Movement patterns and habitat selection by Bighead Carp and Silver Carp within the lower Red River catchment

by

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Abstract

Invasive species are one of the many threats facing native freshwater fish in North America. Invasive fish species can lead to population declines and assemblage-level changes among native fishes. Once established, invasive species are difficult to control and require well-informed management to mitigate their damage. By developing basic information on invasive species life histories and behaviors, managers can work better to minimize their negative effects. Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix*, (hereafter carp) are emblematic of this issue. Carp are characterized by high fecundity, an ability to tolerate a wide range of physicochemical conditions, and effective filter feeding. My study objectives were to determine the movement patterns and habitat selection by carp in the lower Red River catchment. I used active and passive acoustic telemetry technology to locate 50 tagged carp from March 2023 to August 2024. I used generalized additive mixed modeling to determine environmental conditions related to carp movement. Tagged individuals showed mobile and sedentary characteristics. The maximum distance recorded was 336 river-kilometers and a maximum rate of 38 river-kilometers per day. Carp also appeared not to travel outside of my study area in large numbers or travel to the western extent of my study. Carp moved at greater magnitudes during higher discharge variability. I also used a multistate model to estimate transition probabilities among habitats across unique environmental conditions. Carp were more likely to transition between habitats during times of increased water temperature and more variable discharge compared to times of low water temperatures and minimal flows. I modeled the variation in carp habitat selection using a resource selection function. Carp selected habitats that were deeper, had lower-velocities and which were out of the primary channel. This may be due to bioenergetic needs as these habitats require less energy to inhabit and contain higher food abundances. Management of these species must be context dependent as the lower Red River is different than other systems in carps invaded range. My results indicate that carp are making large movement within lower Red River that are consistent with conditions thought to cue spawning migrations. Removal efforts during less variable discharges and lower water temperatures would be the most effective as carp would likely be more congregated in specific habitats. Management targeting low-velocity areas that contain deeper water which are not in the primary channel would also result in more effective removal. Caution is warranted when conducting mitigation efforts as native fish could be inadvertently affected and compensatory responses could occur within carp populations.

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Chapter I

Introduction

The introduction of non-native fishes is one of the many threats facing native freshwater fish in North America (Dudgeon et al. 2006). Direct and indirect interactions with invasive species such as perceived competition, hybridization, and predation can lead to population declines and assemblage-level changes among native fishes (Jelks et al. 2008; Sleezer et al. 2021). For example, Vander Zanden et al. (1999) found that native Lake Trout *Salvelinus namaycush* occupied a lower trophic level in Canadian lakes with non-native Smallmouth Bass *Micropterus dolomieu* and Rock Bass *Ambloplites rupestris* compared to lakes without these species. Further, hybridization between native and non-native species can cause negative effects by decreasing genetic diversity and long-term survivability of native species (McDonald et al. 2008). Non-native Rainbow Trout *Oncorhynchus mykiss* hybridized with threatened native Apache Trout *Oncorhynchus apache*, resulting in 65% of Apache Trout populations now containing Rainbow Trout alleles. (Rhymer and Simberloff 1996; Hitt et al. 2003). Not all non-native species lead to negative consequences on ecological or human systems. However, invasive species, non-native species that cause ecological or economic harm, are of concern to managers (Britton et al. 2011). Introductions of non-native species can occur intentionally through the stocking of desirable sport fish, or unintentionally through aquaculture escapement (Dudgeon et al. 2006; Britton et al. 2011). Once established, invasive species are difficult to eradicate and require well-informed management to control. By developing basic information on invasive species life histories, behavior, and their ecological effects on native fishes, managers can work to better mitigate their damage (Cucherousset and Olden 2011).

Two species emblematic of freshwater invasion due to their life-history traits are Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix*, (hereafter carp). Carp are native to Asia and were introduced in North America in the 1970s to control plankton growth in aquaculture and wastewater treatment ponds. Flooding events allowed both species to enter the Mississippi River basin and establish populations (Kolar et al. 2007). Carp are characterized by high fecundity, an ability to tolerate a wide range of physicochemical conditions, and effective filter feeding (Williamson and Garvey 2005; Solomon et al. 2016; Lenaerts et al. 2023a; Williams et al. 2023). Carp are protracted pelagic-broadcast spawners (hereafter pelagophils, where gametes are released over unprepared, unguarded substrate, absorb water post-fertilization, and become neutrally buoyant. Their eggs then require minimal velocities to maintain the eggs and larvae in suspension during early development (Lenaerts et al. 2023a). Rivers with sufficient velocity and some distance of unimpounded river are typically needed for a proportion of the population to spawn successfully. However, a proportion of other pelagophils populations are known to successfully reproduce in shorter reach lengths (Chase et al. 2015). Once released, eggs drift an estimated 25-100 km before hatching in some river systems (Cuddington et al. 2014; Garcia et al. 2015; Heer et al. 2019). Lenaerts et al. (2023b) found Silver Carp had an averaged batch fecundity (i.e., the number mature eggs within a female) of ~1,200,000 eggs per female and ~1,000,000 for Bighead Carp in the upper Mississippi River. Brewer et al. (2023) estimated the average fecundity of Bighead Carp and Silver Carp in the Red River to be ~780,000 and 1,500,000 eggs, respectively. The high fecundity of both species can lead to rapid population growth in invaded systems. Sass et al. (2010) found an 84% intrinsic rate of increase of carp catches from 1998-2008 in the La Grange reach of the Illinois River.

Carp have the ability to negatively affect native ecosystems and disrupt trophic levels. Carp are filter feeding planktivores which threaten the persistence of native planktivorous fish and larval fish that depend on plankton in early life stages (Sampson et al. 2009; Solomon et al. 2016; Wang et al. 2018; Tillotson et al. 2023). In the upper Mississippi River, larval Freshwater Drum *Aplodinotus grunniens* were found to change diets based on the presence and abundance of Bighead Carp and Silver Carp (Tillotson et al. 2023). These changes can affect the growth and survival of many freshwater fish (DeBoer et al. 2018; Love et al. 2018; Tillotson et al. 2022). Chick et al. (2020b) found sport fish abundances had a negative relationship with Silver Carp abundances in the Mississippi River. As carp continue to invade new river systems, an understanding of the variation in their life-history patterns and ecology would be beneficial to developing meaningful management strategies.

Several strategies are being used to manage carp though they do not appear to be very effective at slowing their spread or eliminating the species. Both species have increased their range into the upper Mississippi River basin including almost all associated tributaries (Lohmeyer and Garvey 2009). Several mitigating techniques have been used to control Bighead Carp and Silver Carp populations (e.g., barriers and removal) (Tsehaye et al. 2013). Large-scale electric barrier systems have been in place in the Chicago Area Waterways System since 2002 to keep carp out of Lake Michigan (Parker et al. 2016). Commercial and recreational fishing programs have been implemented in states to control high carp densities. Illinois signed an agreement with People's Republic of China to export 13.6-22.7 million kg of Bighead Carp and Silver Carp annually. Combinations of air bubbles and sound stimuli have also been used to slow down invasion expansion (Dennis et al. 2019). However, there is little evidence current strategies are useful in controlling carp populations (Tsehaye et al. 2013), except in relatively closed systems (Ridgway et al. 2023a). Due to the variability associated with carp habitat use, movement, and spawning behavior, management strategies are likely to be most effective when catered to local environments.

