximately 16.5 km southeast of Point Pelee, ON (Figure 1.7). Prior to this detection, the fish had been located in the Sandusky River and Bay. Within three days of its detection in the central basin, the fish had moved back into the WB and was detected on a receiver near the outlet of the Detroit River into Lake Erie (Figure 1.7).

The Grass Carp (diploid) that moved into Lake Erie's eastern basin was originally tagged in the Sandusky River in April 2017 but later moved into the Detroit River, Huron River, and Plum Creek. In July 2017, the fish was detected on Toussaint Reef approximately 15 km NW of Port Clinton, OH; however, within five days of this detection the fish had moved approximately 211 km into the central basin and was detected on a receiver just north of the Ohio and Pennsylvania border (Figure 1.8). The following day that Grass Carp had moved into Lake Erie's eastern basin about 7 km west of Presque Isle Bay near Erie, PA. This fish went undetected until October 2017 when it was detected on a receiver just north of Presque Isle Bay. It then went undetected again for approximately 8 months before it was detected on a receiver in Sandusky Bay.

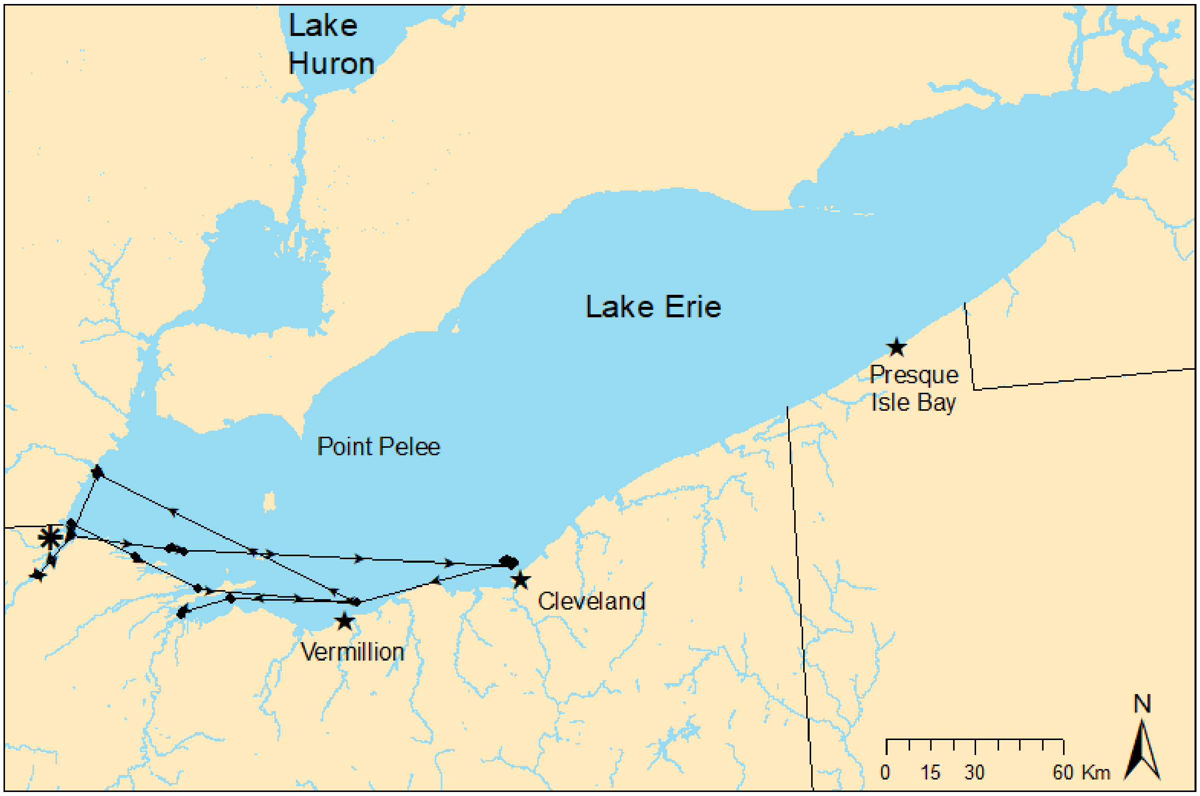

Figure 1.5. Receiver detections (circles) through the end of 2017 and movement directions (lines with arrows) of a tagged Grass Carp that moved into Lake Erie's central basin. The asterisk indicates the approximate location where the fish was released after transmitter implantation.

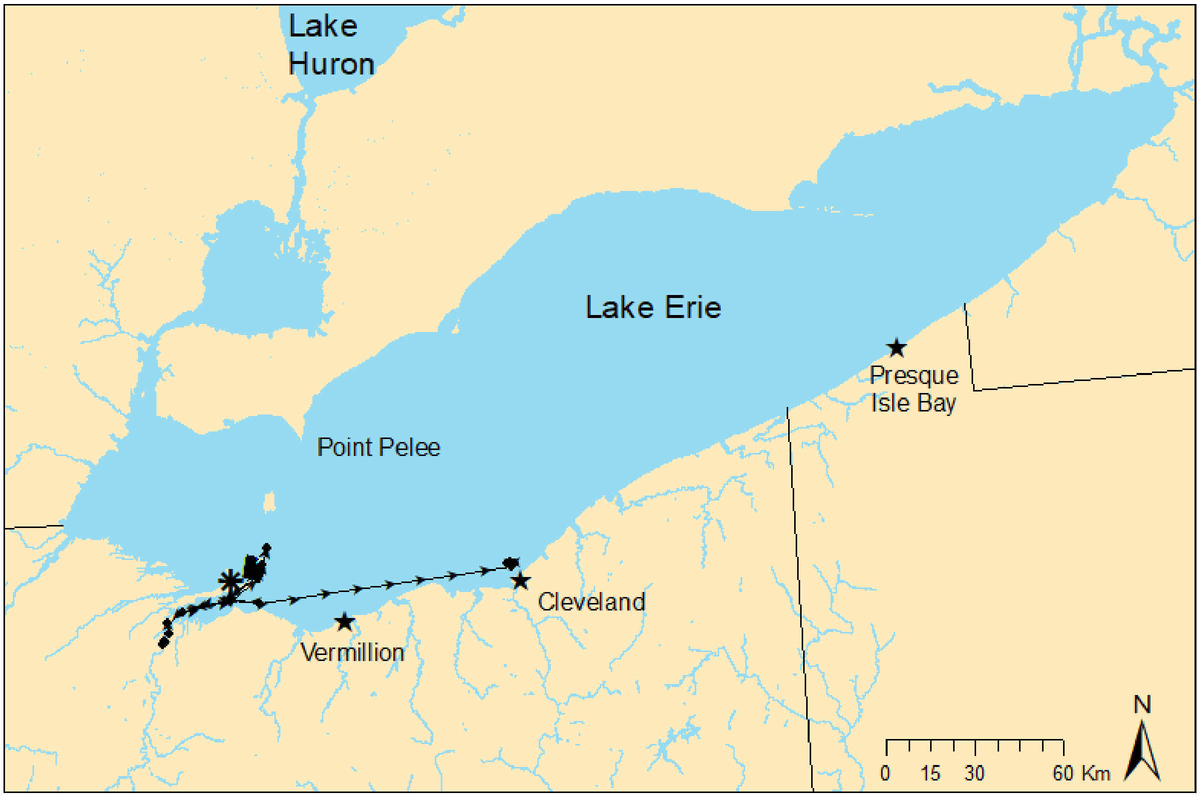

Figure 1.6. Receiver detections (circles) through the end of 2017 and movement directions (lines with arrows) of a tagged Grass Carp that moved into Lake Erie's central basin. The asterisk indicates the approximate location where the fish was released after transmitter implantation. This Grass Carp was intermittently detected on the receiver north of Cleveland, OH in 2018 and moved back into the Sandusky River in early June 2018.

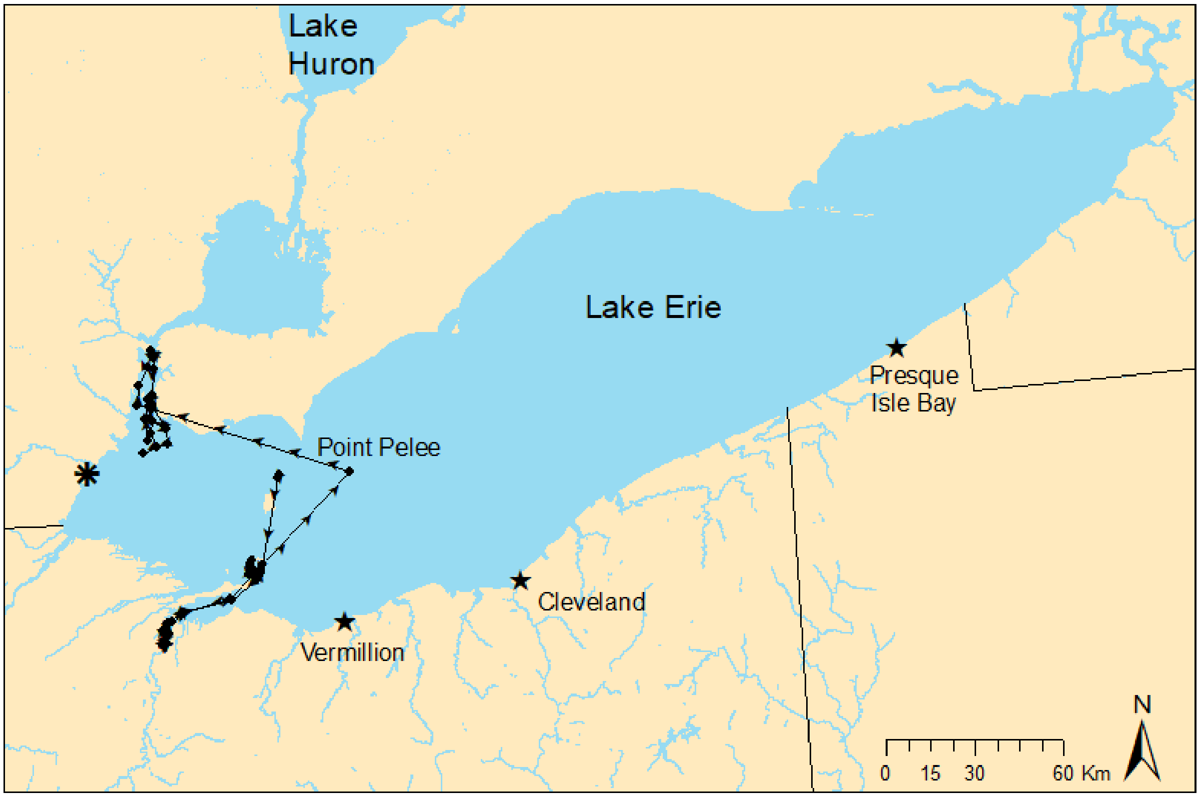

Figure 1.7. Receiver detections (circles) through the end of 2017 and movement directions (lines with arrows) of a tagged Grass Carp that moved into Lake Erie's central basin. The asterisk indicates the approximate location where the fish was released after transmitter implantation.

