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

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Abstract.— Grass Carp *Ctenopharyngodon idella* is an invasive species to the Laurentian Great Lakes first detected in the 1980s. The western basin of Lake Erie is the putative invasion front for the Great Lakes, with spawning known to occur in two of the basin's tributaries (Sandusky and Maumee Rivers). Targeted removal is being used to reduce Grass Carp abundance with an ultimate aim of eradication in part to prevent spread and establishment in the other Great Lakes; response efforts are being concentrated in the Sandusky River due to its heavy use by Grass Carp and being the tributary where spawning occurs consistently. The goal of this research was to identify areas in the Sandusky River where Grass Carp aggregate and identify variables that influence movement to improve efficiency of response efforts. Movement and space use of twenty-seven Grass Carp were monitored using acoustic telemetry. Detection data were used to estimate movement and daily detection rates, and also used in a spatial capture-recapture model to estimate activity centers of tagged fish. Grass Carp movement was highest when daily discharge and water temperature exceeded 31 m^3/s and 18°C, respectively, and next highest when discharge exceeded 31 m^3/s and temperature was between 4.5 and 18°C. Daily detection rates at receivers and concentrations of activity centers suggested that aggregations occurred between river kilometers (RKMs) 34 and 36 and at RKM 45. During spawning conditions, Grass Carp also aggregated near RKM 48.6, which is proximal to suspected spawning locations. We recommend concentrating response efforts in these general locations and using passive capture gear when Grass Carp are the most mobile. Response efforts could be further refined by using a variety of acoustic telemetry monitoring techniques, including fine-scale positioning, real-time receivers, and mobile tracking to provide precise location and timing for removal actions.

Introduction

In the Laurentian Great Lakes of North America, a major issue being confronted by fishery managers is limiting the spread and damaging 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 multiple factors (e.g., importance to global shipping, prevalence of past invasions; Mills et al. 1993; Ricciardi 2001, 2006). Presently, considerable focus in the Great Lakes region is concentrated on preventing invasion by Silver Carp *Hypophthalmichthys molitrix*, Bighead Carp *Hypophthalmichthys nobilis*, and Black Carp *Mylopharyngodon piceus*. Colloquially, these species are referred to as Asian carp or major Chinese carps, which are nomenclatures that also frequently include Grass Carp *Ctenopharyngodon idella*. Unlike Silver, Bighead, and Black Carp, Grass Carp invaded the Great Lakes several decades ago. Management efforts in the region are focused on eradicating Grass Carp to prevent spread, establishment, and negative consequences to aquatic and terrestrial communities (Herbst et al. in press).

Although Grass Carp have been captured from all the Great Lakes except Lake Superior (USGS 2019a), 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 2019a). From the 1980s to 2000s, Grass Carp captures were sporadic and presumed to be triploid (i.e., sterile) individuals that were stocked in small waterbodies for aquatic vegetation control but had escaped to 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 (i.e., fertile) juvenile Grass Carp were caught in the Sandusky River, a tributary to the western basin of Lake Erie. Through otolith microchemistry analysis, it was determined that these fish were naturally produced in the river (Chapman et al. 2013). In 2015, fertilized Grass Carp eggs were collected in the Sandusky River; the most probable spawning location for these eggs was identified as being between the Ballville Dam and the town of Fremont, Ohio (Embke et al. 2016, 2019; Kočovský et al. in press). Fertilized Grass Carp eggs have subsequently been collected in the Sandusky River during years with high discharge events; eggs and a larval Grass Carp were also recently collected from the Maumee River, another tributary to the western basin of Lake Erie (USGS 2019b). Ploidy analysis of 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). Grass Carp captured over a broader temporal (2012-2018) and spatial (entire Lake Erie basin) scale indicated a lower percentage of diploid Grass Carp (64%), though many of the collected diploid fish were likely produced in the Maumee or Sandusky rivers (Whitledge et al. in press)

The combination of elevated catch reports, confirmation of Grass Carp spawning in at least two western basin tributaries, and the prevalence of reproductively viable individuals heightened concerns among fishery management agencies about potential negative effects stemming from increasing population densities in Lake Erie and risk of spread and establishment to the other Great Lakes. This prompted state, provincial, and federal fishery agencies in the basin to develop an adaptive response strategy for eradication of Grass Carp from Lake Erie (Herbst et al. in press). The response strategy was informed using a multi-jurisdiction, collaborative decision analysis with regional experts to determine objectives and potential management actions for Lake Erie response efforts (Robinson et al. in press). The decision analysis process included the development of a quantitative population model that was used to establish an annual removal target of 390 diploid Grass Carp; this target was associated with a population density that was expected to minimize the risk of spread and negative effects on the aquatic and terrestrial communities (DuFour et al. in press). Based on expert elicitation, the most effective and feasible response 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 action by Robinson et al. (in press), enactment of this recommendation is challenged by Grass Carp being notoriously difficult to catch with traditional capture gear and methods (Mitchell 1980; Maceina et al. 1999). In late summer 2014, 10 state, provincial, and federal fishery agencies conducted a coordinated capture response exercise if Silver, Bighead, or Black Carp was detected in Lake Erie. Agencies also targeted Grass Carp during the exercise to accomplish a secondary objective to reduce population abundance. Removal efforts were informed by positive eDNA detections of Grass Carp in Lake Erie over the previous few weeks and consisted of boat electrofishing (219 electrofishing runs = 96 hours of electrofishing time) and gillnetting (53 gillnet lifts = 58.8 hours of soak time). Despite this large amount of effort, only two Grass Carp were captured during the exercise; both fish were caught in Michigan waters near Plum Creek, a small tributary located near the Raisin River (Figure 1; Herbst et al. in press).

For targeted removal to be an effective response method, knowledge of areas where Grass Carp aggregate and how these aggregation areas change temporally is needed. 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, the Sandusky River was the most used system with telemetered fish remaining in the river throughout the year. Grass Carp response strategies for Lake Erie developed by the Ohio Department of Natural Resources (Ohio Department of Natural Resources Division of Wildlife 2019) and the Lake Erie Committee (Lake Erie Committee and Great Lakes Fishery Commission 2018) have each identified the Sandusky River as an area for targeted response efforts due to its high use by Grass Carp and because it is believed to be the tributary where most spawning occurs and likely the largest source of Grass Carp recruitment to Lake Erie (Whitledge et al. in press). Prior to 2018, the Sandusky River was accessible to Grass Carp for approximately 55 km from its outlet into Lake Erie to the Ballville Dam, the first upstream barrier to movement. In July 2018, Ballville Dam was demolished, which increased the accessible river length to 90 km. Consequently, even though the 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 would benefit response efforts.