The goal of my research is to provide ecological data about Bighead Carp and Silver Carp populations in the Red River catchment that may be useful for developing control strategies. Although Bighead and Silver Carp are established in the lower Red River, there are knowledge gaps related to spawning success, movements, and habitat selection that need to be addressed to improve our management strategies (Patton and Tacket 2012). Correspondingly, I have two broad study objectives to help me achieve my goal: 1) determine Bighead Carp and Silver Carp movement patterns in the lower Red River catchment, and 2) assess habitat selection by Bighead Carp and Silver carp during the winter, spring, and summer seasons. My first objective provides valuable information on how and when Bighead Carp and Silver Carp move into different habitats of the lower Red River and the factors that relate to their movement. This allows managers to better understand possible spawning patterns and cues, overwintering refuge locations, and individual variations in movement behavior. My second objective provides more information on which habitats Bighead Carp and Silver Carp are selecting (i.e., using disproportionately to availability) during warm and cold seasons. This, combined with earlier work on native fishes' habitat use in the lower Red River catchment, is useful for determining when there may be overlap with native fishes in key habitats and when carp may be more vulnerable to capture to minimize negative effects on native fishes. Collectively, my study provides important information for developing management strategies in the lower Red River catchment and broadens our knowledge of invasive species behaviors.

Methods

Study area

My study area encompassed approximately 581 river kilometers (rkm) from Denison Dam, Oklahoma to the Arkansas-Louisiana border (Figure 1). The Red River catchment is the southernmost major catchment of the Mississippi River and is located in multiple ecoregions including the San Antonio Prairie, Pleistocene Fluvial Terraces, Tertiary Uplands, Blackland Prairie, Floodplains and Low Terraces, and the Red River Bottomlands (Longing and Haggard 2010; Haggard et al. 2013; EPA 2015). The catchment drains 239,361 km^2 of New Mexico, Texas, Oklahoma, Arkansas, and Louisiana (Bertrand and McPherson 2018). The Red River begins in New Mexico and terminates at the confluence with the Atchafalaya River in Louisiana. The Red River was impounded in 1944 by Denison Dam to create Lake Texoma which separates the upper and lower portions of the catchment (Riggs and Bonn 1959). The upper portion is heavily dammed and experiences cycles of droughts and floods (Bertrand and McPherson 2018). Land use in the upper portion includes rangeland and cropland with an average annual precipitation of 500 mm (Bertrand and McPherson 2018). The upper Red River is characterized by fluctuations in salinity. Salinity sources include oil production, salt springs, and salt seeps (Laughlin and Lacewell 1981). The lower Red River is primarily sand bed with mixed gravel and cobble in the middle portions. Forested land is more common in the lower portions with an average annual precipitation of 1300 mm (Bertrand and McPherson 2018). In the lower Red River, the braided channel of the Oklahoma-Texas portion of the catchment has water temperatures that regularly exceed 36 °C due to the shallow and often unshaded channels (Matthews and Zimmerman 1990). The lower catchment has highly erodible banks of fine sand and silt that translate into suspended sediment loads (Copeland 2002). As the river flows southwest through Arkansas, there are several human modifications to the channel due to dredging and the creation of wing dikes resulting in typically deeper and slower-moving water compared to other reaches in the mainstem.

Passive receiver placement

I placed 22 submersible ultrasonic receivers (VR2Tx InnovaSea Inc; SURs) throughout my study area to determine coarse-scale movements by Bighead Carp and Silver Carp (Figure 2). I prioritized SUR placement in key areas that I hypothesized are important for possible spawning migrations, overwintering habitats, or are necessary to determine if tagged fish leave the study area. I placed two SURs together (hereafter gates) spaced 0.5-3.0 rkm apart for each gate. This configuration prevents simultaneous detection on paired SURs, increases the probability of detecting tagged carp by one of the SURs in a gate, and provides information on movement direction (i.e., by passing by two SURs). Each SUR continuously scans for transmissions and collects the identification number and time stamp of tagged carp when detected. Fifteen of my SURs were placed in tributaries and backwaters which were presumed habitats for feeding and refuge (Birdsall 2023; Werner et al. 2023). For tributary or backwater locations, I placed SURs at least 0.8 rkm away from the mainstem river to avoid detection of tagged carp passing the area in the mainstem river.

I moored SURs and performed range testing to ensure they were in appropriate locations. I moored SURs in place using a 72-kg concrete anchor with a 0.6-m rebar post placed in the middle of the anchor (Figure 3). The rebar post was attached to a near-surface buoy by a 6.35-mm stainless steel cable. The SUR was then attached to a rebar bracket and threaded onto the rebar anchor post, and a secondary rope was then attached from the SUR bracket to the near-surface buoy. The water depth of SUR locations varied by site and season, but locations were chosen to ensure SURs were always submerged. Once deployed, I evaluated SURs using a range testing tag to determine the detection range under a wide range of discharges in my spring and summer seasons. I performed a drifting range test by submerging a test tag ~ 700-m upstream of each SUR. I then drifted downstream marking GPS locations every second until ~ 700-m downstream of the SUR. Next, I calculated the detection probability by dividing the observed detections of the test tag during the drift by the expected detections. Finally, I plotted the detection probability against the distance to visualize the detection range. The distance at which detection probability falls below 50% in poor conditions or 75% in good conditions was ruled as the estimated detection range (Innovasea Inc). This process is important in understanding the range in which tagged fish can be detected. Detection range can be influenced by depth, water temperature, current velocity, and other environmental conditions (Kessel et al. 2014). The detection range of my SURs ranged from 700 m during tests at base flow conditions to 98 m during higher discharge conditions. The average detection range of my SURs during testing was 238 m. The detection range likely varied with seasonal environmental changes; thus, carp detection was less than 100% as with any sampling. I marked the GPS coordinates of each SUR and monitored them every 1-2 weeks to download data and maintain the moorings.

Fish sampling and tagging

I captured Bighead Carp and Silver Carp using monofilament gillnets and electrofishing for subsequent tagging with acoustic transmitters (V16-4X, InnovaSea Inc) at multiple locations in the lower Red River catchment (Figure 4). I targeted areas known to have higher carp counts based on previous sampling in my study area. I used gillnets that were 30.5-m long or 54.4-m long when sampling tributaries and backwaters or the mainstem river respectively. Both gill nets were 3.6-m tall with 8.9, 10.1, and 10.8-cm bar-length mesh panels. I used an 80-amp, high conductivity, DC boat electrofisher (Midwest Lakes; Polo, Missouri) to electrofish. I followed standardized American Fisheries Society electrofishing settings based on conductivity and power during sampling (Miranda 2009). My gillnets were set at chokepoint locations in each reach and then electrofishing was conducted for ~ 1-h. I then pulled gillnets and held any captured carp in an aerated holding tank.