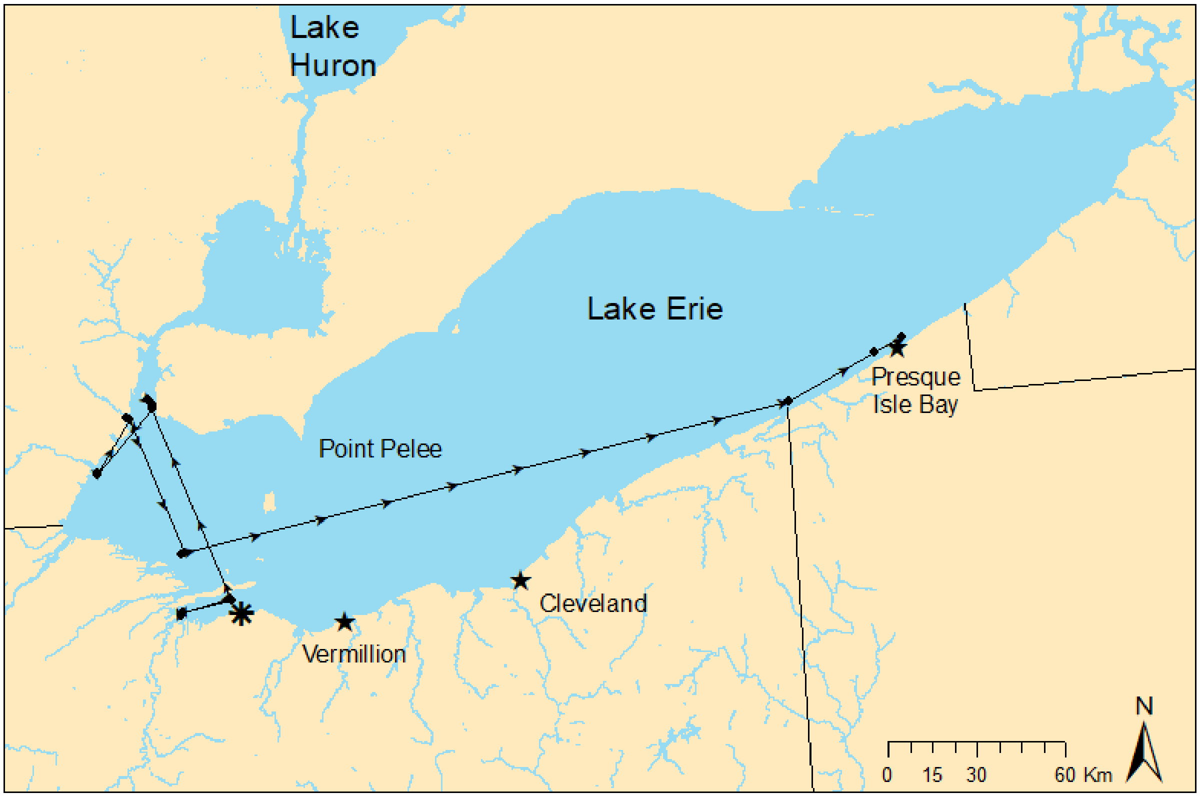

Figure 1.8. Receiver detections (circles) through the end of 2017 and movement directions (lines with arrows) of a tagged Grass Carp that moved into Lake Erie's central basin. The asterisk indicates the approximate location where the fish was released after transmitter implantation. This Grass Carp was subsequently detected on receivers in the Sandusky Bay in July 2018.

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CHAPTER 2

Movement and Space Use of Grass Carp in the Sandusky River, Ohio: Implications for Lake Erie Control Efforts

Introduction

In the Laurentian Great Lakes of North America, a significant issue being confronted by fishery managers is limiting the spread and negative effects of aquatic invasive species and preventing additional invasions from occurring. The Great Lakes are among the planet's most invaded aquatic ecosystems (Ricciardi 2006) and are at risk for additional invasions due to the high volume of international shipping traffic (Mills et al. 1993) and because previous invaders can facilitate establishment of future invaders due to negative effects on native populations and environmental modifications (Ricciardi 2001, 2006). Presently, considerable focus in the Great Lakes region is centered on preventing the invasion of three major Chinese carps, specifically Silver Carp *Hypophthalmichthys molitrix*, Bighead Carp *Hypophthalmichthys nobilis*, and Black Carp *Mylopharyngodon piceus*. Colloquially, these species are referred to as Asian carp, which is a categorization that also frequently includes Grass Carp *Ctenopharyngodon idella*. Unlike Silver, Bighead, and Black Carp, Grass Carp have already invaded the Great Lakes. Management efforts in the region are focused on eradicating Grass Carp or at least reducing population densities to lessen the risk of spread, population establishment, and negative consequences to aquatic and terrestrial communities (Herbst et al. in review).

Although Grass Carp have been captured from all of the Great Lakes except for Lake Superior (USGS 2019), the current invasion front for Grass Carp is believed to be the western basin of Lake Erie. Grass Carp were first caught in Lake Erie in 1985 (USGS 2019). From the 1980s to 2000s, Grass Carp captures were sporadic and presumed primarily to be triploid (i.e., sterile) individuals that were stocked in nearby systems for weed control but had escaped and migrated into Lake Erie (J. Tyson, Great Lakes Fishery Commission, *personal communication*). Beginning in the 2010s, reported captures of Grass Carp by commercial fishers increased in Lake Erie's western basin (Cudmore et al. 2017). In 2012, four diploid juvenile Grass Carp were caught in the Sandusky River, a tributary to the western basin of Lake

Erie, and identified as likely having been produced naturally from that river based on otolith microchemistry analysis (Chapman et al. 2012). In 2015, Embke et al. (2016) collected fertilized Grass Carp eggs from the Sandusky River; the most probable spawning location for these eggs was identified as being between Ballville Dam and the town of Fremont, Ohio (Embke et al. 2019) (Figure 2.1). Fertilized Grass Carp eggs have subsequently been collected nearly annually from the Sandusky River; eggs and a larval Grass Carp were also recently collected from the Maumee River (P. Kočovský, U.S. Geological Survey Great Lakes Science Center, *personal communication*), another tributary to the western basin of Lake Erie. Ploidy analysis of approximately 60 Grass Carp collected from the western basin of Lake Erie between 2014 and 2016 indicated that approximately 87% of the individuals were diploid and capable of viable reproduction (Wieringa et al. 2017).

The combination of elevated catch reports, confirmation of Grass Carp spawning in at least two western basin tributaries, and the prevalence of spawning-capable individuals heightened concerns among management agencies about negative effects stemming from increasing population densities and risk of spread and establishment to the other lakes. This prompted state, provincial, and federal fishery agencies in the Lake Erie basin to develop a coordinated strategy to control Grass Carp. Robinson et al. (in press) conducted a multi-party, collaborative decision analysis to determine objectives and potential management actions for Lake Erie control efforts. The decision analysis project led to the establishment of a goal to annual remove 390 spawning-capable Grass Carp to reduce the risk of spread and negative effects on aquatic and terrestrial communities (DuFour et al. in review). Based on expert elicitation, the most effective control strategy for achieving this suppression goal was targeted removal efforts concentrated in areas of high catchability combined with techniques to disrupt spawning in the Sandusky River (Robinson et al. in press).

Despite targeted removal being identified as a preferred control policy by Robinson et al. (in press), enactment of this policy is difficult because Grass Carp are notoriously difficult to catch with traditional fishing methods (Mitchell 1980; Maceina et al. 1999). In 2014, an exercise involving 10 state, provincial, and federal fishery agencies was conducted on Lake Erie to practice a coordinated response if one of the major Chinese carps was detected in the lake. Although it was intended to be a practice response, the agencies targeted Grass Carp during the exercise to accomplish a secondary objective to reduce population abundance of this species. Control efforts consisted of boat electrofishing (219 electrofishing runs = 96 hours of electrofishing time) and gillnetting (53 gillnet lifts = 58.8 hours of soak time); locations where control efforts were implemented were informed by positive eDNA detections of Grass Carp in Lake Erie over the previous few weeks (S. Herbst, Michigan Department of Natural Resources, *unpublished data*). Despite this large amount of effort, only two Grass Carp were captured during the exercise (S. Herbst, Michigan Department of Natural Resources, *unpublished data*).

For targeted sampling to be a feasible method of control, knowledge of areas where Grass Carp aggregate and how these aggregation areas change temporally would be beneficial. Using detections of Grass Carp implanted with acoustic telemetry transmitters, Harris et al. (in press) identified four areas in Lake Erie that were heavily used by Grass Carp: Sandusky River, Plum Creek, Maumee River, and Detroit River. Of these areas, Sandusky River was the most used system with tagged fish remaining in the river throughout the year. Grass Carp response strategies for Lake Erie developed by the Ohio Department of Natural Resources (ODNR Division of Wildlife 2019) and the Lake Erie Committee (Lake Erie Committee and Great Lakes Fish Commission 2018) have each identified the Sandusky River as an area for targeted control due to its high use by Grass Carp and because it is believed to be the tributary with the most consistent spawning and likely the largest source of Grass Carp recruitment in the lake. Prior to 2018, the Sandusky River spanned approximately 55 km from its outlet into Lake Erie to its first upstream barrier to movement, Ballville Dam. In July 2018, Ballville Dam was demolished, which increased the river run length to 90 km. Consequently, even though Sandusky River has been identified as an area heavily used by Grass Carp, further refinement as to specific areas used by Grass Carp and how use changes seasonally and across years will be beneficial for improving effectiveness of control options.

The purpose of this research was to estimate Grass Carp space use and movement within the Sandusky River and determine how these behaviors were affected by environmental conditions (i.e., discharge and water temperature) to inform control efforts for reducing population densities in Lake Erie.

Grass Carp collected from Lake Erie were implanted with acoustic telemetry transmitters to monitor their movements in the Sandusky River system with passive acoustic receivers deployed throughout the system. Receiver detections were summarized to determine space use and movement and were also used in a spatial capture-recapture model to estimate daily activity (i.e., home range) centers of tagged fish.