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 response 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 accessible portion of the river. 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 1). Prior to 2018, the Ballville Dam was located approximately 55 km from Lake Erie and was the upstream barrier from Lake Erie on the Sandusky River. The dam measured roughly 10.5 m in height and 128 m in width and blocked 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, and complete removal of the dam occurred in July 2018. The lower portion of the Sandusky River, downstream from where the Ballville Dam was located, ranges in width from 32 to 160 m with routine water depths of 5 to 6 m even during low flow conditions (Embke et al. 2016, 2019). The furthest downstream USGS gage station in the Sandusky River is located near Fremont, OH (USGS 04198000; Figure 2); the discharge of the Sandusky River measured at this gage between 2000 and 2019 had a median of 38 m^3/sec (USGS 2019c). Muddy Creek and Sandusky Bays 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.

Data collection.

This study evaluated acoustic tag detection data from Grass Carp (*n*=70) captured from Michigan and Ohio waters of Lake Erie between 2014 and 2019 by either commercial fishing operations or state/federal agency removal efforts and subsequently implanted with acoustic telemetry transmitters (Model V16H, Vemco, Halifax, Nova Scotia; hereafter transmitters). Details of Grass Carp collection and the procedures used to implant transmitters are described in detail in Harris et al. (in press) but 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 three seconds, similar to the process described by Vandergoot et al. (2011). While immobilized, transmitters were inserted into the coelom through a ventral incision that was closed with two to three 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) resulting in an estimated transmitter lifespan of approximately 6.7 years. The external portion of the first two dorsal rays were removed for age estimation by clipping the rays as close to the body as possible with a pair of wire cutters; each fish was externally marked below the anterior portion of the intact 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 regained equilibrium.

For this study, only detections between 1 May 2017 and 31 July 2019 were used in analyses because this was the time period when receiver coverage in the Sandusky River was most comprehensive. 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 as part of the Great Lakes Acoustic Telemetry Observation System (GLATOS) network (Krueger et al. 2019). In some instances, tagged Grass Carp were detected beyond 60 days post-tagging; however, subsequent examination of detection histories suggested these detections were likely from a dead fish or a shed tag, which would bias results. Four individuals experienced with telemetry detection data examined detection histories of all tagged fish that occurred in the Sandusky River, and voted whether certain detections were likely from live 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. Most (22) of these fish were captured, tagged, and released in the Sandusky River and five were captured, tagged, and released elsewhere in Lake Erie (Catawba Island: 2 fish; Maumee River: 1 fish; River Raisin: 2 fish) (Figure 1) but were later detected on receivers in the Sandusky River. Estimated age of Grass Carp using dorsal fin rays ranged from 4 to 12 years ($\bar{x}$ = 6 years), although the accuracy of these age estimates is unknown given that we are not aware of age validation studies being conducted for this hard structure. Total lengths and body mass of tagged Grass Carp ranged from 78.2 to 106.7 cm ($\bar{x}$ = 91.7 cm) and 5.3 to 16.3 kg ($\bar{x}$ = 9.6 kg), respectively. Blood samples were used to determine ploidy of tagged fish using methods described in Krynak et al. (2015). Of the 27 telemetered 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 laboratory results, blood samples being coagulated prior to testing, or blood samples not being collected.

Grass Carp detections were recorded with acoustic telemetry receivers (hereafter receivers) deployed throughout the Sandusky River as part of the GLATOS network. Three 69 kHz receiver models (VR2W, VR2TX, and VR2C; Vemco, Halifax, Nova Scotia) were used to monitor movements. Although site-specific acoustic detection range evaluations (Melnychuk 2012) were not conducted, ancillary experiments conducted to determine detection ranges of transmitters estimated a 500-m detection probability of at least 50% in the Sandusky River (C. Vandergoot, Michigan State University, *unpublished data*). Receivers recorded date, time, and unique transmitter ID code of telemetered Grass Carp. In 2017, a total of 12 receiver stations were installed in the Sandusky River. As additional receivers became available, receiver stations were added 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). Receivers extended approximately 40 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 river was too large to cover with a single receiver. In such cases, multiple receivers were deployed in-line across the width of the system to increase the probably of detecting a telemetered fish. Even though multiple receivers were deployed, detections on any of these in-line receivers were treated as a single detection at that RKM, 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 receivers were not recovered due to complications that prevented retrieval (e.g., excessive woody material obstructing retrieval). Situations where receiver retrieval was prevented occurred infrequently and although they resulted in some gaps of coverage were not deemed to be detrimental to analyses because they occurred later in the study when receiver coverage was most dense.

Environmental covariates

Based on prior research (Stanley et al. 1978; Bain et al. 1990), Grass Carp space use and movement were hypothesized to be affected by river discharge and water temperature, which also could influence the effectiveness of response efforts in the Sandusky River. 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 upstream of the former Ballville Dam, near Fremont, Ohio (Figure 2). 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 about Grass Carp spawning in the Sandusky River and published and unpublished sources 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, response efforts targeting Grass Carp do not typically occur in the Sandusky River from December to February. The average water temperature in 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 response 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 based on the combination of spawning thresholds and sampling effectiveness: 1) daily maximum discharge ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C (high discharge and high temperature); 2) daily maximum discharge ≥ 31 m^3/s and daily mean water temperature between 4.5°C and 18°C (high discharge and low temperature) 3) daily maximum discharge < 31 m^3/s and daily mean water temperatures ≥ 18°C (low discharge and high temperature); 4) daily maximum discharge < 31 m^3/s and daily mean water temperature between 4.5°C and 18°C (low discharge and low temperature); 5) daily mean water temperature < 4.5°C (winter). During this study (822 days), the five categories occurred on a total of 97, 133, 109, 282, and 201 days respectively.

Detection data filtering

Using the GLATOS package (Holbrook et al. 2019) in R (R Core Team 2019), Grass Carp detections were filtered to remove the potential occurrence of false detections (i.e., detection of a transmitter code 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, a criterion recommended by Pincock (2012).

RKM receiver detection rates

Using the filtered receiver detection data, we constructed encounter histories $(y_{i,j,d})$ for each tagged fish (i=1, 2, …, 27) 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 histories were based on 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 rates for individual fish at each RKM receiver. This detection rate accounted for the fact that not all telemetered 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 transmitters in unmonitored areas between receivers. Not accounting for these potential tag fates could lead to negatively biased detection rates because of excess zero detections. 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 (Harris et al. in press). The identification of tagged Grass Carp that possibly died or shed their tags 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 (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

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

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 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 (unobserved) variable for the daily activity centers of the tagged fish (Raabe et al. 2014). We were primarily 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); we believed the activity centers would identify areas of aggregation in the Sandusky River that could be targeted with response 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 estimating daily movement (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 (identified the last day of availability to be detected) Grass Carp that permanently emigrated from the Sandusky River (as described above), as well as two individuals captured and killed during agency response efforts 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 during the study period). 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 $z_{i,d} \sim$ 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

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

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 possibilities (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 exploratory model comparison using deviance information criteria.