I anesthetized, measured morphometrics, and tagged each carp to later quantify movement dynamics. My procedures followed the appropriate animal care and use procedure (2022-5088). I anesthetized each fish using an electrosedation table until stage IV of sedation (Summerfelt and Smith 1990; Kim et al. 2017). Briefly, stage IV sedation causes the fish to have total loss of equilibrium, muscle tone, and responsiveness to visual and tactile stimuli, while still maintaining a slow opercular movement. Species, total length (mm), and mass (g) of each fish were quantified. Only carp large enough to meet an appropriate transmitter burden (i.e., < 2% of total body weight) (Winter 1996) were tagged. I made a 5-6 cm incision on the left-ventral side of the body between the anal and pelvic fins. Sex was determined based on visual observation of the gonads when possible or the presence of sperm when handling an individual. I inserted the transmitter into the coelomic cavity of the carp and then closed the incision with barbed sutures (PDO-Adjustable Loop, 0 Violet 60cm, CP-2 Rev Cut 26mm 1/2C, Corza Medical, Westwood, MA, USA) by passing the suture needle through the skin on either side of the incision, ensuring the sutures are secured and close the incision completely. I placed a looped FT-4 Lock-on external tag (Floy Tag & Mtg Inc, Seattle, Washington) at the posterior end of the dorsal fin (Coulter et al. 2022a). These tags were used for external identification by the researchers and public. I then held the fish in a recovery tank until it could swim on its own (typically only a few minutes). I disinfected all surgical instruments between surgeries with 90% ethanol for one minute. Tagged fish were released within 50 m of their captured location. Post release, I remained in the area for a minimum of five minutes to ensure no tagged carp resurfaced in distress. I then repeated this process until no greater than 12 total carp had been tagged from a single location. I excluded all detections from tagged fish for 14 days after tagging due to the possibility of movements being related to the stress of handling rather than typical behavior (Frank et al. 2009).

I omitted tagged fish from my data set when I had reason to believe either the tag was shed, or the fish had died. A proportion of tagged fish tend to shed surgically implanted transmitters (e.g., 26% (Ridgway et al. 2023b), 14% (Lawrence et al. 2023), 53% (Byrd et al. (2019)). It is often unclear whether a tag is shed, or the fish has died. Methods for determining mortality events vary among studies and species (Klinard and Matley 2020). Knowledge of the species' behavior and equipment limitations are also important considerations (i.e., detection range of passive and active receivers). Although my data showed that individuals became more sedentary during certain periods of time (e.g., remaining in backwater habitats), constant detections at a single receiver or lack of movement greater than 50-m from previous locations acquired via active tracking were likely due to mortality or tag loss. My criteria for estimating possible mortality included detections every day from a single passive receiver over a 90-day period, detections without movement from the previous location over a 90-day period via active tracking. My 50-m cut off was due to the limitations in the spatial extent where I could reasonably determine whether a fish had moved (see Coulter et al. 2016). I was unable to confirm fish positions < 50 m. This general approach is consistent with other telemetry studies with variability in the distance or amount of time. Khan et al (2016) used a categorization of loss of detections by reef fish to infer mortality, Gerber et al. (2017) used date of last movement and instances of fish not visiting multiple receivers as a post tagging metric to estimate tag loss or mortality, and Zemeckis et al. (2019) used lack of movement over a 30-day period to determine possible mortality.

Chapter II

Movement patterns of Bighead Carp and Silver Carp within the lower Red River catchment

Introduction

Fish movements are important to understanding their ecology, life-history, and is informative to managers. Fish movements can be influenced by both environmental factors and individual traits (Taylor and Cooke 2012; Albanese et al. 2004). Due to the spatial and temporal distribution of heterogeneous habitat, fish may not have access to all required habitats in a relatively small area (Fausch et al. 2002). Thus, movement is important for many fish to complete their life cycles. For example, Brook Trout *Salvelinus fontinalis* showed increased movements related to their spawning requirements (i.e., different pool depths) (Mollenhauer et al. 2013). Movement is also key to species dispersal and gene flow (Radinger and Wolter 2014), recolonizing habitats (Wedgeworth et al. 2023), and invading new habitats (Cooper et al. 2021). Gosset et al. (2006) found that Brown Trout *Salmo trutta* were restricted from quality spawning habitat due to weirs and dams. Identification of barriers to fish movement and the environmental conditions that are associated with successful passage can help managers adapt these structures, remove them, or increase their effectiveness in preventing movements of invasive species (Kallis et al. 2023). Understanding the temporal and spatial patterns of movements gives insight into fish behavior and results in more informed management (Cooke et al. 2022). By understanding the movements of invasive species, managers can designate important habitats (Cooke et al. 2016) or seasons when removal may be more effective (Degrandchamp et al. 2008).

Fish movements are cued by a myriad of factors that are both biological and environmental. Fish movements can be influenced by environmental cues such as changes in water temperature or discharge, but the magnitude of these movements varies based on catchments and species (Taylor and Cooke 2012). These cues direct fish to move into specific habitats to better feed, recruit, or find refuge. For example, flow and temperature influence the downstream migrations of juvenile fish species from spawning sites to nursery habitat (Pavlov et al. 2017). Water temperature can also trigger hormone increases such as testosterone in males and estradiol-17β in females which can influence movement to find spawning locations or spawning itself (Ferguson et al. 2019). Individual traits such as sex or weight can also influence the timing and magnitude of fish movements (Mollenhauer et al. 2013). For example, male Brook Trout *Salvelinus fontinalis* moved 2.5 times the distance of female Brook Trout (Hutchings and Gerber 2002). Stiver et al. (2007) found large male Cichlids, *Neolamprologus pulcher* dispersed at higher rates than smaller individuals of both sexes. Sánchez-González and Nicieza (2021) found within hatchery reared Brown Trout *salmo trutta* larger bodied individuals tended to be more sedentary than smaller individuals. Individual personality across sizes and sex can also influence movement and dispersal rates. For example, Leatherside Chub *Lepidomeda aliciae* had clear distinctions between explorer and non-explorer traits (Rasmussen et al. 2012). Understanding movements of individual invasive species such as carp gives more insights into their ecology and behavior.