Methods

Study site

The Sandusky River watershed drains approximately 4,700 km^2 in northwest Ohio (Tetra Tech Inc. 2014). The total length of the Sandusky River is approximately 207 km (Forsyth et al. 2016); the river flows into Muddy Creek Bay and subsequently Sandusky Bay before entering Lake Erie (Figure 2.1). Prior to 2018, Ballville Dam, located approximately 55 km from Lake Erie, was the furthest downstream barrier on the Sandusky River. The dam measured roughly 10.5 m in height and 128 m in width, and was believed to block upstream fish passage (Gillenwater et al. 2006; Kočovský et al. 2012). In September, 2017, a roughly six meter notch was created at the south spillway to incrementally lower the impoundment behind the dam, followed by complete removal of the dam in July 2018. The lower portion of the Sandusky River, downstream from where the Ballville Dam was located, ranges in width from 32 m to 160 m and commonly has depths of five to six meters at low flow conditions (Embke et al. 2016, 2019). The furthest downstream USGS gauge station in the Sandusky River is located near Fremont, OH (USGS 04198000); the discharge of the Sandusky River measured at this gage between 2000 and 2018 averaged 40 m^3/sec and ranged from 0.5 to 736 m^3/sec (USGS 2016). Muddy Creek Bay and Sandusky Bay have a combined surface area of approximately 143 km^2 with a maximum depth of approximately 3 m. The Sandusky River, Sandusky Bay, and Muddy Creek Bay in combination are hereafter referred to as the Sandusky River.

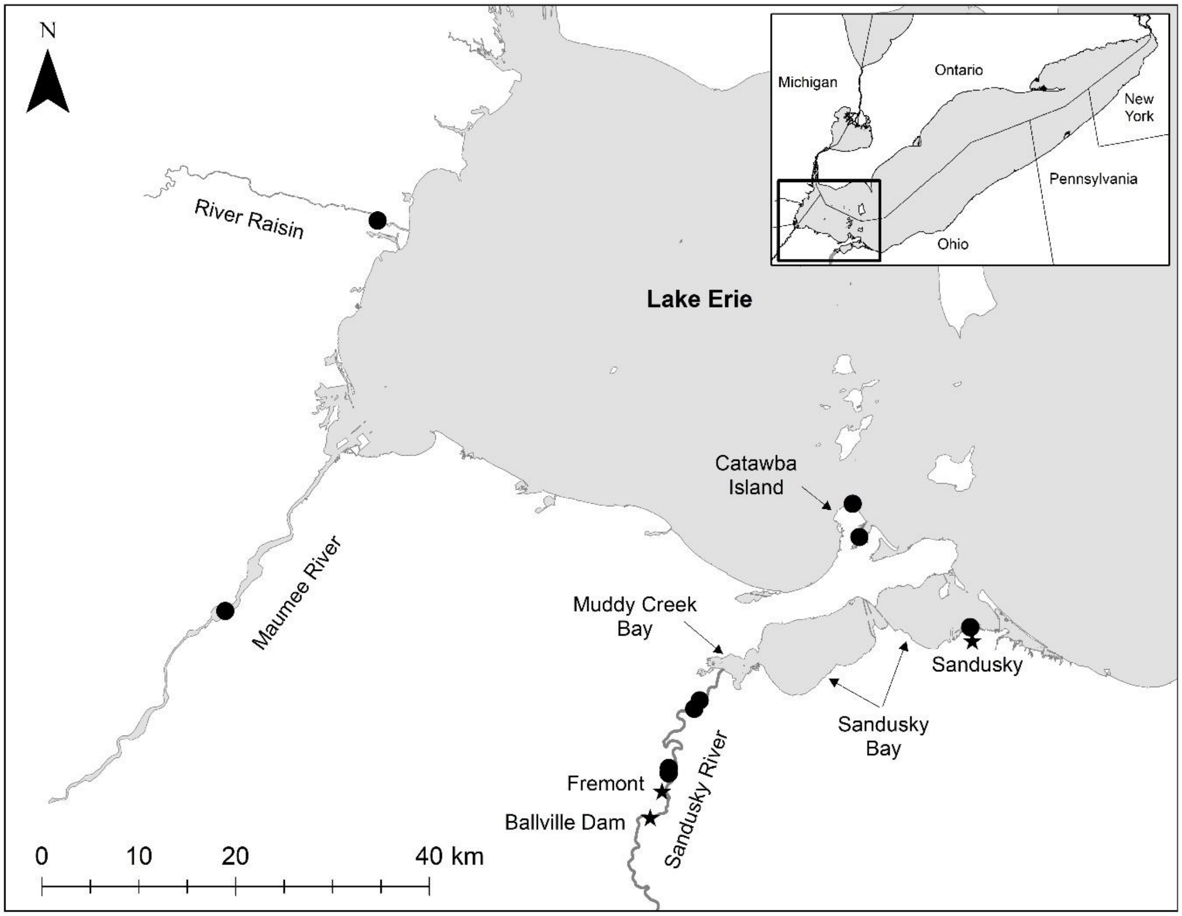

Figure 2.1. Map of the western basin of Lake Erie showing release locations of the 27 Grass Carp that provided detections used in this study (2014-2019). Twenty-two fish were released in the Sandusky system, two fish in Lake Erie near Catawba Island, one fish in the Maumee River, and two fish in the River Raisin.

Data collection.

This study used detection data from Grass Carp (*n* = 70) implanted with acoustic telemetry transmitters (Model V16H, Vemco, Halifax, Nova Scotia; hereafter transmitters) that were captured from the Michigan and Ohio waters of Lake Erie between 2014 and 2019 by either commercial fishing operations or state/federal agency sampling efforts. Details of Grass Carp collection and the procedures used to implant transmitters are described in detail in Harris et al. (in press) and are summarized here. Prior to surgery, fish were anesthetized to stage-4 as recommended by Bowzer et al. (2012) using a portable electroanesthesia system (Smith-Root, Inc., Vancouver, Washington) set to pulsed-direct current at 30 V, 100 Hz, and 25% duty cycle for 3 seconds. While anesthetized, transmitters were inserted into the coelom through ventral incisions that were then closed with 2 to 3 absorbable sutures (PDS-II, 3-0, Ethicon, Somerville, NJ) following methods described in Cooke et al. (2011) and Hayden et al. (2014). Transmitters were programed to produce a tag-specific code at a frequency of 69 kHz every 120 s on average (range: 60 to 180 s). Estimated transmitter lifespans were approximately 6.7 years. Each fish was externally marked, below the anterior portion of the dorsal fin, with an external lock-on loop tag (Model FT-4; Floy Tag & Manufacturing Inc., Chattanooga, TN) that had a unique number for each fish along with a phone number for contact if the fish was recaptured. Fish were held in an aerated tank for 30 to 60 minutes after surgery and released once they could maintain equilibrium independently.

For this study, only detections between 1 May 2017 and 31 July 2019 were used in analyses as that is the time period when receiver coverage in the Sandusky River was the most intensive. Only detections of tagged fish determined to be alive and in good condition during the study period were incorporated in analyses. This filter was accomplished by only using detections from tagged Grass Carp that were detected more than 60 days post tagging on any acoustic receiver deployed in the Great Lakes region. In some instances, tagged Grass Carp were detected on 1 or more receiver more than 60 days post tagging; however, subsequent examination of detection histories suggested these detections were possibly from a dead fish or a shed tag, which could bias results. Four professionals experienced with telemetry detections examined detection histories of all tagged fish detected in the Sandusky River, and voted whether certain detections were from alive fish or from dead fish or a shed tag. The majority decision was used to decide whether suspect detections would be included in further analyses.

Of the 70 originally tagged Grass Carp, 27 fish met the criteria for inclusion in subsequent analyses. Of the 27 Grass Carp, 22 were tagged in the Sandusky River and 5 were tagged elsewhere in Lake Erie (Catawba Island: 2 fish; Maumee River: 1 fish; River Raisin: 2 fish) (Figure 2.1) but which later moved into the Sandusky River. Ages of tagged Grass Carp estimated from dorsal fin rays ranged from 4 to 12 years ($\bar{x}$ = 6 years), with total lengths ranging from 78.2 to 106.7 cm ($\bar{x}$ = 91.7 cm). Body mass ranged from 5.3 to 16.3 kg ($\bar{x}$ = 9.6 kg). Blood samples were used to determine the ploidy of the tagged fish following methods described in Krynak et al. (2015). Of the 27 tagged fish, 59% (16 of 27 fish) were diploid, 15% (4 of 27 fish) were triploid, and 26% (7 of 27 fish) were unknown. Ploidy status results reported as unknown were due to inconclusive results, blood samples being coagulated prior to testing, or blood samples not being collected.

Transmissions from tagged Grass Carp were recorded with acoustic telemetry receivers (hereafter receivers) deployed throughout the Sandusky River. Three 69 kHz receiver models (VR2W, VR2TX, and VR2C; Vemco, Halifax, Nova Scotia) were used at different locations. Receivers recorded date, time, and unique transmitter ID code of tagged Grass Carp transmission. In 2017, a total of 12 receiver stations were located in the Sandusky River. As additional receivers became available, receiver stations were added to the existing array in 2018 (total of 27 receiver stations) and 2019 (total of 65 receiver stations) to improve coverage in the river and to better understand use of Sandusky and Muddy Creek Bays (Figure 2.2). Receivers extended approximately 40 river kilometers (RKMs) from an area separating inner and outer Sandusky Bay (RKM 10.6) upstream to an area just below Ballville Dam (RKM 50.2). In Muddy Creek and Sandusky Bays and one location in the Sandusky River, the width of the area was too large to cover with a single receiver. In such cases, multiple receivers were deployed in-line across the width of the system. Even though multiple receivers were deployed, detections on any of these in-line receivers were treated as a single detection at that RKM location, which we refer to as RKM receivers. Most receivers were deployed year-round, although some receivers were removed to prevent loss during the winter. Additionally, some deployed receivers could not be recovered during the timeframe of this study due to complications that arose during retrieval (e.g., excessive woody material obstructing retrieval).