The spatial capture-recapture model used in this study deviated from that described in Raabe et al. (2014) in how daily activity centers were modeled after the first day of detection. In Raabe et al. (2014), activity centers after the first day of detection were modeled with 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 in our model, 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 aggregated and influence response effort effectiveness. We attempted to fix this drifting issue using several different approaches, including changing the distributional assumption on the observed encounter histories conditional on the "alive" state of tagged fish (e.g., binomial, negative binomial, zero-inflated 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

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

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 the two receivers deployed upstream of where the dam was located.

The spatial capture-recapture model was fit using Bayesian inference methodology in JAGS (Plummer 2015) executed from within R via the jagsUI package (Kellner 2019). The following vague prior probability distributions were specified for model parameters: $\phi \sim$ Unif.$(0,1)$, $\tau \sim$ Unif.$(0,50)$, $\sigma_j \sim$ 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.

Movement

Daily ranges of movement for tagged Grass Carp in the Sandusky River were estimated as the distance between the furthest upstream RKM receiver detection and furthest downstream RKM receiver detection on a daily basis for each fish. Range of movement 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 total movements of tagged Grass Carp were estimated in R by interpolating paths from the filtered detection data using the interpolate_path function from the GLATOS package (Holbrook et al. 2019). For most fish, movement paths were interpolated using one-day increments. For a few fish, movement paths were interpolated using 1/6 day increments because of the extent of their movements in the river so that distance calculations respected the boundaries of the river. Distances between subsequent detections (interpolated or actual) were calculated using the distGeo() function from the geosphere library (Hijmans 2019) if detections were in Muddy Creek or Sandusky Bays or by differences in RKMs of the detections if they were in the Sandusky River. Daily movements for fish with multiple detections or interpolated locations per day were calculated by summing distances between detections or interpolated movement paths. If during a day a fish was only detected on a single receiver, its daily total movement was assumed to be 0 km.

Differences in daily range of movement and total 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. The linear mixed models were fit in R using the lmer() function in the lme4 library (Bates et al. 2015). Overall differences in daily range of movement and total movement among 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 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 throughout the Sandusky River (Figure 3). This distribution included Grass Carp detected in the area generally associated with spawning activity ($\approx$ RKM 51) during times when spawning activity likely was not occurring (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 some Grass Carp moved into these bays particularly during the summer months (Figure 3).

Daily detection rates

Daily detection rates varied among the RKM receivers overall and among the five temperature and discharge categories (Figure 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 4A). Under conditions of high discharge and high temperatures, 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 4B). Under low temperature conditions, the highest detection rates were at RKM receivers 45.1 and 33.8 regardless of discharge (Figures 4 C and D). When discharge was low and water temperature was high, the detection rate was highest at RKM receiver 45.1 with fairly equal detection rates at RKM receivers 17.9, 25.8, 33.8, and 36.3 (Figure 4E). Under winter conditions, 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 4F).

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 daily activity centers) were 3.51 (95% highest posterior density credible interval: 3.48 – 3.55) and 3.14 (3.06 – 3.21), respectively (Table 1). The mean of the posterior distribution for ϕ (i.e., daily apparent survival probability) was 0.999 (0.998 – 1.000) (Table 1). Scaled to an entire year, this equated to annual apparent survival rate of approximately 66%, which is likely 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 0.39 (0.08 – 0.70) to 5.004 (4.87 – 5.13) (Table 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 5). A general tendency occurred 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 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 5).

Overall, daily activity centers were concentrated near RKMs 10.6 and 27.7 (Figure 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 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 (Figure 6) should actually be distributed more broadly across RKMs throughout Muddy Creek Bay, Sandusky Bay, and into 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. Under high discharge and high temperature conditions, activity centers were concentrated near RKMs 34.3, 44.8, and 49.7 with the highest concentration at RKM 49.7 (Figure 6B). Under high discharge and low temperatures, 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 6C). Under low discharge and low temperature conditions, activity center concentrations were highest near RKMs 36.6 and 44.8, with slightly lower concentrations near RKMs 34.3 and 49.7 (Figure 6D). Under low discharge and high temperature conditions, activity center concentrations were the highest near RKM 44.8 with slightly lower concentrations near RKM 34.3 (Figure 6E). Under winter conditions, activity center concentrations were highest near RKMs 34.3 and 36.6, with slightly lower concentrations near RKMs 44.8 and 49.7 (Figure 6F).

Movement

Mean daily range of movement of tagged Grass Carp (furthest distance upstream and downstream in a day) ranged from 0 to 2.2 km, with an overall mean daily range of movement of 0.69 km (SE =

0.11). Most tagged Grass Carp had an average daily range of movement of less than 1 km, although 22% of tagged Grass Carp had an average daily range of movement of more than 1 km. Daily range of movement significantly differed among the five temperature and discharge categories (Table 2). Under high discharge and high temperature conditions, mean daily range of movement ($\bar{x}$ =1.65 km, SE = 0.18) was significantly greater than for other categories. The second highest daily range of movement ($\bar{x}$ =0.53 km, SE = 0.044) was observed under high discharge and low temperature conditions; this daily range of movement was significantly greater than the daily ranges of movement for the other three temperature and discharge categories (Table 2). Daily ranges of movement between the remaining three temperature and discharge categories were not significantly different, with mean daily ranges of movement from 0.21 km (SE = 0.02 km) (winter) to 0.29 km (SE = 0.04 km) (low discharge and high temperature) (Table 2).

Mean daily total movement (total distance traveled in a day) of tagged Grass Carp ranged from 0 to 19.67 km, with an overall mean daily total movement of 1.17 km (SE = 0.06). Many Grass Carp (63%) moved more than 1 km/day on average and 30% moved more than 2 km/day on average. Like daily range of movement, mean daily total movement was significantly different among the five temperature and discharge categories (Table 3). Under high discharge and high temperature conditions, mean daily total movement ($\bar{x}$=3.32 km/day, SE = 0.34) was significantly greater than for the other categories. The second highest mean daily total movement ($\bar{x}$=1.18 km/day, SE = 0.80) occurred under high discharge and low temperature conditions; this mean daily total movement was significantly greater than the mean daily total movement for the other three temperature and discharge categories (Table 3). Mean daily total movements between the remaining three temperature and discharge categories were not significantly different, with mean daily movement averages ranging from 0.59 km (SE = 0.04) (temperature < 4.5°C) to 0.70 km (SE = 0.04) (low discharge and low temperature) (Table 3).