Movement distances and the timing of both Bighead Carp and Silver Carp are variable within their non-native range. Similar to other fish species, carp populations are comprised of both mobile and sedentary individuals, where mobile fish can colonize new areas and sedentary fish provide resilience in populations as they increase abundance in favorable habitats (Coulter et al. 2022b). For example, Prechtel et al. (2018) found that most of the Silver Carp in the Wabash River, Indiana had total home range sizes of either <26 or >102 rkm. LaBrie and Wesner (2023) found approximately equal numbers of Silver Carp moving <50 rkm and > 50 rkm in the James River in South Dakota. Likewise, movement rates vary among populations. Vallazza et al. (2021) found Bighead Carp and Silver Carp moved as far upstream as 440 km upstream from their tagging site to 360 km downstream of their tagging site in the upper Mississippi River. In the Illinois River, carp had a maximum movement rate of 64 rkm/d (DeGrandchamp et al. 2008) and a maximum of 409 rkm traveled in the Wabash River (Coulter et al 2016). The timing of carp movements can also vary throughout the year. For example, Bighead Carp in the Illinois and Wabash rivers moved at greater frequencies during late spring and early summer (Peters et al. 2006; Erickson et al. 2016). Silver Carp, alternatively, moved greater distances and more frequently in September and October in the Wabash River (Coulter et al. 2016). Fritts et al. (2020) found Bighead Carp and Silver Carp had no seasonal patterns in the downstream approach of a lock and dam in the Mississippi River, but upstream approaches become more frequent in the summer and autumn months. Carp spawning movements are thought to be influenced by increased discharge and rising temperatures (Peters et al. 2006; Coulter et al. 2016 Hintz et al. 2017a), but with substantial individual variability (Coulter et al. 2022b).

Because of the variability in movement patterns across space and time among other catchments within the non-native range of Bighead Carp and Silver Carp, the Red River catchment provides an interesting study area as the physicochemical conditions are typically more variable than in catchments for previous studies. Thus, the objective of my second chapter was to determine movement patterns of Bighead Carp and Silver Carp. I hypothesized that both species of carp would have similar movement patterns, with greater movements during the spring when they would be expected to spawn (Calkins et al. 2012; Coulter et al. 2016; Vallazza et al.

2021). I also hypothesized that carp would be more likely to transition among coarse-habitat features during spring and summer months (Coulter et al. 2018a; Prechtel et al. 2018).

Methods

Seasons

Because fish tend to make changes in their movements seasonally, I developed criteria for sampling seasons within the lower Red River. Each season encompassed different patterns in water temperature and discharge in the catchment. I used the USGS stream gage near Index AR 07337000 from 1990 to 2022 to define my seasons. Typically, winter (i.e., Dec-Feb) is characterized by low water temperatures (mean temperature of 9.9° C) and low discharge (mean 17.7 m^3/s). During the spring (i.e., March-May), water temperatures are typically warm (mean temperature of 19.9° C) and there is an increase in discharge conditions (mean discharge of 336 m^3/s). The summer season (i.e., June-August) is typically characterized by declining discharges to base flow conditions (mean discharge of 170 m^3/s) and warm water temperatures (mean temperature of 29.9° C). The river tends to begin cooling during autumn (i.e., September-November) (mean water temperature 21.1° C) with typically low to moderate flows (mean discharge of 130 m^3/s).

Fish tracking

My team and I used both passive and active tracking across multiple seasons to determine fish movement patterns. In addition to my passive tracking data collected by my SURs (see Chapter 1), I actively tracked in three seasons: Winter (Dec 1st-Feb 28th), Spring (Mar 1st-May 31st), and Summer (Jun 1st-Aug 31st). We also tracked supplementally during autumn (September 1st-November 30th). All tracking was completed during the day (~0700-1900 hours). My team and I actively tracked multiple reaches of the mainstem river and tributaries within the lower Red River catchment in Arkansas, Oklahoma, and Texas. My tracking reaches varied in length and distribution within the catchment due to limited boat access and varying water levels (Figure 5). My team and I, actively tracked 3-5 days each week within my winter, spring, and summer seasons. My team and I also tracked 1-2 days per week during my autumn season. We tracked by boat, moving downstream at approximately 7-9 km/h. I towed a VHTx-69k transponding omni-directional hydrophone behind the boat which scanned for tagged carp. The hydrophone was paired with a VR100-300 manual receiver to detect the presence of tagged carp. Once a carp was detected, we used the omni-directional hydrophone to approach a fish's location until decibels read ≥75 (Coulter et al. 2016). We then used a directional hydrophone to triangulate and confirm the approximate location of the fish (i.e., within 50 m) (Calkins et al. 2012). Once a location was determined, I recorded GPS coordinates, date, and several habitat characteristics. If the fish moved while we were tracking, we maintained the initial contact point as the detection.

Environmental covariates

I quantified coarse-scale physicochemical conditions I hypothesized to relate to both Bighead Carp and Silver Carp. I defined movements as the distance traveled between consecutive detections and rate as the distance traveled per day between consecutive detections. My covariates included average daily discharge per movement (1.0 m^3/s), average discharge of the three days prior to each movement (1.0 m^3/s), average water temperature of the three days prior to each movement (1.0°C), day of study (1 day), average daily water temperature per movement (1.0°C), coefficient of variation (CV) of daily water temperature per movement, CV of daily discharge per movement, and average daily photoperiod per movement (1.0 min) (

Table 1). I took environmental measurements at coarser scales (i.e., catchment and segment) due to both species' capacity for large-scale movements and the positioning of USGS stream gages.

I obtained average daily discharge and water temperature from several locations in the lower Red River catchment. I collected mean daily discharge measurements from USGS stream gages near Denison Dam TX 07331600, Arthur City TX 07335500, De Kalb TX 07336820, Index AR 07337000, Fulton AR 07341500, and Spring Bank AR 07344370. I also collected water release data from Hugo Dam in Oklahoma and Millwood Dam in Arkansas (Figure 6). I compiled discharge data from the closest location to the most recent carp detection for each movement made by an individual carp. I obtained water temperature data from my SURs placed across the catchment (Figure 2). SURs recorded water temperature every hour starting at the time of deployment. I calculated the mean daily water temperature from each SUR, and compiled water temperature data from the closest SUR to the most recent carp detection.

I developed three hypotheses (and associated flow metrics) about how flow patterns might be related to carp movements. I hypothesized that carp movement distances and rates (i.e., kilometers per day) would be positively related to more variable (i.e., CV of discharge) and increased discharges (i.e., mean daily discharge) and that movements would be biased in an upstream direction. The importance of discharge variability has been described for other species of pelagic broadcast spawning minnows of the Southern Great Plains (Matthews 1988; Worthington et al. 2018; Wedgeworth et al. 2023). Although diminutive compared to carp, I hypothesized variability to be important to carp given the shared reproductive traits. I calculated average daily discharge and CV of discharge between redetections of tagged carp. Carp made larger movements under higher discharge conditions in the Wabash and Illinois rivers (Peters et al. 2006; DeGrandchamp et al. 2008; Coulter et al. 2016). Higher daily discharge conditions can initiate spawning migrations, cue fish to use different habitats, and are associated with successful reproduction in pelagic broadcast spawners (Schrank et al. 2001; Durham and Wilde 2009). Lastly, fish often do not react to changing environmental conditions immediately (Forsythe et al. 2012); therefore, examining conditions prior to a movement may better explain possible cues. The conditions leading up to a movement must be captured sufficiently thus, I averaged the discharge of the three days before each movement following Forsythe et al. (2012) and Vine et al. (2019).