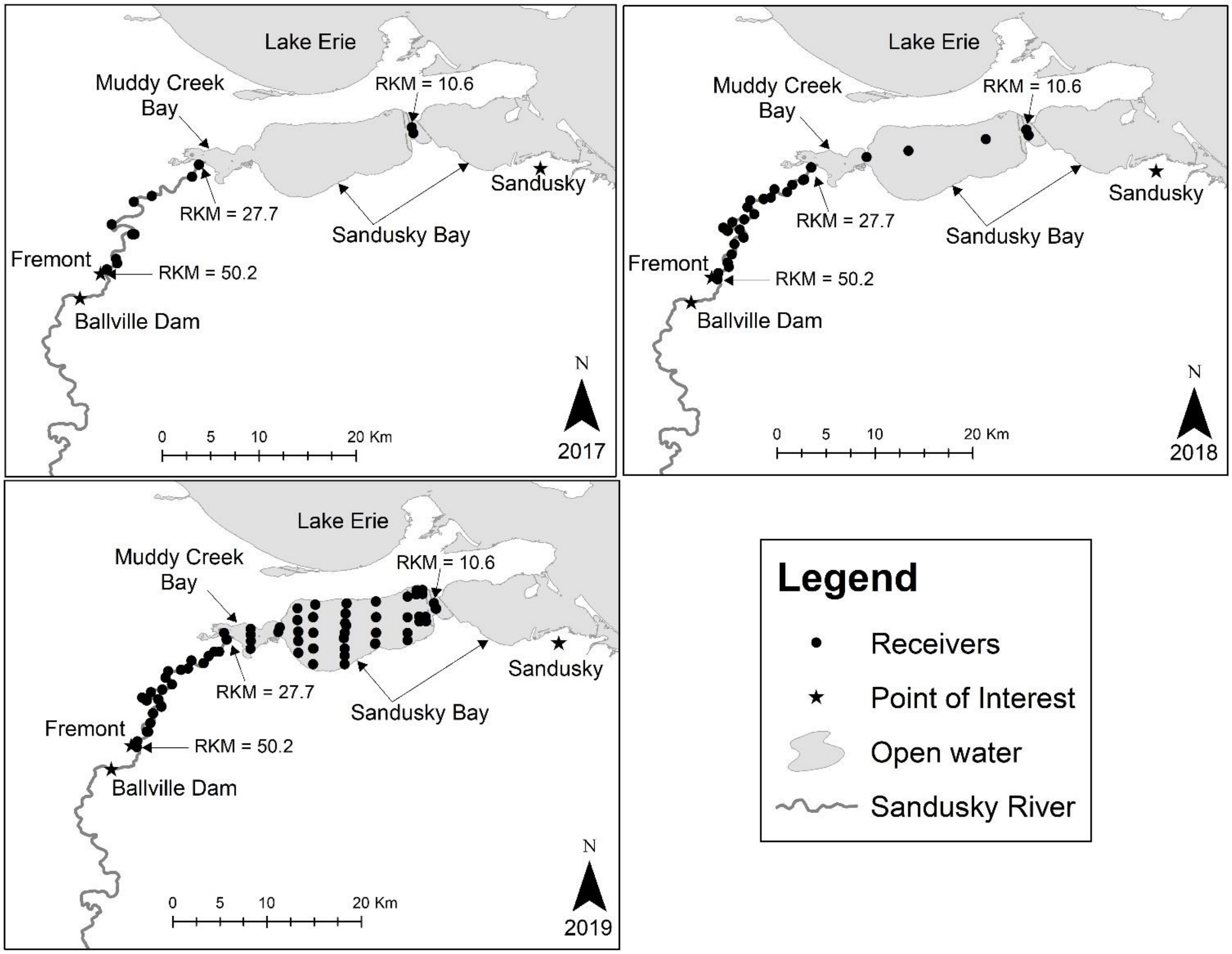

Figure 2.2. Locations (black circles) where acoustic receivers were deployed in the Sandusky River during each year this study was conducted.

Environmental covariates

Based on prior research (Stanley et al. 1978; Bain et al. 1990), Grass Carp space use and movement in the Sandusky River were hypothesized to be affected by river discharge and water temperature, which also could influence the effectiveness of control efforts. Consequently, we incorporated measures of river discharge and water temperature when describing space use and movement. River discharge data were obtained from the US Geological Survey (USGS) National WaterWatch Website (https://waterwatch.usgs.gov/) collected at the National Water Information System

Station 04198000, located near Fremont, Ohio. Water temperature data were collected by a VR2C (Vemco, Halifax, Nova Scotia) receiver with a built in thermometer, deployed at RKM 49.5.

Information available for Grass Carp spawning in general and specifically in the Sandusky River were used to develop categories of space use and movement for Grass Carp. Prior research reported that the onset of Grass Carp spawning occurs at approximately 18°C (Duan et al. 2009; Cudmore et al. 2017; Embke et al. 2019). Additionally, Murphy and Jackson (2013) identified that a discharge of at least 31 m^3/s was needed in the Sandusky River to keep Grass Carp eggs suspended. According to unpublished information collected by state and federal agencies, control efforts targeting Grass Carp do not typically occur in the Sandusky River during December, January, or February. The average water temperature during those three months during the study was 2.1°C (SE = 2.4°C); consequently, we chose a water temperature of 4.5°C to represent the lower threshold when targeted efforts for Grass Carp would occur. Based on this temperature and discharge information, we developed the following categorization for summarizing Grass Carp space use and movement: 1) daily maximum discharge $\geq 31\ m^3/s$ & daily mean water temperatures $\geq$ 18°C; 2) daily maximum discharge $\geq 31\ m^3/s$ & daily mean water temperature $\geq$ 4.5°C and < 18°C; 3) daily maximum discharge $< 31\ m^3/s$ & daily mean water temperatures $\geq$ 18°C; 4) daily maximum discharge $< 31\ m^3/s$ & daily mean water temperature $\geq$ 4.5°C and < 18°C; 5) daily mean water temperature < 4.5°C.

Detection data filtering

Using the GLATOS package (Holbrook et al. 2019) in R (R Core Team 2019), detections of tagged fish on receivers were filtered to remove the potential occurrence of false detections (i.e., detection of a transmitter code that is not actually present) in the recapture database (Simpfendorfer et al. 2015). Detections were filtered by deleting individual detections more than 60 minutes apart from another detection of the same unique and tag-specific code, which is 30 times the nominal delay of the transmitters used to tag Grass Carp and was a criterion recommended by Pincock (2012).

RKM receiver detection rates

Using the filtered detection data from the receivers, we constructed encounter histories $(y_{i,j,d})$ for each tagged fish (*i*=1, 2, …, *I*) that consisted of the number of hourly detections (*y*) at each RKM receiver (*j*=1, 2, …, 34) per day (*d*=1, 2, …, 822). As these were hourly detections, the number of detections on any receiver for an individual tagged Grass Carp ranged from 0 to 24. From these encounter histories, we calculated daily detection rate for tagged fish at each RKM receiver. Calculations of this detection rate accounted for the fact that not all tagged fish were at liberty in the Sandusky River for the same amount of time because of differences as to when fish were tagged or moved into the Sandusky River and the possibility that fish could leave the Sandusky River, die from various causes, or shed their tags in areas where transmissions could not be detected by receivers. Not accounting for these factors could lead to negatively biased detection rates because of excess zero detections. Tagged Grass Carp were considered to have emigrated from the Sandusky River if they were detected on the lowest RKM receiver and then were either never detected again or detected on another acoustic telemetry receiver, outside the Sandusky River, in Lake Erie (Harris et al. in press). The identification of tagged Grass Carp that possibly died or shed their tag in the Sandusky River was informed by fitting a state-space spatial capture-recapture (SCR) model to the encounter history data (described below). One of the estimated parameters from this SCR model is the "alive" state of each tagged individual for each modeled time period. The estimated "alive" state for each tagged Grass Carp was used in setting the time frame for calculating hourly detection rate at each RKM receiver for each fish. Specifically, let $L_{i,j}$ equal the length of time (i.e., days) that individual *i* was in the Sandusky River and estimated to be "alive" while the *j*-th receiver was deployed. The detection rate at each RKM receiver for each tagged fish was calculated as

$$\bar{y}_{i,j} = \frac{\sum_d y_{i,j,d}}{L_{i,j}}. \qquad (1)$$

We then calculated the mean detection rate at the RKM receivers by averaging across the tagged individuals

$$\bar{y}_j = \frac{\sum_i \bar{y}_{i,j}}{I}. \quad (2)$$

Mean detections rates were calculated overall and separately for the five discharge and water temperature categories described in the environmental covariates section.

Spatial capture-recapture analysis.

A state-space spatial capture-recapture (SCR) model patterned after the model described in Raabe et al. (2014) was fit to the encounter history data [i.e., number of hourly detections (y) at each RKM receiver for tagged Grass Carp]. The SCR model was based on a Cormack-Jolly-Seber formulation and consisted of an observational model for the observed encounter histories of tagged Grass Carp, a state model for the "alive" state of the fish on a given day, and a latent (hidden) variable for the daily activity centers of the tagged fish (Raabe et al. 2014). We primarily were interested in estimates of the activity centers of the tagged Grass Carp as these represented the central locations (i.e., home range centers) of Grass Carp space use (Muñoz et al. 2016), and we believed the activity centers could identify areas of aggregation in the Sandusky River to be targeted during control efforts. Although we primarily were interested in estimates of activity centers, the estimates of the "alive" state of fish were also beneficial for summarizing receiver detection rates and for estimates daily movements (see below).

The daily "alive" state $z_{i,d}$ of tagged Grass Carp was a Bernoulli distributed random variable that equaled 1 when a Grass Carp was estimated to be alive and in the study area and 0 when a Grass Carp was estimated to be dead or to have left the study area. We censored Grass Carp that permanently emigrated from the Sandusky River (as described above), as well as two individuals captured and killed during agency control actions, and one individual found to have shed its transmitter upon recapture. We did not censor Grass Carp that temporarily emigrated from the Sandusky River (i.e., Grass Carp that left the Sandusky River but later returned to the river). On the first day a Grass Carp was detected on a receiver, its alive state was set to 1 with a probability of 1 (Raabe et al. 2014). For all other days, the alive state was defined as $z_{i,d} \sim \text{Bernoulli}(\phi z_{i,d-1})$, where ϕ is the daily apparent survival probability.

Observed encounter histories of tagged Grass Carp were conditional on the alive state and assumed to be distributed as a Poisson random variable

$$y_{i,j,d}|z_{i,d} \sim \text{Poisson}\left(o_{j,d}\lambda_o \exp\left(-\left|s_{i,d} - x_j\right|^2/2\sigma_j^2\right)\right) \tag{3}$$

where $o_{j,d}$ is an indicator variable for whether the j-th receiver was deployed and operational on the d-th day, λ_0 is the baseline encounter rate at the receivers (i.e., the expected number of detections when an individual's activity center is located precisely at the location of a receiver), $s_{i,d}$ is the activity center location for the i-th individual on the d-th day, x_j is the RKM location of the j-th receiver, and σ_j is a receiver-specific scale parameter that determines the rate of decline in detection probability as a function of distance from the activity center to a receiver location. This model structure was selected over other possible structures [e.g., receiver-specific baseline encounter rates and constant sigma, observed encounter histories distributed as a binomial random variable as described in Dorazio and Price (2019)] based on deviance information criteria.