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 efforts to eradicate this invasive species and lessen the risk of spread and establishment to the other Great Lakes. RKM receiver detection rates and distributions of Grass Carp activity centers pointed to areas of aggregation in the Sandusky River that appear to shift with changing discharge and water temperature. Locations between RKMs 34 and 36 and RKM 45 in particular appear to be areas of possible Grass Carp aggregations. During high discharge and high temperature, the conditions when Grass Carp moved the most, there was an additional aggregation area around RKM 49. This location is slightly downstream from the likely spawning location of Grass Carp in the Sandusky River, which is near 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 receivers located near RKMs 17.9 and 25.8, which perhaps could be associated with staging behavior that Grass Carp may show prior to spawning. We recommend that future response efforts in the Sandusky River target these areas to increase the probability of catching Grass Carp.

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 spawn 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 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 our expectation, and first reported by Harris et al. (in press), we found adult Grass Carp remained in the Sandusky River throughout the year and moved widely throughout the river. Similarly, Chapman et al. (2013) reported that juvenile grass carp caught in the Sandusky River likely spent their entire lives in the Sandusky River based on otolith microchemistry analysis. We observed other behaviors as well that did not match up with previous beliefs regarding Grass Carp behavior in rivers, such as fish being located in Muddy Creek Bay and Sandusky Bay even during late spring and early summer when spawning normally occurs.

The daily movements that we observed in this study were generally greater than what has been reported for Grass Carp in other studies. We observed mean daily total movements ranging from 0 to 19.67 km and daily ranges of movement from 0.0 km to 2.2 km. The mean daily total movement found in this study (1.17 km) was somewhat higher than the mean daily total 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 et al. 1999). Weberg et al. (2020) found juvenile grass carp averaged 2.0 and 3.4 km per month for two stocked cohorts of juvenile grass carp in an Appalachian reservoir. 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 in the Sandusky River was greatest at discharge exceeding 31 m^3/s matches results reported 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. Greater movements were attributed to the occurrence of spawning events or movement into inundated floodplain habitat for feeding purposes (Sullivan et al. 2019). Movement also could be linked to fish seeking habitats that provide some refuge to fast water velocities (Brenden et al. 2006). Regardless of the underlying reason for greater movement, knowledge as to the variables that lead to increased mobility can inform protocols for efforts to remove invasive aquatic species. 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 in the Sandusky River was the highest when discharge exceeded 31 m^3/s, we recommend response efforts consider deploying passive capture gear when discharge exceeds this threshold because Grass Carp encounters with deployed gear ostensibly should be high and lead to increased 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, response efforts should continue to 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 involves 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). 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 removal methods in other parts of Lake Erie (K. Robinson, Michigan State University, *personal communication*).

Although this study was based on observations from fewer than 30 fish, we believe our study results will nevertheless prove valuable for informing Grass Carp response efforts on the Sandusky River. Because these results are new and unique for the Grass Carp in the Great Lakes, they are being incorporated into eradication strategies being implemented by resource agencies (Herbst et al. in press). Using detection information from a few tagged individuals to identify locations of untagged fish for removal efforts is referred to as the "Judas" technique and has been identified as a beneficial tool for efforts to reduce abundances of invasive species (Lennox et al. 2016; Crossin et al. 2017). Aquatic species for which the Judas technique has proven successful in helping to inform response 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; Williams et al. 2020). 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 the inherent risk of releasing the individuals in the wild rather than simply killing them. The high-use areas identified by the tagged Grass Carp in this study should be targeted by future removal efforts coupled with mobile tracking techniques, to improve the effectiveness of the Lake Erie Grass Carp adaptive response program (Herbst et al. in press).

The Ballville Dam removal occurred in stages over the course of this study and though habitat changes were not the focus of this study, there were no substantial habitat alterations apparent in the downstream portion of the Sandusky River. The former dam was considered a "run-of-the-river" dam and therefore did not substantially impact discharge in downstream area (USFWS 2014), suggesting data from USGS gage station 04198000 remained relevant to the focus area for this study. The real-time data from this gage station provided through US Geological Survey (USGS) National WaterWatch Website (https://waterwatch.usgs.gov/), along with our findings of aggregation areas and movement, can be used to inform the deployment of grass carp targeted efforts on a daily basis for the Sandusky River.

Information provided through this study could also be used to inform future risk assessments for Grass Carp along with informing potential space use of other Asian carp species if they were to invade 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 gained from this study adds to the insights related to Grass Carp large-scale movements and tributary use in Lake Erie described by Harris et al. (in press). 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. Methods used in this study could also be used to inform aggregation areas for novel or rare species using a riverine system.

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 used 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, response 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 capture methods. This information 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 response efforts (Robinson et al. in press).

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Table 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
λ_0	3.51	3.48 – 3.55	2,691	σ_{16}	0.64	0.61 – 0.67	2,567
τ	3.14	3.06 – 3.21	1,883	σ_{17}	1.16	1.11 – 1.23	2,664
ϕ	0.999	0.998 – 1.000	3,000	σ_{18}	1.69	1.65 – 1.74	2,667
σ_1	5.00	4.87 – 5.13	3,000	σ_{19}	0.83	0.80 – 0.87	2,669
σ_2	4.45	4.19 – 4.73	3,000	σ_{20}	0.99	0.96 – 1.03	2,387
σ_3	3.94	3.66 – 4.20	3,000	σ_{21}	1.27	1.22 – 1.30	3,000
σ_4	0.98	0.92 – 1.05	3,000	σ_{22}	1.62	1.57 – 1.67	3,000
σ_5	2.44	2.31 – 2.59	3,000	σ_{23}	1.67	1.62 – 1.71	3,000
σ_6	3.04	2.88 – 3.21	3,000	σ_{24}	1.57	1.53 – 1.62	3,000
σ_7	0.39	0.08 – 0.70	3,319	σ_{25}	1.71	1.66 – 1.76	2,791
σ_8	2.34	2.20 – 2.51	3,163	σ_{26}	1.46	1.35 – 1.55	3,000
σ_9	1.97	1.86 – 2.08	3,231	σ_{27}	1.02	0.97 – 1.08	2,692
σ_{10}	1.54	1.45 – 1.62	3,000	σ_{28}	3.41	3.33 – 3.50	2,738
σ_{11}	1.63	1.54 – 1.72	3,390	σ_{29}	0.93	0.90 – 0.96	2,503
σ_{12}	2.07	1.95 – 2.19	2,800	σ_{30}	1.24	1.19 – 1.29	2,455
σ_{13}	2.21	2.15 – 2.26	2,675	σ_{31}	4.63	4.34 – 4.84	3,207
σ_{14}	1.22	1.20 – 1.25	2,157	σ_{32}	2.77	2.72 – 2.83	3,000
σ_{15}	1.12	1.09 – 1.15	3,000	σ_{33}	2.01	1.94 – 2.08	3,153