I developed three hypotheses about how my temperature metrics would relate to carp movements. First, I hypothesized that carp movement distances and movement rates would have a quadratic relationship with average daily water temperature. I anticipated that carp would move upstream as temperatures increase and downriver as temperatures cooled due to the associations with upstream movements during spawning migrations and need for refuge habitat in colder seasons (Hintz et al. 2017a; Vallazza et al. 2021). I calculated the mean daily water temperature over the period between consecutive fish detections to relate to carp movement. I hypothesized that carp would move more under moderate temperatures that would correspond to spawning (i.e., carp tend to spawn in conditions above 18°C, Jennings 1988; Nico et al 2005) and that fish would begin to move less as temperatures continued to warm because of the tradeoff between energy expenditure for movement and feeding (Prechtel et al. 2018; Glubzinski et al. 2021). Second, I hypothesized carp would have a positive linear relationship with the variability (i.e., CV) in water temperatures. Variation in water temperature is a key aspect in natural thermal regimes to which riverine fish have adapted. Variation in temperature could cue carp to find spawning habitat (Olden and Naiman 2010). Lastly, because conditions leading up to fish movements may have a greater relationship with movement distances and rates than the conditions during a movement (Forsythe et al. 2012), I calculated the mean water temperature three days prior to each movement following Forsythe et al. (2012).

I hypothesized carp movement rates and absolute distances would have a positive relationship with mean photoperiod. Photoperiod is known to influence the timing of large movements through the increase in hormone production in male and female fish (Jonsson 1991; Norberg et al. 2004). I recorded the photoperiod of each day through sunrise and sunset timing using Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil) data, using Idabel, OK as the reference location. I took the difference between the two times of each day to obtain a quantitative metric for the length of photoperiod per day (Munz and Higgins 2013). I then calculated the mean photoperiod of the period between consecutive detections for each fish.

I also hypothesized that time of year, sex, and size of fish would be related to movements by carp. I recorded the date of each movement and used calendar day to represent the timing of each movement. I hypothesized carp would move more in the spring and autumn as was found in the Illinois and Wabash Rivers (DeGrandchamp et al. 2008; Coulter et al. 2022b). Several species of fishes exhibit sex-based movement trends related to spawning and dispersal (e.g., Cichlids, Stiver et al. (2007), Brook Trout, Hutchings and Gerber (2002), and Coho Salmon, Rodnick et al. (2008)). I hypothesized female carp would move greater distances and at faster rates than males because of their role in seeking out spawning habitat (Waters and Noble 2004; Miller and Scarnecchia 2011). Regardless of sex, larger individuals may be able to swim greater distances or seek different habitats compared to smaller individuals (Radinger and Wolter 2014). I hypothesized Bighead Carp would move greater distances and at faster rates than Silver Carp.

Although both Bighead Carp and Silver Carp are assumed to hold similar trophic levels and have similar habitat needs (DeGrandchamp et al. 2008; Yao et al. 2016), many other species sharing those traits exhibit different movement dynamics with some being more mobile than others (e.g., Rock Bass *Ambloplites rupestris*, Redbreast Sunfish *Lepomis auritus* compared to Largemouth Bass *Micropterus salmoides*, Bluegill *Lepomis macrochirus*, Gatz and Adams (1994)).

Movement pattern analyses

I used detection locations from both active and passive tracking to model the variation in movement patterns of Bighead Carp and Silver Carp. I analyzed movement patterns by adding each detection locations onto a map of the study area using ArcGIS Pro (ESRI, Redlands, CA, USA). I calculated absolute distance, movement rate, and direction (i.e., upstream or downstream) between fish detection. Only one detection per day per fish were analyzed. Multiple detections within the same day occurred regularly. I used the detection which indicated the greatest movement from the last known location. Multiple movements could be made between SURs within a gate on the same day, but I only used one movement to minimize autocorrelation. I calculated daily movement rate (km/d) by dividing the distance moved between two consecutive detections by the number of days the fish was at large. I considered these movements to be conservative (i.e., minimum estimates) as the fish likely moved nonlinearly between detections (Coulter et al. 2016). I measured movement direction by assessing the order in which detections occurred (i.e., detections occurring upstream or downstream compared to the last detection).

I standardized and transformed my data as needed and checked multicollinearity among my covariates prior to model development. I log transformed mean discharge, CV of discharge, three days before movement discharge, and CV of water temperature due to right-skewness. This promotes convergence of the model and ensures I am meeting the regression assumptions of linearity and homoscedasticity. I then tested for multicollinearity among variables using Pearson's correlation coefficient. Any variable set with a |r| >0.6 were considered multicollinear; thus, I proceeded using only one of the variables in the set for my model development following Roever et al. (2014) (Table 2). Multicollinearity was a concern with several variable sets thus, I retained mean discharge, mean water temperature, CV of discharge, CV of water temperature, and carp weight for model building. These variables were believed to be more directly related to carp movements compared to photoperiod, day of study, and lagged temperature and discharge covariates. All continuous variables were then standardized to have a mean of 0 and standard deviation of 1. I used the software R (version 4.4.1 R Core Team 2024) to conduct all analysis.

I made three overarching hypotheses regarding movement magnitudes of Bighead Carp and Silver Carp. My first hypothesis was that carp movement would primarily be related to individual traits. Individual traits have been shown to be a key aspect of fish movement in several species (e. g., Paddlefish, Miller and Scarnecchia 2011; Lingcod *Ophiodon elongatus* Okamura et al. 2014; Brown Trout, Sánchez-González and Nicieza 2021). Body size within the same species can be related to differences in movement patterns. For example, Mollenhauer et al. (2013) found larger Brook Trout tended to move more in fall compared to Winter. These individual characteristics could be related to differences between individuals and environmental conditions, causing a particular group of individuals to move at different rates or distances compared to other groups (Radinger and Wolter 2014; Lamarins et al. 2022). Unique subsets of covariates including mean discharge, mean temperature, sex, and weight as additive effects, and an interactive effect of discharge and species were used to test this hypothesis. I hypothesized that larger individuals and females would move at greater magnitudes than smaller individuals and males due to bioenergetic costs and differences in swimming performance. I hypothesized an interactive effect between mean discharge and species. I hypothesized that Silver Carp movements would be more related to higher discharge and Bighead Carp movements would be more related to lower discharges because Silver Carp have been shown to have higher endurances in greater velocities (Hoover et al. 2017).

My second hypothesis was that carp movement would be primarily related to season or direction. Seasonality of movement has been well documented in fish (Winemiller and Jepsen 1998; Taylor and Cooke 2012; Cooke et al. 2022). Seasonal patterns in water temperature, discharge, and photoperiod are associated with important fish behavior changes that cue fish to spawn, find ideal habitat, or feed (Schlosser 1991; Norberg et al. 2004 Taylor and Cooke 2012; Radinger and Wolter 2014; Ferguson et al. 2019). Carp are known to make large spawning migrations that typically coincide with spring and summer (Peters et al. 2006; Hintz et al. 2017a; Coulter et al. 2022b). Vallazza et al. (2021) found that most dam passages occurred from April to July. Direction could also relate to carp movement magnitudes as other studies have found greater upstream movements during conditions associated with spawning (Peters et al. 2006; Erickson et al. 2016). I hypothesized an interactive effect between temperature and direction and discharge and direction. I expected to see greater movement magnitudes in the upstream direction when discharges and temperatures were increasing and greater movements downstream as discharge and temperatures were at low or intermediate values due to the associations with upstream movements during spawning migrations (Yu et al. 2018; Vallazza et al. 2021). I hypothesized carp may only be influenced by specific covariates during certain times of the year. Environmental conditions (i.e., mean discharge and mean temperature) and their interactive effects between seasons allowed me to test this hypothesis. I hypothesized that mean discharge and mean temperature would only have a positive relationship with movement rates and distances in the spring and summer months because these seasons typically contain spawning cues and the winter season does not.