One of the deviations from the spatial capture-recapture model used in this study from the one described in Raabe et al. (2014) concerned the modeling of daily activity centers of tagged Grass Carp after the first day of location. In Raabe et al. (2014), activity centers after the first day of location were modeled through a random walk process where the activity center for day *d* was from a normal distribution truncated to the bounds of the study system with a mean equal to the activity center for day *d*-1 and an estimated standard deviation of τ. When we attempted this formulation for the Grass Carp encounter history data, we encountered instances where estimated activity centers would drift past several RKM receiver locations to areas where large gaps in receiver coverage occurred even though the next recorded detection on a RKM receiver was close to the last recorded detection. The occurrence of this drift could lead to biased estimates of activity centers, which could affect the identification of areas where Grass Carp aggregate and influence control effort effectiveness. We attempted to fix this drifting issue using several different approaches, including changing distributional assumption on the observed encounter histories conditional on the "alive" state of tagged fish (e.g., binomial, negative binomial, zeroinflated Poisson) and varying the truncation bounds depending on fish location. The most stable approach found was to model daily activity centers differently depending on whether Grass Carp were detected or not detected on a given day. If a Grass Carp was detected, the activity center for the day was modeled as described above. However, if a Grass Carp was not detected on a given day, that day's activity center was drawn from a normal distribution truncated to the bounds of the study system with a mean equal to the location of the last RKM receiver on which the fish was detected and an assumed standard deviation of 0.5. In other words, activity centers after the first day of detection were assumed to follow

$$s_{i,d} \sim \begin{cases} Normal\left(s_{i,d-1}, \tau\right)\mathrm{T}(x_L, x_U) & \text{if fish is detected on day } d \\ Normal(LL_i, 0.5)\mathrm{T}(x_L, x_U) & \text{if fish is not detected on day } d \end{cases} \tag{4}$$

where LL_i is the last recorded detection location of the i-th Grass Carp prior to it going missing, and x_L and x_U are the assumed lower and upper boundaries for the study area. A standard deviation greater than 0.5 for modeling activity centers when fish were not detected resulted in activity centers drifting past areas where receivers were deployed. Regardless of whether Grass Carp were detected or not, x_L and x_U were set equal to 5 and 55 RKM. Adjustment of x_U for time periods after removal of the Ballville Dam was not necessary as we never detected Grass Carp on receivers deployed upstream from the dams former location.

The spatial capture-recapture model was fit using Bayesian inference methodology in JAGS (Plummer 2015) executed from within R (R Core Team 2019) via the jagsUI package (Kellner 2019). The following vague prior probability distributions were specified for model parameters: $\phi \sim \mathrm{Unif.}(0,1)$, $\tau \sim \mathrm{Unif.}(0,50)$, $\sigma_j \sim \mathrm{Unif.}(0,100)$, and $\lambda_0 \sim \mathrm{Gamma}(0.05, 0.05)$. Three parallel MCMC chains, each consisting of 20,000 iterations, were run from random initialization values with an initial 1,000 iterations as an adaptive phase for the MCMC sampling algorithm. The first 10,000 iterations were discarded as burn-ins and every 10^{th} iteration was retained resulting in a total of 3,000 saved samples across the chains. Chain convergence for parameters was determined by examining trace plots and scale reduction factors constructed and calculated using the coda package (Plummer et al. 2006). For most parameters, means of the saved MCMC chains were used as point estimates for parameters and derived variables and 95% highest posterior density intervals (HPD) were used as measures of uncertainty for the point estimates. For the “alive” state of tagged fish, we used the medians of the saved MCMC chains.

Daily dispersal and movement

Daily dispersal of tagged Grass Carp in the Sandusky River was estimated as the distance between the furthest upstream RKM receiver detection and furthest downstream RKM receiver detection on a daily basis for each fish. Dispersal on a given day was assumed to be 0 km if a tagged individual was either only detected on a single receiver or not detected on any receiver on that day. Daily movements of tagged Grass Carp were estimated in R (R Core Team 2018) through interpolated paths from the filtered detection data estimated with the interpolate_path function from the GLATOS package (https://gitlab.oceantrack.org/GreatLakes/glatos). 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 km. When fish were undetected for a period of several days and subsequently detected on a different receiver from their prior location, daily movements were calculated as the distance between receiver locations divided by the number of days that elapsed between detections.

Differences in daily dispersal and movement among and between the five discharge and water temperature categories described in the environmental covariates section were tested through linear mixed models. The five discharge and water temperature categories were treated as a fixed effect in the linear mixed models. Individual fish identifiers were included in the linear mixed models as a random effect in part to account for multiple observations for each tagged fish as these observations were likely autocorrelated. The linear mixed models were fit in R (R Core Team 2019) using the lmer() function in the lme4 library (Bates et al. 2015). Overall differences in daily dispersal and movement among the discharge and water temperature categories were tested through an *F*-test with a Satterthwaite correction for the denominator degrees of freedom using the anova() function in the lmerTest library (Kuznetsova et al. 2017). Overall significant differences among the discharge and water temperature categories were followed up with pairwise tests between the categories using the contest1D() function in the lmerTest library (Kuznetsova et al. 2017). Pairwise tests were based on linear contrasts of the mean values of the category levels and also involved a Satterthwaite correction for degrees of freedom.

Results

Hourly detections of tagged Grass Carp at the RKM receivers indicated that individual Grass Carp were broadly distributed in the area of the Sandusky River where receivers were deployed (Figure 2.3). This included tagged Grass Carp detected on receivers in the area generally associated with spawning activity (≈ RKM 50) during times when spawning activity likely was not occurring (i.e., winter months). Receiver coverage in Muddy Creek and Sandusky Bays was sparse until the end of the study; however, detections on these receivers indicated that Grass Carp moved into these bays particularly during the summer months (Figure 2.3).

Daily detection rates

Daily detection rates varied among the RKM receivers overall and among the five temperature and discharge categories (Figure 2.4). Overall, the highest detection rates were at RKM receivers 36.3 and 45.1 followed by RKM receivers 33.8 and 17.9 (Figure 2.4A). When daily maximum discharge was ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C, the highest detection rates were at RKM receivers 25.8 and 48.5 followed by detection rates at RKM receivers 17.9 and 45.1 (Figure 2.4B). When daily mean water temperatures were between 4.5 °C and 18°C, the highest detection rates were at RKM receivers 45.1 and 33.8 regardless of discharge (Figure 2.4 C & D). When water temperature was greater than 18°C but discharge was < 31 m^3/s, the highest detection rate was at RKM receiver 45.1 with fairly equal detection rates at RKM receivers 17.9, 25.8, 33.8, and 36.3 (Figure 2.4E). When water temperature was < 4.5°C, detection rates were more evenly spread across RKM receivers ranging from 33.8 to 38.5 as well as RKM receivers 45.1 and 48.5 (Figure 2.4F).

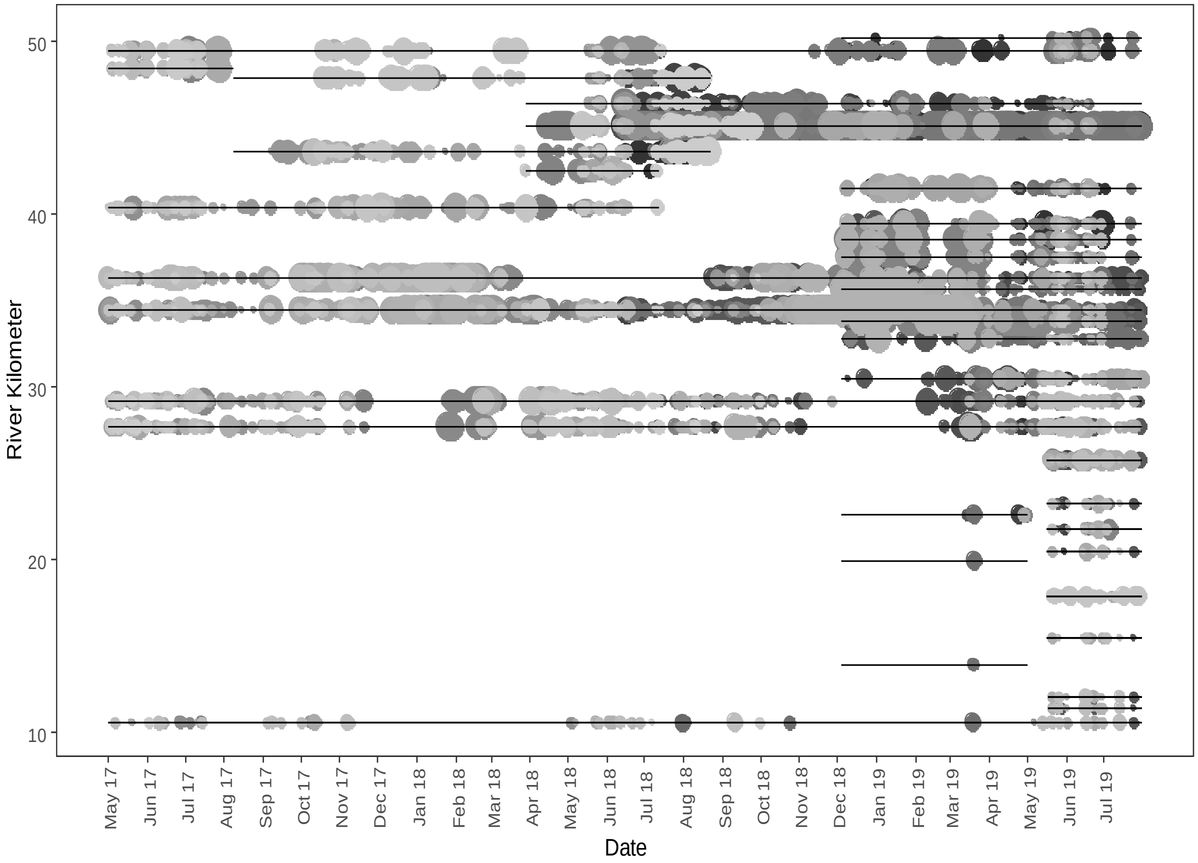

Figure 2.3. Hourly detection counts per day for each tagged Grass Carp at each RKM receiver in the Sandusky River from May 1, 2017 to July 31, 2019. The size of the symbol is indicative of the number of counts. The horizontal lines indicate period of operation for the deployed receivers, although several of the receivers are identified as non-operational because they could not be recovered at the end of the study. Different shades of gray differentiate tagged Grass Carp.