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

Test	Test statistic value	Degrees of freedom	P-value
Overall difference among categories	131.51	4, 14,204	< 0.01*
High disc./high temp. vs. high disc./low temp.	-18.15	14,203	< 0.01*
High disc./high temp. vs. low disc./high temp.	-19.27	14,143	< 0.01*
High disc./high temp. vs. low disc./low temp.	-17.07	14,165	< 0.01*
High disc./high temp. vs. winter	-21.41	14,091	< 0.01*
High disc./low temp. vs. low disc./high temp.	4.36	14,226	< 0.01*
High disc./low temp. vs. low disc./low temp.	3.86	14,227	< 0.01*
High disc./low temp. vs. winter	6.03	14,227	< 0.01*
Low disc./high temp. vs. low disc./low temp.	0.35	14,214	0.73
Low disc./high temp. vs. winter	0.88	14,198	0.38
Low disc./low temp. vs. 5 winter	0.35	14,216	0.73

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

Test	Test statistic value	Degrees of freedom	P-value
Overall difference among categories	117.29	4, 9,890	< 0.01*
High disc./high temp. vs. high disc./low temp.	-2.12	9,890	< 0.01*
High disc./high temp. vs. low disc./high temp.	-2.57	9,892	< 0.01*
High disc./high temp. vs. low disc./low temp.	-2.79	9,899	< 0.01*
High disc./high temp. vs. winter	-2.60	9,894	< 0.01*
High disc./low temp. vs. low disc./high temp.	0.45	9,886	< 0.01*
High disc./low temp. vs. low disc./low temp.	0.66	9.898	< 0.01*
High disc./low temp. vs. winter	0.48	9,888	< 0.01*
Low disc./high temp. vs. low disc./low temp.	0.22	9,891	0.13
Low disc./high temp. vs. winter	0.03	9,881	0.77
Low disc./low temp. vs. winter	-0.18	9,894	0.19

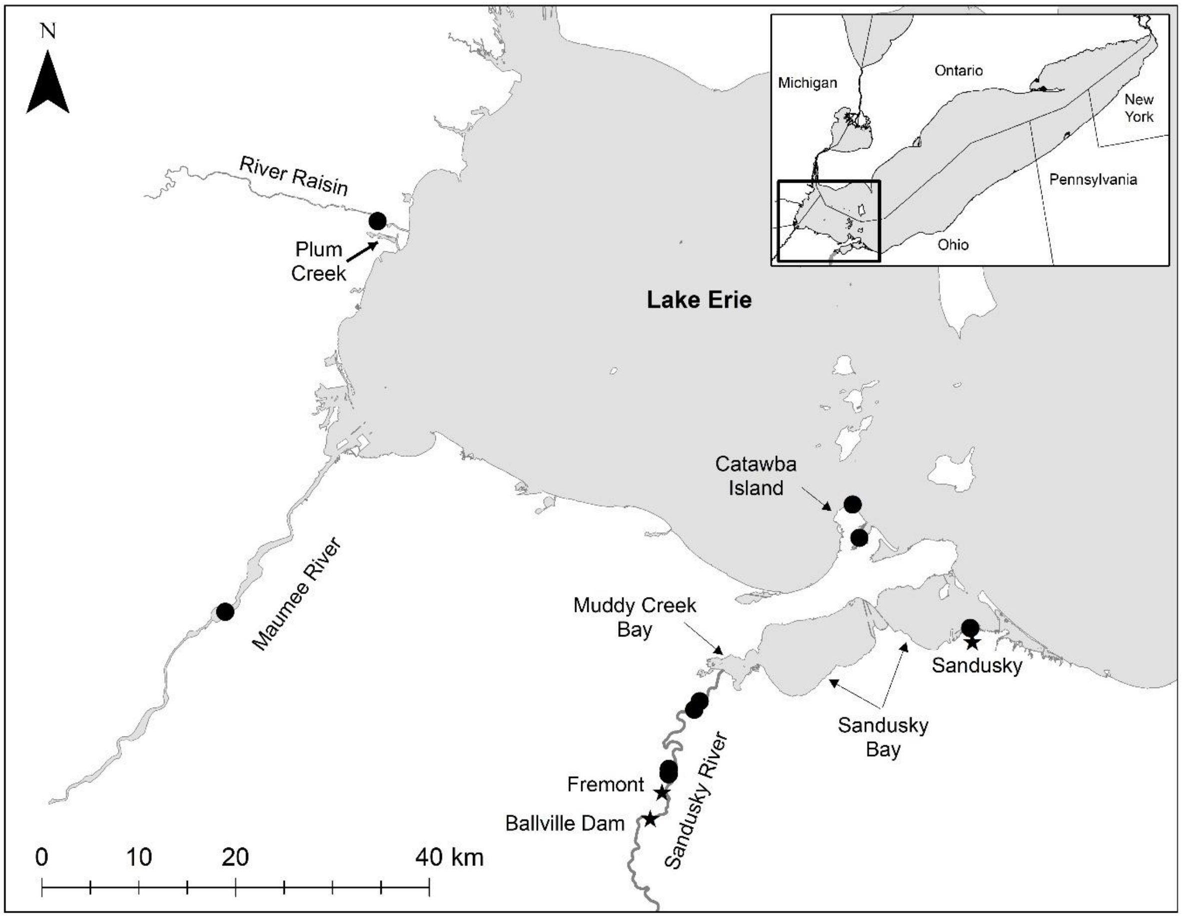

Figure 1. Map of the western basin of Lake Erie showing release locations of the 27 Grass Carp that provided detections used in this study (2014-2019). Twenty-two fish were released in the Sandusky system, two fish in Lake Erie near Catawba Island, one fish in the Maumee River, and two fish in the River Raisin.