My third hypothesis was that carp movement magnitudes would be more associated with variability in environmental conditions rather than mean environmental conditions. Variability in environmental factors can be a key aspect of fish movement (Moore and Thorp 2008; Taylor and Cooke 2012; Coulter et al. 2016). Large variability in discharges and temperatures are normally associated with spring flood pulses which are also associated with spawning cues in carp (Hintz et al. 2017a; Yu et al. 2018). Main effects of CV of discharge and CV of temperature were used to evaluate this hypothesis. I expected both covariates to have a positive relationship with movement magnitudes as the flow variability has shown to be important in other cyprinids (Moore and Throp 2008; Alexandre et al. 2016). I also hypothesized an interactive effect between CV of water temperature and mean discharge. I expected that movement magnitudes would have a minimal relationship with CV of temperature at low and moderate discharges and a positive relationship at higher discharge values because of the specific conditions associated with carp spawning migrations (Li et al. 2013; Lubejko et al. 2017; Lenaerts et al. 2023a). For similar reasons, I also hypothesized an interactive effect between CV discharge and mean water temperature. I expected to see minimal relationships between movements and discharge variability until higher values of both discharge variability and mean water temperature were reached.

I used a generalized additive mixed-effect model (GAMM) to determine the relationships between my covariates and carp movement distances and rates (i.e., two models). I used the hypotheses above to create several subsets of main effects and interactions. All models contained a random effect of individual. Using a random effect of individual accounts for the repeated observations of tagged fish (Otis and White 1999). Both species were included in all analyses as a binary fixed effect. I fit models using the mgcv package in R (Wood 2023). I used thin-plate regression splines and a restricted-maximum likelihood (REML) procedure (Wood 2017).

Model 1: I modeled my covariates related to absolute movement distance (i.e., distance traveled by a single carp between consecutive detections).

Distance model:

$yi = f1(xi1) + f2(xi2) + \ldots + fp(xip) + Zibi + \epsilon$

yi = response variable for observation i

$f1(xi1) + f2(xi2) + \ldots + fp(xip)$ = series of smoothing functions for each predictor variable

$Zibi$ = random effect of individual

ϵ = error term

Model 2: I modeled my covariates related to movement rate (i.e., distance traveled by a single carp divided by the number of days between consecutive detections.

Movement rate model:

$\mathrm{yi = f1(xi1) + f2(xi2) + \ldots + fp(xip) + Zibi} + \epsilon$

yi = response variable for observation i

$\mathrm{f1(xi1) + f2(xi2) + \ldots + fp(xip)}$ = series of smoothing functions for each predictor variable

Zibi = random effect of individual

ϵ = error term

I first evaluated the assumption of temporal independence of residuals by comparing simple models with and without autocorrelation structures. I fit movement rate and distance models with day of study only to evaluate if movements were temporally autocorrelated. I then compared movement distance and rate models using Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002).

Next, I examined the need for including smoothing terms. I created a series of six models that contained the main effects of mean water temperature, mean discharge, CV of discharge, CV of water temperature and weight. Within the base model all variables had a smoothing term. I used an iterative process by removing the smoothing term from a different variable in each model to examine any possible linear relationships (Hunsicker et al. 2016; Wood 2017). I then compared all candidate models using Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). The decision to characterize a term as linear or non-liner in future models was also based on the effective degrees of freedom (EDF). Terms with an EDF of one are linear whereas terms further from one tend to be more non-linear (Wood 2017; Wood 2023).

Next, I built a series of hypothesis-based models to investigate movement patterns by carp. Hypothesis models were the same among my movement distance and movement rate analysis except for the response variable. I built several models for each overarching hypothesis (stated above) that examined a unique subset of covariates as additive and interactive effects to evaluate the relative support for each hypothesis (Table 3). I compared all models using Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) to determine which model had the greatest support among those considered. The model with the lowest AICc score was designated as my top model. All models with ΔAICc< 2 were considered to have equal empirical support. If models had ΔAICc< 2, the simpler models with fewer parameters were favored to avoid unnecessary model complexity (Burnham and Anderson 2002).

I assessed model validation by performing a 10-fold cross-validation using the CVgam function of the gamclass R package (Robertson et al. 2015; Maindonald 2023; Mazziotta et al. 2024). This approach generates a scale parameter (GAMscale) based on the complete data, and an estimate of mean squared error scale parameter from cross-validation (CV-mse-GAM). Models were considered to have good predictive capacity if the mean squared error estimate are slightly larger than the scale estimate (Robertson et al. 2015; Mazziotta et al. 2024)

Multistate analysis

I used detection locations from both active and passive tracking to develop a multistate model (Laake and Rexstad, E. 2008; Lebreton et al. 2009; Kéry and Schaub 2011) to estimate transition probabilities of Bighead Carp and Silver Carp between habitat types. I used the GPS coordinates of each detection from individual carp to determine the date (i.e., period) and habitat (i.e., state) that fish were located in. This formed a detection history across my entire study period. This detection history represents the observation process of individual fish (i.e., where and when I detected a tagged carp). This analysis differs from my GAMM analysis because it does not consider movement distance. Within my multistate model carp could move large magnitudes but remain in the same habitat. My multistate analysis provides additional information because it emphasizes transitions among habitats rather than movement magnitudes. Understanding the probability of carp transitioning to and from habitats during specific time periods can improve management efforts.

I defined three states based on habitats hypothesized to be important to Bighead Carp and Silver Carp. I defined my states based on observed coarse-habitat used by carp during the study. I limited my analysis to three states to avoid having an overly complicated model because the number of parameters being estimated increases exponentially with the number of states which quickly becomes prohibitive (White et al. 2006). My states included backwater habitat (B), tributaries (T), and mainstem river (M). Backwater habitats may be important areas where carp congregate during certain times of year (MacNamara et al. 2018; Prechtel et al. 2018) and may be important for removal as gear recapture probability is higher in backwaters compared to mainstem habitats (Birdsall 2023). Likewise, tributaries have been identified in some rivers as congregation areas (Chapman 2006; Camacho et al. 2023), whereas mainstem habitats could be important for carp dispersal and spawning (Coulter et al. 2016; Werner et al 2023). Understanding conditions that may be related to transitions among major habitats is important because they can inform managers when removal effort may be most effective (Ridgway et al. 2023a).