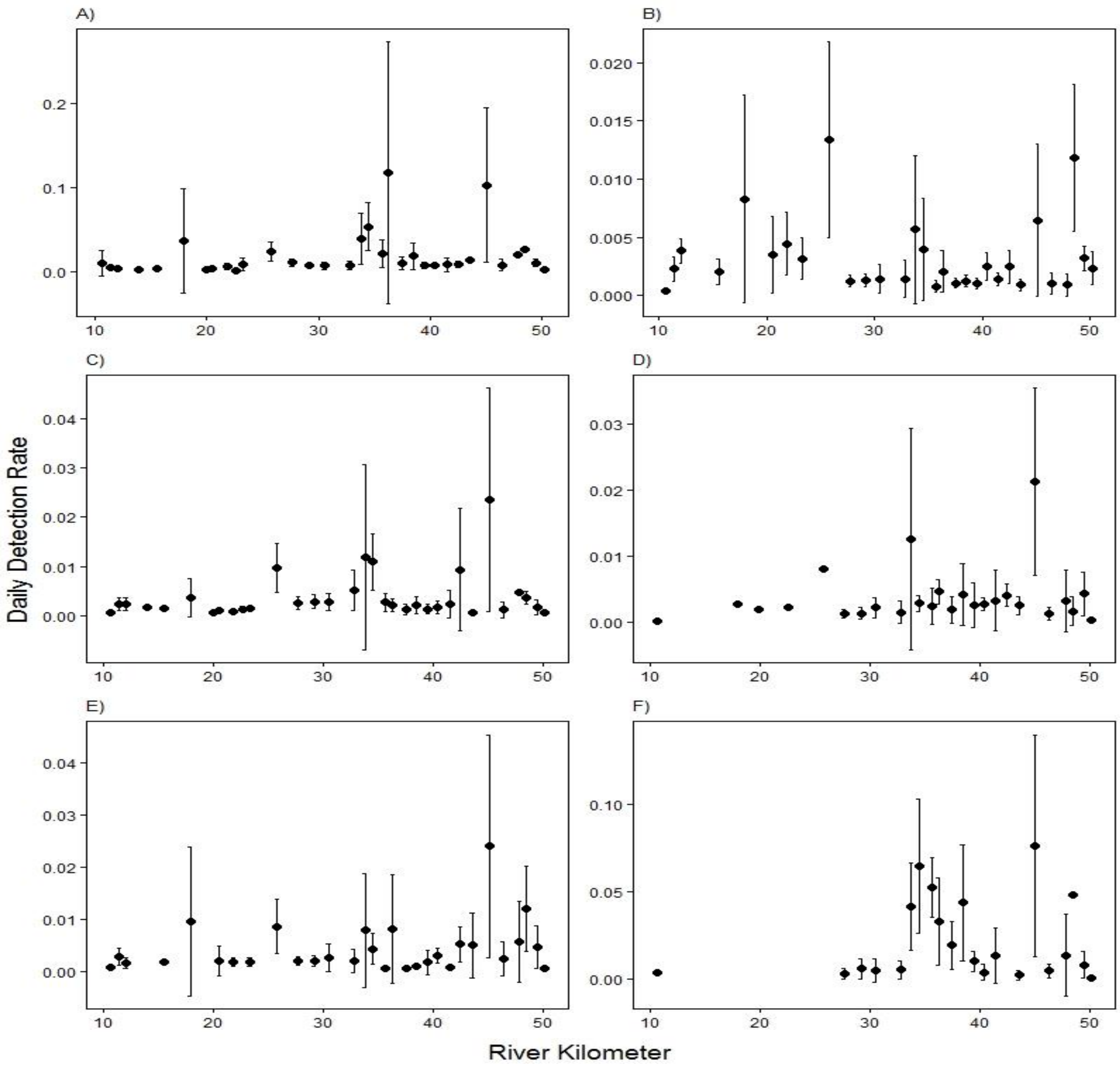

Figure 2.4. Mean daily detection rates and 95% confidence limits at each RKM receiver overall and for the 5 temperature and discharge categories described in the text (A = overall, B = daily maximum discharge ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C; C = daily maximum discharge ≥ 31 m^3/s and daily mean water temperature ≥ 4.5°C and < 18°C; D = daily maximum discharge < 31 m^3/s and daily mean water temperature ≥ 4.5°C and < 18°C; E = daily maximum discharge < 31 m^3/s and daily mean water temperatures ≥ 18°C; F = daily mean water temperature < 4.5°C).

Spatial capture-recapture analysis

The MCMC chains for all parameters of the spatial capture-recapture model converged on stationary and stable distributions based on examination of trace plots and the upper 95% confidence interval for the potential scale reduction factor for each parameter being less than 1.1. Means of the posterior distributions for λ_0 (i.e., receiver baseline encounter rate) and τ (i.e., standard deviation of the normal distribution for the daily activity centers) were 3.514 (95% highest posterior density credible interval: 3.478 – 3.54) and 3.135 (3.060 – 3.210), respectively (Table 2.1). The mean of the posterior distribution for ϕ (i.e., daily apparent survival probability) was 0.999 (0.998 – 1.000) (Table 2.1). Scaled to an entire year, this equates to annual apparent survival probability of approximately 66%, which is likely biased low compared to actual survival as the model is likely estimating some alive fish to be dead because they went undetected near the end of the study. Means of the posterior distributions for σ_j (i.e., receiver-specific scale parameters that determine the rate of decline in detection probability as a function of distance from the activity center to a receiver location) ranged from 0.393 (0.078 – 0.701) to 5.004 (0.078 – 0.701) (Table 2.1).

The average of the daily estimated activity centers for Grass Carp ranged from RKM 25.9 to 39.4 over the course of the study (Figure 2.5). There was a general tendency for the RKM location for average daily activity centers to increase from early/mid-summer to early/mid-winter and then decrease through to the early spring (Figure 2.5). Locations of average daily activity centers were much more variable during mid and late spring, likely due to spawning activity of tagged fish (Figure 2.5).

Table 2.1. Means of posterior probability distributions, 95% highest posterior density intervals, and effective sample size for the posterior means for the parameters of the spatial capture-recapture model fit to encounter histories of tagged Grass Carp in the Sandusky River. Results are not shown for daily activity centers or the daily "alive" status of each tagged fish.

Param.	Mean	95% HPD	Eff. Size	Param.	Mean	95% HPD	Eff. Size
l_0	3.514	3.478 – 3.549	2,691	σ_{16}	0.636	0.605 – 0.665	2,567
τ	3.135	3.060 – 3.210	1,883	σ_{17}	1.164	1.108 – 1.225	2,664
ϕ	0.999	0.998 – 1.000	3,000	σ_{18}	1.693	1.654 – 1.736	2,667
σ_1	5.004	4.873 – 5.127	3,000	σ_{19}	0.833	0.795 – 0.869	2,669
σ_2	4.453	4.189 – 4.726	3,000	σ_{20}	0.994	0.963 – 1.025	2,387
σ_3	3.936	3.664 – 4.198	3,000	σ_{21}	1.269	1.215 – 1.304	3,000
σ_4	0.984	0.921 – 1.053	3,000	σ_{22}	1.619	1.570 – 1.666	3,000
σ_5	2.444	2.306 – 2.590	3,000	σ_{23}	1.666	1.616 – 1.712	3,000
σ_6	3.037	2.876 – 3.205	3,000	σ_{24}	1.574	1.531 – 1.621	3,000
σ_7	0.393	0.078 – 0.701	3,319	σ_{25}	1.708	1.659 – 1.757	2,791
σ_8	2.344	2.196 – 2.512	3,163	σ_{26}	1.457	1.353 – 1.550	3,000
σ_9	1.970	1.861 – 2.079	3,231	σ_{27}	1.024	0.973 – 1.079	2,692
σ_{10}	1.535	1.452 – 1.621	3,000	σ_{28}	3.414	3.332 – 3.501	2,738
σ_{11}	1.627	1.538 – 1.723	3,390	σ_{29}	0.929	0.901 – 0.960	2,503
σ_{12}	2.069	1.951 – 2.186	2,800	σ_{30}	1.241	1.192 – 1.292	2,455
σ_{13}	2.206	2.153 – 2.257	2,675	σ_{31}	4.625	4.340 – 4.835	3,207
σ_{14}	1.222	1,195 – 1.252	2,157	σ_{32}	2.774	2.719 – 2.828	3,000
σ_{15}	1.119	1.086 – 1.154	3,000	σ_{33}	2.012	1.939 – 2.083	3,153

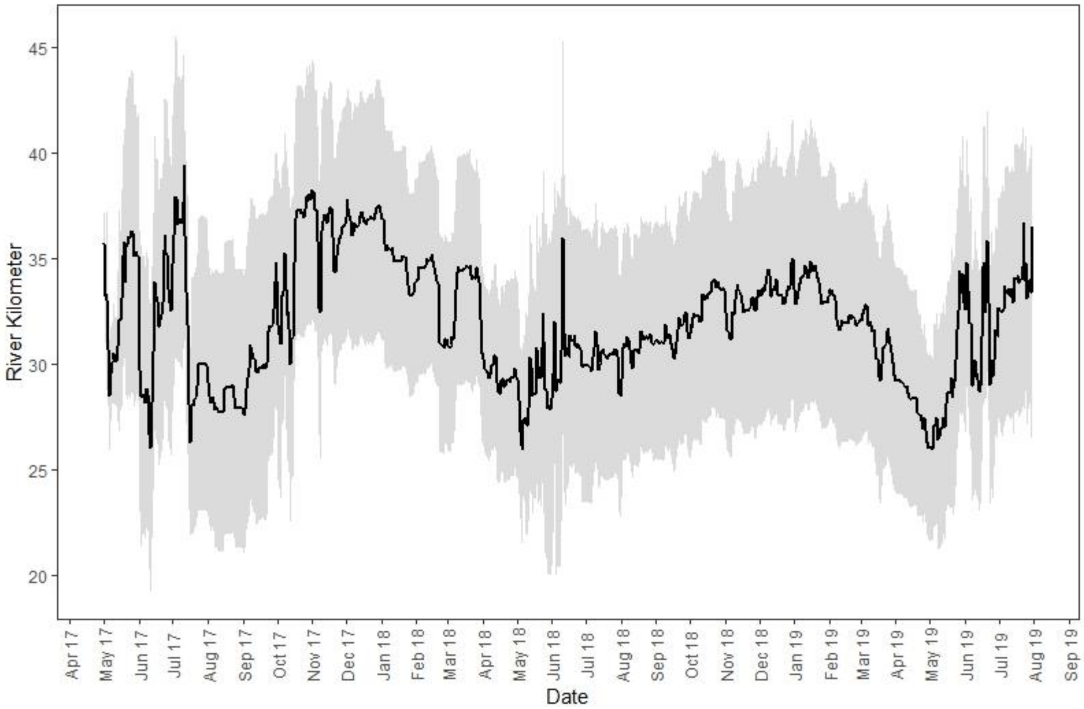

Figure 2.5. Daily mean RKM (black line) for all Grass Carp activity center posterior daily means along with the 95% CI (gray ribbon) for the Sandusky River from May 1, 2017 through July 31, 2019.