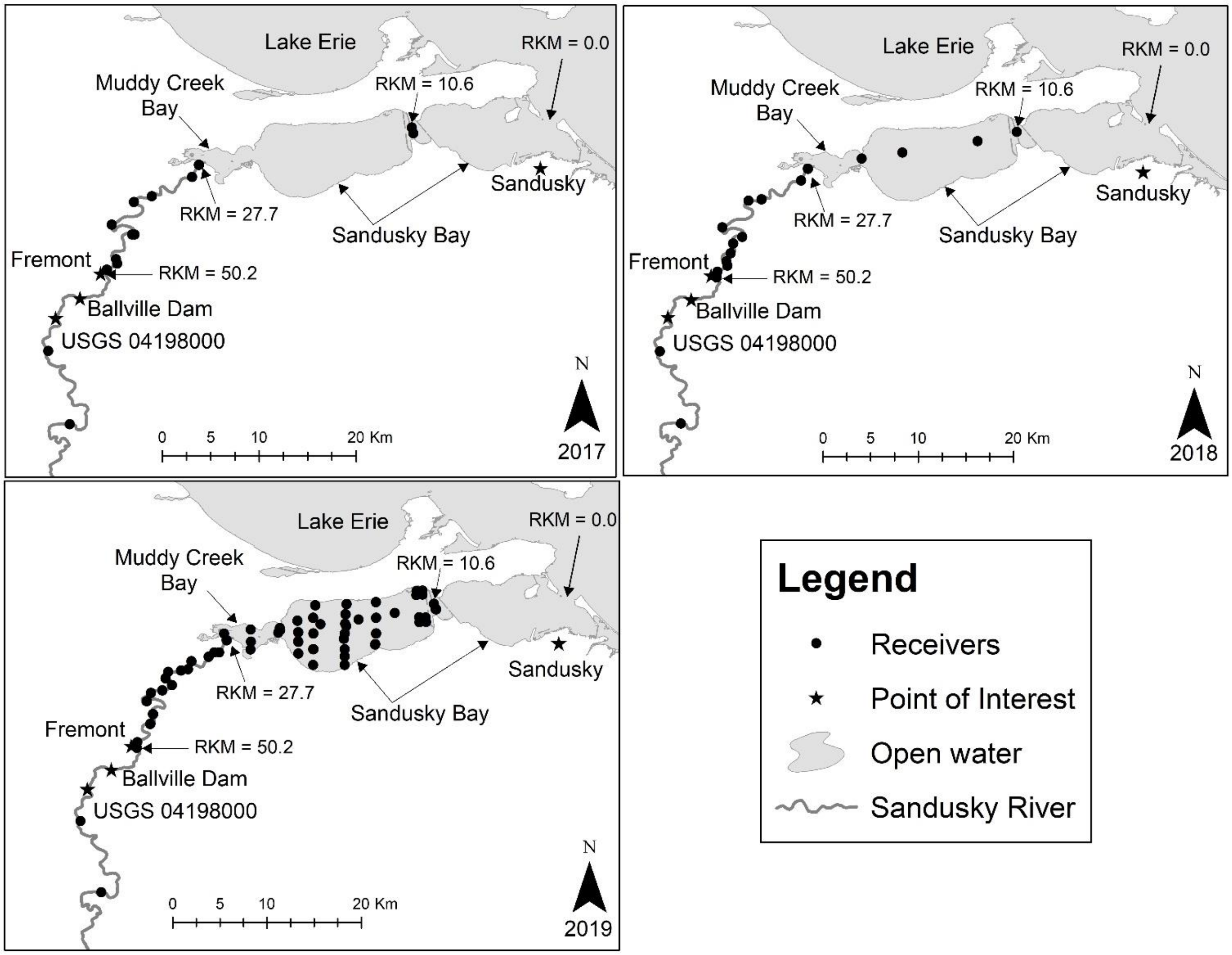

Figure 2. Locations (black circles) where acoustic receivers were deployed in the Sandusky River during each year this study was conducted.

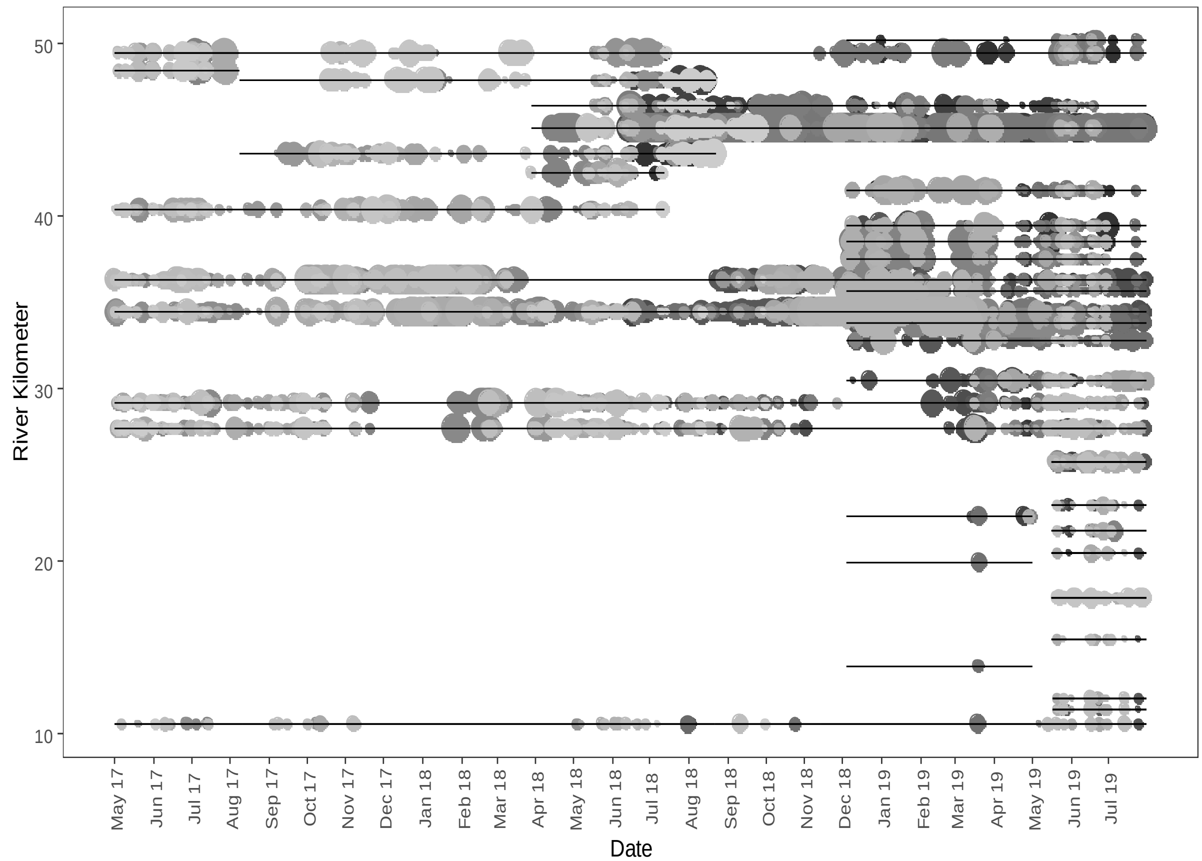

Figure 3. Hourly detection counts per day for each tagged Grass Carp at each RKM receiver in the Sandusky River from May 1, 2017 to July 31, 2019. The size of the symbol is indicative of the number of counts. The horizontal lines indicate period of operation for the deployed receivers, although several 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.