I defined six irregularly spaced time periods based on water temperature and discharge patterns throughout the study period to reflect unique environmental conditions between each period (t1, t2, t3, t4, t5, and t6) (Table 4) (Figure 7). Briefly, time intervals between t1 to t2, t4 to t5, and t5 to t6 were periods of increasing and variable discharge with increasing water temperatures. Time intervals t2 to t3 and t3 to t4 were periods of decreasing water temperatures and consistently low discharges with single increases in discharge magnitude above the mean for the study period (170 m^3/s). I made hypotheses predicting movement probabilities of tagged individuals between each time period. I hypothesized some periods would have a greater effect on the probability that carp transition among habitats. I hypothesized that during the time intervals t4 to t5 the probability of transitioning would be higher than the probability of remaining in a single state. This period encompassed environmental conditions that have shown to cue carp to move greater distances and seek different habitat (Jennings 1988; Schrank et al. 2001; Nico et al 2005). I also hypothesized that during conditions associated with lower movement (t2 to t3 and t3 to t4) the probability of remaining in a state would be greater than transitioning to other states. I believe these times do not provide the ideal cues for carp movements.

Multistate models are a generalized form of Cormack-Jolly-Seber models (Cormack, 1964; Jolly, 1965; Seber, 1965). The general assumptions of a CJS model that are shared by multistate models include tagging does not affect survival, all individuals have an equal probability of recapture, tagging marks are permanent, sampling occasions are instantaneous, populations are open with emigration considered permanent (Kéry and Schaub 2011). CJS models estimate the probability of apparent survival (s) across open periods and recapture (p) within each period after the initial capture period. Where transitions are constrained to either an "alive" or "dead" latent state. Estimates of apparent survival are not estimates of mortality due to emigration and mortality being confounded with each other. Multistate models introduce a transition probability parameter (ψ) for multiple "alive" states, where individuals can transition back and forth unlike the "dead" state which is permanent. ψ is also estimated across open periods. My primary interest was in transition probabilities between habitats of carp among discrete time periods. The estimation of ψ across periods allows me to extend traditional mark-recapture models to investigate transitions by carp to and from designated habitats. An assumption of multistate models is that individuals cannot occupy multiple states within the same sampling period and will transition among states during open periods. Within my detection history a single individual violated this assumption. I only retained the detection of this carp in the first state to avoid violation of the model assumption (Perry et al 2010; Labuzzetta et al. 2024; Van Vleet et al. 2024).

I adjusted my detection history to deal with shed or missing tags. Some individuals either died or shed their transmitters during my study. The distinction between dead individuals or individual that shed their tag was not possible. For these individuals, a distinction was made in my detection history that censored all further detections. This removed the individual from contributing to parameter estimations after it was presumed to have died or shed its tag. This censoring avoided biasing recapture probabilities. Six of these individuals died or shed their tag before the first period. I removed these individuals from the detection history because they provided no information to the model as well. A major assumption of the multistate framework is that all individuals in a state have the same likelihood to transition and be detected at each time period (Kéry and Schaub 2011). Throughout the study, I made needed adjustments to my SUR array. Some SURs were lost at various times and 10 additional SURs were added to my array in winter 2024 (Table 5). However, due to the mobile capabilities of both species and my wide distribution of active tracking reaches (Figure 5), I believe this assumption was reasonably met for the different state groups. When constructing my detection history there were multiple instances in which individuals were not found during a closed period but were detected in close temporal proximity to a closed period (i.e., in an open period). These instances result in the model not capturing transitions that occurred in the previous open period. For these instances, I moved individual detections into the closest closed period if the detection was <14 days from the closed period. There were three individuals that were never detected in any closed period but were detected during at least one open period. I moved these detections into closed periods to avoid biasing my survival and recapture estimates (Table 6). The focus of my analysis was on coarse-scale habitat transitions over coarse-scale time periods, thus moving individual detections allowed me to retain as much information as possible. This technique is used by other multistate studies (Melnychuk et al. 2017; Coulter et al. 2018a). Transitions are assumed to occur during the open period and including these detections may better reflect transitions than detections only occurring in the closed periods.

I first fit a multistate model using all three states, where transitions probabilities did not vary across the six time periods.

State process:

$Z_{i,fi} = fs_i$

$z_{i,t+1} \mid z_{i,t} \sim \text{categorical}(\Omega_{zi,t,1 \ldots S,i,t})$

Where $z_{i,t}$ is the true state of an individual i at time t. The state process represents the actual transitions of an individual (Kéry and Schaub 2011).

Observations process:

$y_{i,t} \mid z_{i,t} \sim \text{categorical}(\Theta_{zi,t,1 \ldots O,i,t})$

Where $y_{i,t}$ is the observed state of individual i at time t. The observed process represents the transitions that are observed and cannot be the same as the state process due to imperfect detection (Kéry and Schaub 2011).

Estimated parameters : s(B,.), s(M,.), s(T,.), Ψ(B-B), Ψ(B-M), Ψ(B-T), Ψ(M-B), Ψ(M-M), Ψ(M-T), Ψ(T-B), Ψ(T-M), Ψ(T-T), p(B,t), p(M,t), p(T,t), Where s is survival probability, Ψ is habitat-transition probability, and p is recapture probability.

Derived parameters: Φ(B,t), Φ(M,t), Φ(T,t),

where Φ is cumulative survival probability.

Model estimates are reported as the mode (most likely value) with 95% credibility intervals from the posterior distribution (Marjoram et al. 2003). These models indicated transitions between tributaries and backwater habitats were rare. Recapture and survival estimates were also similar between backwater and tributary states (Table 7, Figure 8). This indicated that minimal information would be lost by combining the backwater and tributary states. This is consistent with observed data, where most transitions were associated with the mainstem. Combining the two states also allows for time varying estimates of transitions probabilities to be made because there are far fewer parameters in a two-state model. The conditions of the lower Red River also support combining tributary and backwater states as they both provide low-velocity habitats where carp congregate (MacNamara et al. 2018; Birdsall 2023). I made time varying transition probabilities a random effect to generalize my findings to a broader temporal scale (Wagner et al. 2006). I defined the backwater/tributary state as state “A” The two-state model can be expressed as:

Estimated Parameters:

s(A,.), s(M,.),

p(A,t), p(M,t),

Ψ_{A-Mt} ~ Normal $(\mu_{\Psi A-M,} \sigma^2_{\Psi A-M})$,

$\Psi_{M\text{–}At} \sim \text{Normal}\,(\mu_{\Psi M-A,}\, \sigma^2_{\Psi M-A})$,

Derived Parameters: Ψ(M–Mt), Ψ(A–At),

Where:
$z_{i,t}$ = the true state of an individual i at time t
$y_{i,t}$ = the observed state of individual i at time t
s = survival probability
p = the time-varying recapture probabilities
Ψ = time-varying transitioning probabilities,
μ = the group means associated variance σ^2.