Overall, daily activity centers were concentrated near RKMs 10.6 and 27.7 (Figure 2.6A), with other peaks in activity center locations occurred at RKMs 34 to 37, 44.8, and 49.7. The concentration of daily activity centers at RKMs 10.6 and 27.7 partly reflect assumptions that were made in analyses and lack of receiver coverage in Muddy Creek and Sandusky Bays during the early part of the study. RKM 10.6 is the furthest downstream location of RKM receivers in the Sandusky River. Grass carp that left the Sandusky River and later returned were not censored from analyses. Therefore, daily activity centers for fish that left the Sandusky River and later returned to the river would have been estimated near this RKM location until they later returned to the river, resulting in this concentration of activity centers at that downstream location. Similarly, during the early part of the study when receiver coverage was sparse in Muddy Creek and Sandusky Bays, if a tagged Grass Carp moved downstream from the river into one of these bays, the estimated daily activity centers for those fish would have remained close to the RKM receiver located just upstream from the bays (RKM 27.7) until fish either moved back into the river or exited Sandusky Bay. This means the concentration of activity centers at RKMs 10.6 and 27.7 should actually be distributed more broadly across Muddy Creek Bay, Sandusky Bay, and Lake Erie itself, and we do not believe these are reflective of Grass Carp aggregation areas.

Activity centers varied among the five temperature and discharge categories. When daily maximum discharge was ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C, activity centers were concentrated near RKMs 34.3, 44.8, and 49.7 with the highest concentration at RKM 49.7 (Figure 2.6B). When daily maximum discharge was ≥ 31 m^3/s and daily mean water temperatures were between 4.5°C and 18°C, the highest concentrations of activity centers were still at RKMs 34.3, 44.8, and 49.7 although under these conditions the highest concentration was at RKM 34.3 (Figure 2.6C). When daily maximum discharge was ≤ 31 m^3/s and daily mean water temperatures were between 4.5°C and 18°C, activity center concentrations were highest near RKMs 36.6 and 44.8, with slightly lower concentrations near RKMs 34.3 and 49.7 (Figure 2.6D). When daily maximum discharge was ≤ 31 m^3/s and daily mean water temperatures ≥ 18°C, activity center concentrations were the highest near RKM 44.8 with slightly lower concentrations near RKM 34.3 (Figure 2.6E). When daily mean water temperatures were ≤ 4.5°C activity center concentrations were highest near RKMs 34.3 and 36.6, with slightly lower concentrations near RKMs 44.8 and 49.7 (Figure 2.6F).

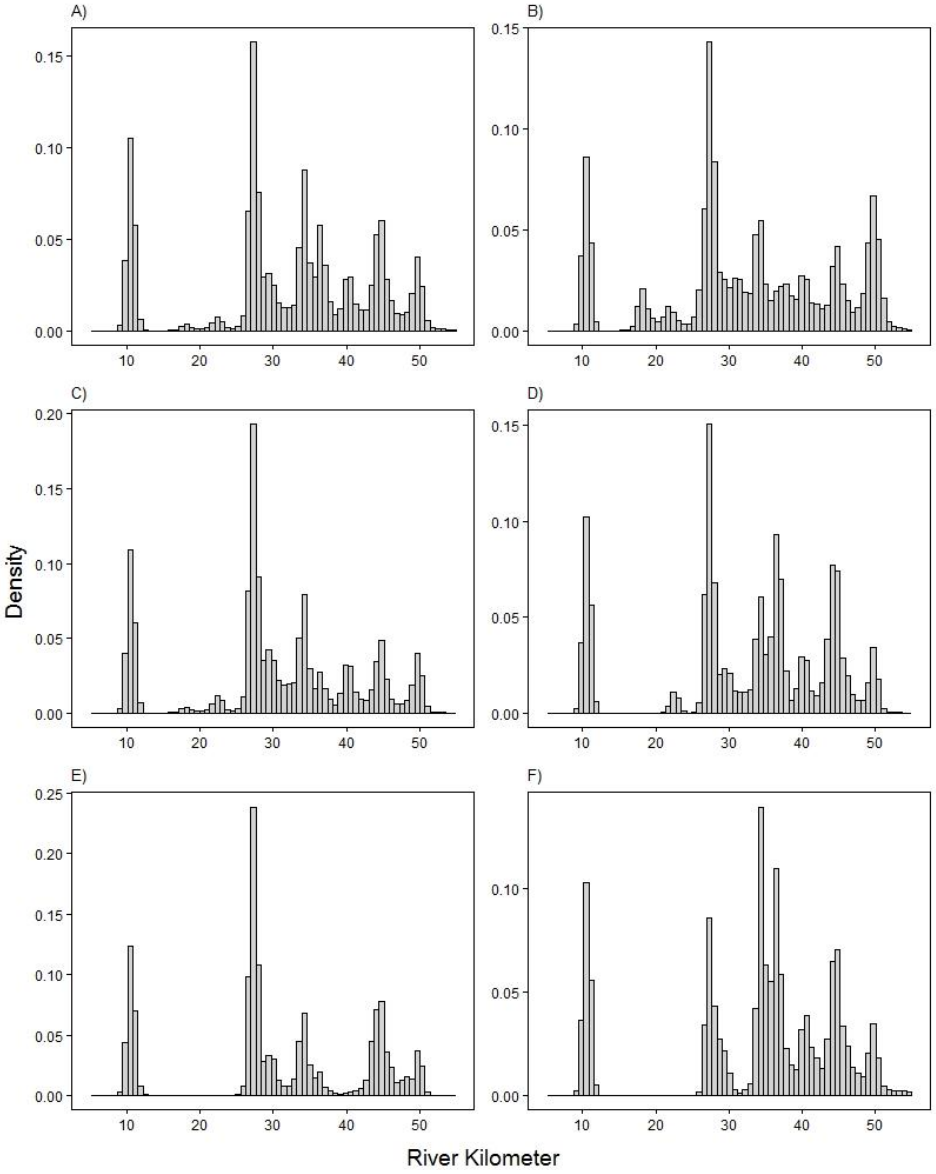

Figure 2.6. Activity center posterior frequencies at river kilometers throughout the study site overall and for the 5 temperature and discharge categories described in the text (A = overall, B = daily maximum discharge ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C; C = daily maximum discharge ≥ 31 m^3/s and daily mean water temperature ≥ 4.5°C and < 18°C; D = daily maximum discharge < 31 m^3/s and daily mean water temperature ≥ 4.5°C and < 18°C; E = daily maximum discharge < 31 m^3/s and daily mean water temperatures ≥ 18°C; F = daily mean water temperature < 4.5°C).

Daily dispersal and movement

Mean daily dispersal of tagged Grass Carp ranged from 0 to 2.2 km, with an overall mean daily dispersal of 0.69 km (SE = 0.11). Most tagged Grass Carp had an average daily dispersal of less than 1 km, although 22% of tagged Grass Carp had an average daily dispersal of more than 1 km. Daily dispersal significantly differed among the five temperature and discharge categories (Table 2.2). When discharge was ≥ 31m^3/s and temperature was ≥ 18°C, mean daily dispersal ($\bar{x}$ =1.65 km, SE = 0.18) was significantly greater than for the other categories. The second highest daily dispersal ($\bar{x}$ =0.53 km, SE = 0.044) was when discharge was ≥ 31m^3/s and temperature was between 4.5°C and 18°C; this daily dispersal was significantly greater than the daily dispersals for the other three temperature and discharge categories (Table 2.2). Daily dispersals between the remaining three temperature and discharge categories were not significantly different, with mean daily dispersals ranging from 0.21 km (SE = 0.02 km) (temperature < 4.5°C) to 0.29 km (SE=0.04 km) (discharge ≤ 31m^3/s and temperature ≥ 18°) (Table 2.2).

Table 2.2. ANOVA and pairwise comparison results for the daily dispersals of Grass Carp under five environmental covariate categories: 1) daily maximum discharge ≥ 31 m^3/s & daily mean water temperatures ≥ 18°C; 2) daily maximum discharge ≥ 31 m^3/s & daily mean water temperature ≥ 4.5°C and < 18°C; 3) daily maximum discharge < 31 m^3/s & daily mean water temperatures ≥ 18°C; 4) daily maximum discharge < 31 m^3/s & daily mean water temperature ≥ 4.5°C and < 18°C; 5) daily mean water temperature < 4.5°C.

Test	Test statistic value	Degrees of freedom	P-value
Overall difference among categories	131.51	4, 14,204	< 0.0001
Category 1 vs. 2	-18.15	14,203	< 0.0001
Category 1 vs. 3	-19.27	14,143	< 0.0001
Category 1 vs. 4	-17.07	14,165	< 0.0001
Category 1 vs. 5	-21.41	14,091	< 0.0001
Category 2 vs. 3	4.36	14,226	< 0.0001
Category 2 vs. 4	3.86	14,227	0.0001
Category 2 vs. 5	6.03	14,227	< 0.0001
Category 3 vs. 4	0.35	14,214	0.7294
Category 3 vs. 5	0.88	14,198	0.3809
Category 4 vs. 5	0.35	14,216	0.7273

Mean daily movement of tagged Grass Carp ranged from 0.05 to 2.91 km, with an overall mean daily movement of 0.86 km (SE = 0.12). Most tagged Grass Carp moved less than 1 km/day on average but 26% of fish moved more than 1 km day/day on average. Similar to daily dispersal, mean daily movement was significantly different among the five temperature and discharge categories (Table 2.3). When discharge was ≥ 31m3/s and temperature was ≥ 18°C, mean daily movement ($\bar{x}$=1.94 km/day, SE = 0.18) was significantly greater than for the other categories. The second highest mean daily movement ($\bar{x}$=0.71 km/day, SE = 0.049) occurred when discharge was ≥ 31m3/s and temperature was between 4.5°C and 18°C; this mean daily movement was significantly greater than the mean daily movement for the other three temperature and discharge categories (Table 2.3). Mean daily movements between the remaining three temperature and discharge categories was not significantly different, with mean daily movement averages ranging from 0.34 km (SE = 0.02) (temperature < 4.5°C) to 0.41 km (SE=0.04) (discharge < 31m^3/s and temperature ≥ 18°) (Table 2.3).

Table 2.3. ANOVA and pairwise comparison results for the mean daily movement of Grass Carp under five environmental covariate categories: 1) daily maximum discharge ≥ 31 m^3/s & daily mean water temperatures ≥ 18°C; 2) daily maximum discharge ≥ 31 m^3/s & daily mean water temperature ≥ 4.5°C and < 18°C; 3) daily maximum discharge < 31 m^3/s & daily mean water temperatures ≥ 18°C; 4) daily maximum discharge < 31 m^3/s & daily mean water temperature ≥ 4.5°C and < 18°C; 5) daily mean water temperature < 4.5°C.