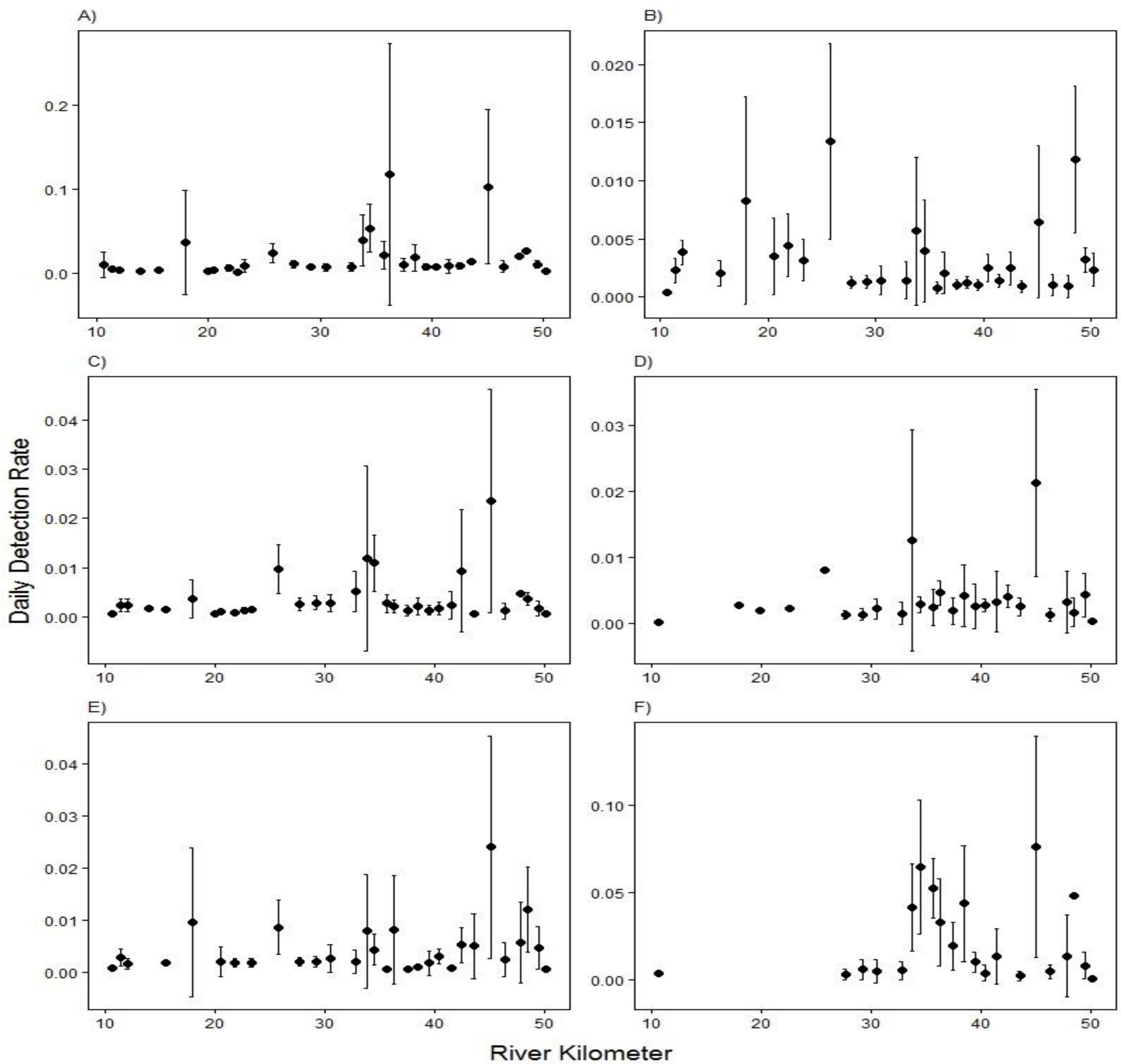

Figure 4. Mean daily detection rates and 95% confidence limits at each RKM receiver overall and for the 5 temperature and discharge categories described in the text (A = overall, B = daily maximum discharge ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C; C = daily maximum discharge ≥ 31 m^3/s and 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).

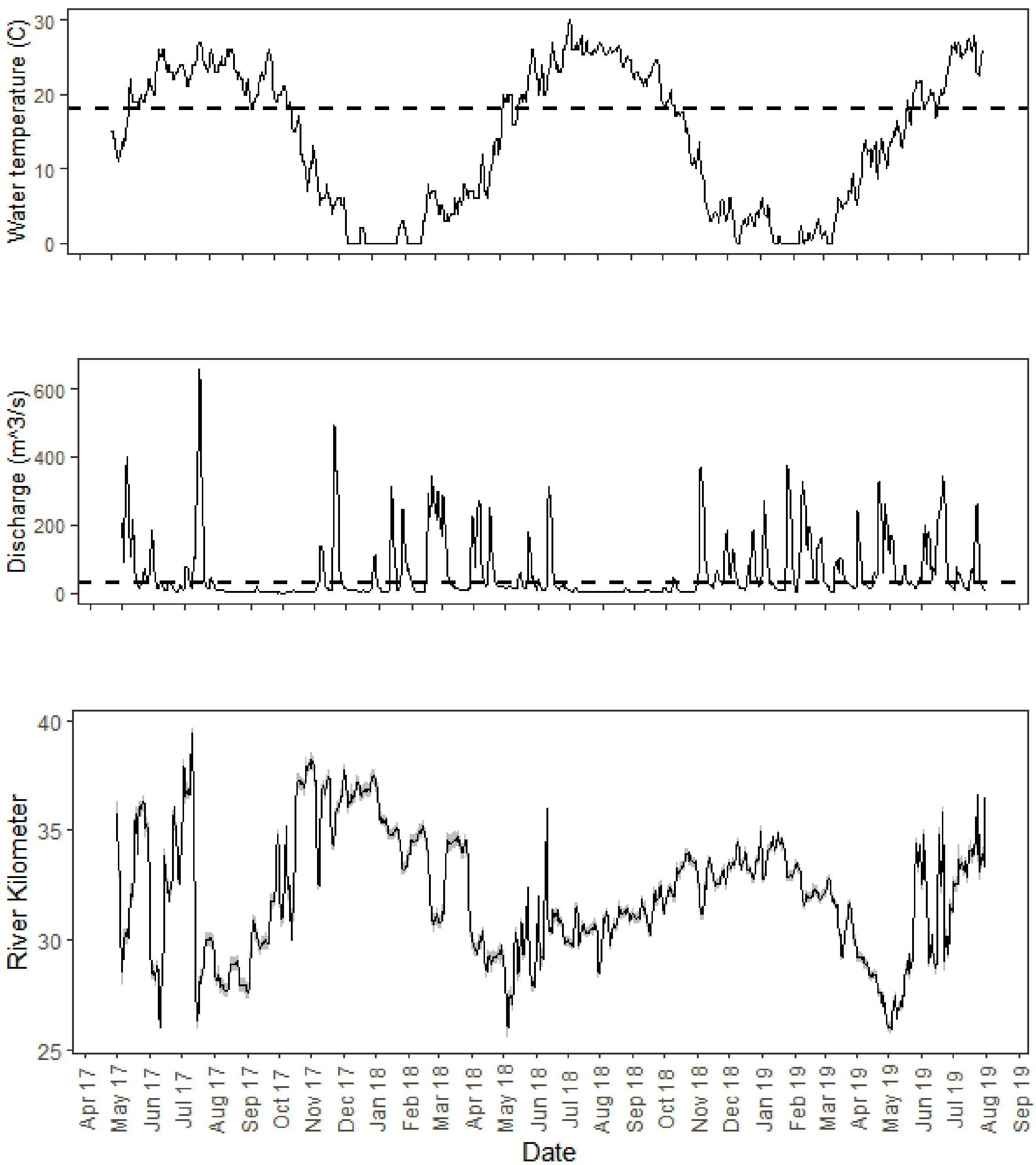

Figure 5. Daily water temperature (top panel; solid line), daily maximum discharge (middle panel; solid line) and average of the daily estimated RKM activity centers (bottom panel; solid line) for Grass Carp along with the 95% Bayesian credible intervals (bottom panel: gray ribbon) for the Sandusky River from May 1, 2017 to July 31, 2019. The dashed lines on the daily water temperature and maximum discharge panels delineate 18 °C and 31 m^3/s.

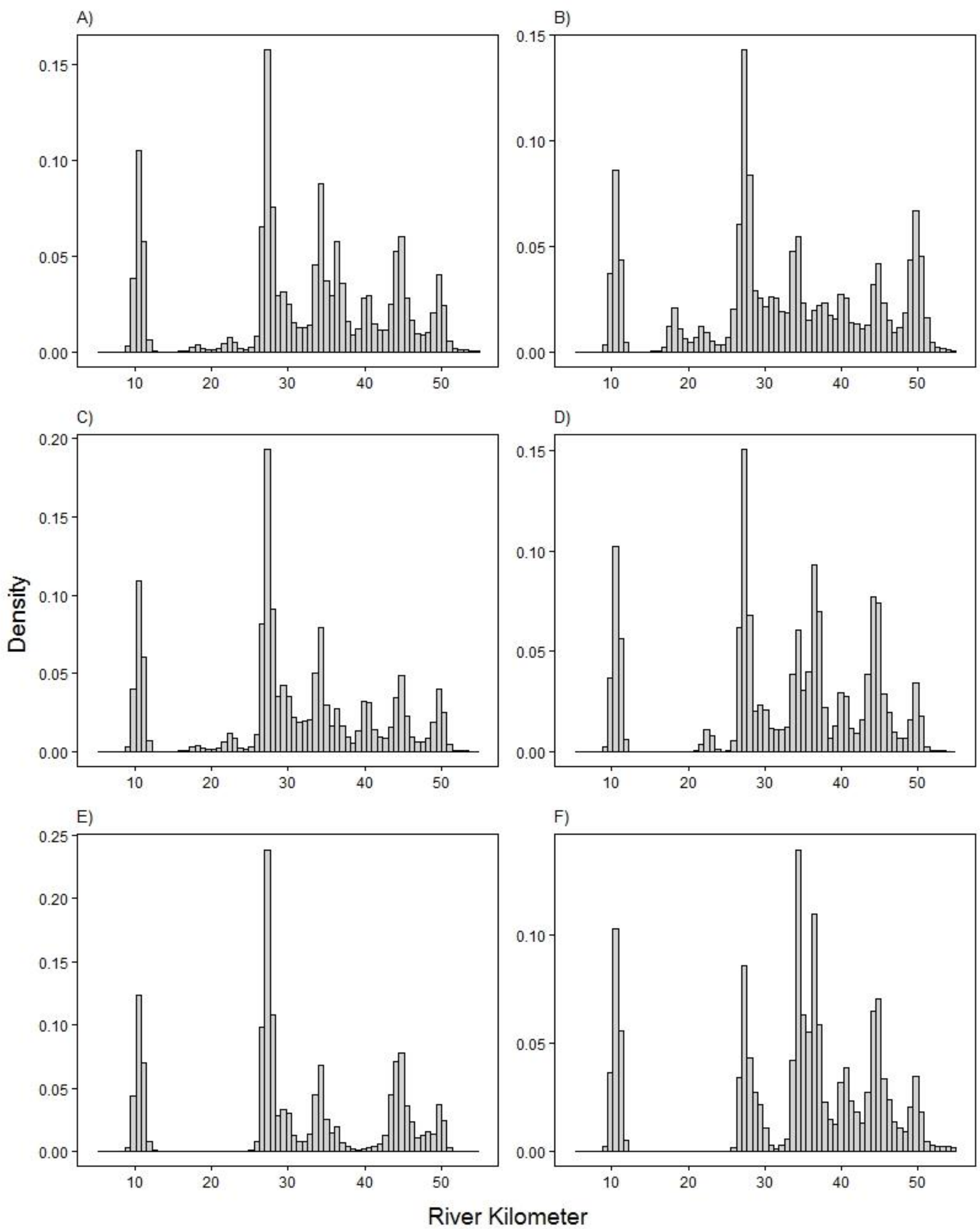

Figure 6. Activity center posterior frequencies at river kilometers throughout the study site overall and for the five temperature and discharge categories described in the text (A = overall, B = daily maximum discharge ≥ 31 m^3/s and daily mean water temperatures ≥ 18°C; C = daily maximum discharge ≥ 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).