Test	Test statistic value	Degrees of freedom	P-value
Overall difference among categories	147.91	4, 13,957	< 0.0001
Category 1 vs. 2	-17.85	13,948	< 0.0001
Category 1 vs. 3	-20.55	13,892	< 0.0001
Category 1 vs. 4	-19.34	13,923	< 0.0001
Category 1 vs. 5	-22.39	13,887	< 0.0001
Category 2 vs. 3	6.08	13,985	< 0.0001
Category 2 vs. 4	6.29	13,973	0.0001
Category 2 vs. 5	7.74	13,985	< 0.0001
Category 3 vs. 4	1.22	13,977	0.2234
Category 3 vs. 5	0.78	13,971	0.4334
Category 4 vs. 5	-0.63	13,985	0.5263

Discussion

Through this study, we were able to provide insight into Grass Carp space use and movement in the Sandusky River that can assist with control efforts to reduce population densities in Lake Erie and lessen the risk of spread and establishment to the other Great Lakes. Both RKM receiver detection rates and distributions of Grass Carp activity centers point to areas of aggregation in the Sandusky River that appear to shift with changing discharge and water temperature; these different areas of aggregation can be selectively targeted depending on environmental conditions during future control efforts. Grass Carp movement behavior appeared variable with individuals tending to be the most mobile during higher discharges and warmer water temperatures. Because certain types of capture gear are more effective when fish are actively moving, this movement information can be used to design collection protocols that could lead to greater reductions in Grass Carp densities in Lake Erie.

Using data collected through 31 December 2017, Harris et al. (in press) identified an area approximately 8 RKM upstream of Muddy Creek Bay (i.e., between RKMs 27 and 35) as an area where Grass Carp were frequently detected. Through this study, which included a higher number of tagged Grass Carp and more intensive coverage of receivers in Sandusky River, we pinpointed areas between RKMs 34 and 36 and RKM 45 as possible aggregation areas based on daily RKM receiver detection rates and concentrations of estimated daily activity centers; we recommend that future control efforts target these areas. An additional aggregation area of Grass Carp when discharge was $\geq 31m^3/s$ and water temperature was ≥ 18°C was around RKM 49, which was also the environmental conditions when Grass Carp moved the most. This location is slightly downstream from the likely spawning location of Grass Carp in the Sandusky River, which is around RKM 51 (Embke et al. 2019). Receiver detection rates under conditions typically associated with spawning (i.e., high discharge and high temperature) also were high at a receiver located near RKMs 17.9 and 25.8, which perhaps could be associated with some staging behavior that Grass Carp exhibit prior to spawning.

Despite Grass Carp having been first introduced to waterbodies in North America in the 1960s and being widely stocked for aquatic vegetation biocontrol throughout the 1970s, little published information exists about Grass Carp space use and movements in rivers. According to Shireman and Smith (1983), Grass Carp spawning in upstream areas of rivers associated with rapids, islands, sandbars, or tributary junctions. After spawning, Grass Carp were thought to move into floodplains, lakes, and backwaters to feed on aquatic and flooded terrestrial vegetation (Shireman and Smith 1983). Given these descriptions, we anticipated at the onset of this study that Grass Carp would be mostly located in the Sandusky River between mid-spring and early summer, and then either move into Muddy Creek or Sandusky Bays or Lake Erie during the remainder of year. Contrary to this expectation, however, and first reported by Harris et al. (in press), we found Grass Carp remaining in the Sandusky River throughout the year and moving widely throughout the river. We also observed a variety of behaviors, as fish were detected in Muddy Creek Bay and Sandusky Bay even during late spring and early summer when spawning normally occurs.

The daily movements and dispersals that we observed in this study were generally greater than what has been reported for Grass Carp in other students. We observed mean daily movements ranging from 0.05 to 2.91 km and daily dispersals ranging from 0.21 km to 1.65 km. The mean daily movement found in this study (0.86 km) was slightly higher than the mean daily movement of 0.76 km reported by Harris et al. (in press) for all of Lake Erie, but results were still fairly consistent between the two studies. Both movement rates are higher than what has been reported from telemetry studies conducted on stocked Grass Carp in reservoirs and other impoundments. Reported daily movements ranged from 0.03 to 0.66 km from Grass Carp studies conducted in Lake Texana, Texas (Chilton and Poarch 1997) and Lake Seminole, Georgia (Maceina 1999). Whether Grass Carp movement in rivers is typically greater than in reservoirs and impoundments is not currently known but could be evaluated through additional Grass Carp telemetry studies in both lentic and lotic systems.

Our finding that Grass Carp movement and dispersal in the Sandusky River was greatest at discharge exceeding 31 m^3/s matches results from previous Grass Carp studies. Using occupancy modeling, Sullivan et al. (2019) determined that probability of Grass Carp local colonization in Iowa tributaries to the Upper Mississippi River was most positively influenced by high discharge. Sullivan et al. (2019) attributed the higher movements due to the occurrence of spawning events or movement into inundated floodplain habitat for feeding purposes. Movement also could be linked to fish seeking habitats that provide some refuge to faster water velocities (Brenden et al. 2006). Regardless of the underlying reason for greater movement, knowledge as to the factors that lead to greater mobility can inform protocols for control efforts. Fish capture methods are generally categorized as passive or active techniques (Zale et al. 2013). Passive capture techniques, which include setting gillnets, trap nets, or trammel nets, are stationary gear that requires fish to swim into the gear to be captured (Hubert et al. 2013). Active capture techniques, which involve actively moving gear through the water such as electrofishing or trawling, generally are meant to target fish that are stationary or not swimming faster than the gear is moved through the water (Hayes et al. 2013). Given that Grass Carp movement and dispersal in the Sandusky River was the highest when discharge exceeded 31 m^3/s, we recommend control efforts consider deploying passive capture gear when discharge exceeds this threshold as Grass Carp encounters with deployed gear ostensibly will be higher and lead to higher captures. If high discharge prevents passive gear deployment directly in the main channel of the Sandusky River, capture gear could be deployed in backwater areas behind obstructions or islands.

When discharge is less than < 31 m^3/s and Grass Carp are less mobile, control efforts should perhaps focus on active capture methods or pairing active and passive capture methods to target Grass Carp. Paired active (i.e., electrofishing) and passive (i.e., trammel nets) capture techniques, which has involved using the active method to drive fish and force them to encounter the passive gear, has been used to successfully capture Grass Carp in other systems (Sullivan et al. 2019) and similar methods have been used by Department of Fisheries and Oceans Canada in an effort to remove Grass Carp from Lake Erie (B. Cudmore, Department of Fisheries and Oceans Canada, *unpublished data*) and its effectiveness is currently being evaluated against other sampling methods in other parts of Lake Erie (K. Robinson, Michigan State University, *personal communication*).

Although the result from this research were collected from fewer than 30 tagged individuals, we nevertheless believe our study results will prove valuable for informing Grass Carp control efforts on the Sandusky River. Using detection information from a few tagged individuals to identify locations of untagged fish for control purposes is referred to as the Judas technique and has been identified as a beneficial tool for efforts to control invasive species (Lennox et al. 2016; Crossin et al. 2017). Aquatic species for which the Judas technique has proven successful in helping to inform control efforts include Common Carp (*Cyprinus carpio*; Bajer et al. 2011; Taylor et al. 2012), Northern Snakehead (C*hanna argus*; Lapointe et al. 2010), Silver Carp (Coulter et al. 2016), and Lake Trout (*Salvelinus namaycush*; Dux et al. 2011). The premise of the Judas technique is that tagging and releasing fish back into the system will provide the information needed to increase capture rates in the future so as to justify releasing the individuals in the wild rather than simply killing them in the first place.

Information provided through this study could be used to inform future risk assessments for Grass Carp along with informing potential space use if other Asian carp were to be present in the Great Lakes.

Behavior and movement were two knowledge gaps identified in the most recent risk assessment for the Great Lakes (Cudmore et al. 2017) and the information in this study adds to the insights found by Harris et al. (in press) to reducing that knowledge gap. Grass Carp information about spawning preferences has been used as a surrogate for understanding other Asian carp, such as Bighead Carp (Kočovský et al. 2012), and our findings of aggregation areas and movement rates could be applied to these species in context of their spawning season.

Although the information presented in this study provides more refined information as to Grass Carp space use and movement in the Sandusky River, additional monitoring in the river with the more intensive receiver configuration used in 2019 would be useful. In particular, a longer time series of detection histories than in this study could allow the spatial capture-recapture model to include environmental covariates that could be used to predict activity centers of fish in the system (Royle et al. 2014). Further, control efforts in the Sandusky River and elsewhere in Lake Erie could be informed by obtaining fine-scale space use information on Grass Carp through the use of an acoustic telemetry positioning system (Espinoza et al. 2011; Binder et al. 2016), particularly in areas of greatest aggregation (i.e., RKMs 34 to 36 and RKM 45). The deployment of an acoustic telemetry positioning system in select areas of the river could also provide direct information concerning Grass Carp catchability to different survey gear, which would be beneficial for estimating Grass Carp densities in different areas of Lake Erie, which are key uncertainties influencing expected benefits from different types of control efforts (Robinson et al. in press).

MANAGEMENT RECOMMENDATIONS

Understanding Grass Carp spatial use and movement can provide fisheries managers with insights into behaviors outside of just point of capture information. Since 2018, Grass Carp captures by fishery management agencies have increased and biologists are using summaries of detections from passive receivers, detections from real-time receivers, and active tracking to inform response effort locations (L. Nathan, Michigan Department of Natural Resources, *personal communication*). Use of the Sandusky River was twice as high as the next most used tributary. Although Plum Creek was not as heavily used as the Sandusky River, tagged Grass Carp were observed making repeated visits to this area, which could serve as a focal point for control efforts as well. Other tributaries that are candidates for control efforts are the Maumee and Detroit rivers. Grass Carp generally spent more time in the Detroit River than the Maumee River, however, the Maumee River has had confirmed spawning activity (P. Kočovský, U.S. Geological Survey Great Lakes Science Center, *personal communication*) which may elevate it as a focal point for fisheries managers.

Further refinement of the spatial use and movement in the Sandusky River will aid fisheries managers focusing efforts in the highest used tributary. Control efforts targeting Grass Carp should be focused on the areas between RKMs 34 and 36 and RKM 45, as they are potential aggregation areas in the Sandusky River based on daily RKM receiver detection rates and concentrations of estimated daily activity centers. When discharge is $\geq 31 m^3/s$ and water temperature is $\geq 18°C$, control efforts should focus around RKM 49, which we identify as a potential aggregation area under these conditions. Given that Grass Carp movement and dispersal in the Sandusky River was the highest when discharge exceeded $31\ m^3/s$, we recommend control efforts consider deploying passive capture gear when discharge exceeds this threshold as Grass Carp encounters with deployed gear ostensibly will be higher and lead to higher captures. If high discharge prevents passive gear deployment directly in the main channel of the Sandusky River, capture gear could be deployed in backwater areas behind obstructions or islands. When discharge is less than $< 31\ m^3/s$ and Grass Carp are less mobile, control efforts should focus on active capture methods or pair active and passive capture methods to target Grass Carp.

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