I fit the multistate model using the direct, state-space formulation described by Kéry and Schaub (2012). I estimated distributions with Markov chain Monte Carlo (MCMC) methods using the program JAGS (version 4.3.1, Plummer 2003) via the package jagsUI (Kellner 2024) in the statistical software R. All probability estimates were given broad uniform priors between 0–1. Adequate MCMC convergence (i.e., chain mixing) was achieved using four chains of 35,000 iterations each ran in parallel after a 10,000-iteration burn-in phase (thinning = 100). I considered convergence a potential scale reduction factor $\hat{R}<1.05$ (Brooks and Gelman 1998).

Results

Fish Tracking

I tagged carp at an approximately even sex ratio and equal numbers of each species over a range of sizes. I tagged 16 male and 9 female Bighead Carp, and 13 male and 12 female Silver Carp. Bighead Carp had a mean total length (TL) of 1040.12 mm (SD: 104.75, range: 964-1340 mm) and a mean weight of 21698 g (SD: 5952.98, range: 11750-36000). Silver Carp had a mean

TL of 871.68 mm (SD: 96.71, range: 609-1052 mm) and a mean weight of 9632 g (SD: 3822.76, range: 2500-16900) (Table 8).

My team and I detected 82% of my tagged carp. I conducted 171 active tracking events and obtained 1519 detections from Bighead Carp and 2596 detections from Silver Carp using active and passive telemetry. I detected 41 individuals at least twice (i.e., a minimum of two detections were needed to record a movement by an individual for my GAMM analysis). Eight of my tagged fish were presumed to have died or shed their tag (Table *8*).

Environmental conditions

Environmental conditions varied among seasons but mostly followed typical seasonal patterns for the lower Red River catchment. Higher discharges were recorded in the spring months and lower discharges in the late summer into autumn and winter. Discharge had a range of (7.58 - 1282.75 m^3/s) during the study period. Discharges were highest during my spring season (range: 33.69 - 1282.751) and lowest during my winter season (range: 8.44 - 458.73). As expected, water temperatures were highest during the late summer (range: 23.4 - 33.6), lowest during the winter (range: 2.6 - 17.7), with a range of (2.6 - 33.6 °C) over the study period (Figure 7)

Fish Movement

Bighead Carp and Silver Carp exhibited variability in their movement magnitudes. Bighead Carp had a mean movement distance of 2.37 km (SD: 18.05, range: 0-336.57) and mean movement rate of 0.46 km/d (SD: 1.8, range: 0-37.89). Silver Carp had a mean movement distance of 1.01 km (SD: 9.61, range: 0-206.99) and mean movement rate of 0.36 km/d (SD: .95, range: 0-18.02). The greatest movement distance (336.57 km) was recorded by a female Bighead Carp during my summer season (Table 9).

Detections of tagged fish varied across my SUR array. The greatest number of detections came from my SURs located in oxbows and tributaries (e.g., oxbows close to the OK-AR border, Kiamichi River, and Muddy Boggy Creek). Several SURs had no detections during their deployment including gates located at the upper extent of the catchment near Denison Dam, the Sulphur River, and Big Pine Creek. SURs located at the southern extent of my study area (i.e., AR-LA border) recorded only a few detections possibly indicating only a few fish left the study area (Table 5, Figure 2).

Movement Pattern analysis

My initial model comparisons indicated support for not including autocorrelation structures, whereas including smoothing terms for my parameters had more support than not including smoothing terms. For the distance model, the simplest model with no autocorrelation structure (AICc = 21181.78, log-likelihood = -10586.89, df = 4) had the most support compared to the same model with an autocorrelation structure (AICc = 21190.59, log-likelihood = -10590.29, df = 5). For my movement rate model, the simpler model (AICc = 6698.372, log-likelihood = -3345.181, df = 4) also had more support than the more complex model (AICc = 6697.675, log-likelihood = -3343.83 df = 5). Although the ΔAICc was <2 between the two models, I choose the simpler model with no correlation structures for all future models (Wood 2017). For both movement models, exploratory models with all terms containing a smoothing term had the greatest support compared to other models (Table 10).

My top-ranked model of absolute movements by carp contained an additive effect of CV of discharge and an interactive effect between CV of water temperature and discharge (Table 11 and Table 12). My top ranked model explained 71% of the deviance in these data. The random effect of individual explained 9% of the deviances in these data. My model validation indicated reasonable results with (GAMscale = 162.52) and (CV-mse-GAM = 165.1262). This similarity in estimates indicates that the model generalizes well to new data and is likely not overfit. The model was >2 ΔAICc away from all other models indicating this model had the greatest support among those considered. Both species moved at greater distances at higher CV of discharge values (Figure 9). The interactive effect between water temperature variability and mean discharge showed varying effects of discharge at different water temperatures variability. I divided discharges based on two standard deviations below and above the mean to show the effect of CV of water temperature on movement distances at low, medium, and high discharge. During low and medium discharge conditions, water temperatures variability had a minimal effect on movement distances. During high discharges, movement distances increased at greater water temperature variability values (Figure 10).

My top ranked movement rate model included an additive effect of CV of discharge and an interactive effect between CV of water temperature and discharge (Table 13 and Table 12). This model explained 39.2% of the deviance in the data. The random effect of individual explained 12% of the deviance in these data. My model validation indicated reasonable fit (GAMscale = 1.6819) and (CV-mse-GAM = 1.6880). The similarity in estimates indicates that the model generalizes well to new data and is likely not overfit. This model was >2 ΔAICc away from all other models that I considered. Carp moved at higher rates during higher values of CV of discharge (Figure 11). The interactive effect between CV of temperature and mean discharge indicated varying effects water temperature variability at different discharge conditions. I divided discharges based on two standard deviations below and above the mean to show the effect of CV of water temperature on movement distances at low, medium, and high discharge. During low discharges movement rates were higher at low to intermediate values of variability, during mean discharge levels water temperature had little effect on movement rate, during high discharges movement rates were also greater at low to intermediate values of water variability. (Figure 12).

Multistate analyses

The transition probabilities varied between my two states and over time. Transition probabilities from state A to state M were the highest between t1 and -t2 and t4 and -t5 and the lowest between t2 and -t3, t3 and -t4, and t5 and -t6 (Figure 13). Transition probabilities from state M to state A were highest between t1 and t2, t4 and -t5, and t5 and -t6 and lowest between t2 and -t3 and t3 and -t4 (Figure 14). The level of uncertainty was higher for transitions estimates from state M to state A. This uncertainty also occurred in the probability of remaining in state M (Table 14). Average apparent survival in state A was higher than in state M (Table 14). Recapture probability of my tagged fish was also variable through time. Recapture probability of my tagged carp was lower in state M with higher levels of uncertainty (Table 15).

Discussion

The variation among movement patterns in my tagged carp indicates there is a subset of highly mobile fish and many that move very little, and these two movement characteristics may be displayed by the same individual over time. I found both species' average movements were <3 km over my study period indicating a relatively sedentary population. Whereas other studies found carp to move at larger magnitudes, on average. For example, mean movement distances of 12.4 km and 4.13 km for Silver Carp and Bighead Carp, respectively, in the Wabash and Illinois rivers (Peters et al. 2006; Coulter et al. 2016). However, a subset of my tagged fish also made long distance movements (maximums were 336.57 km and 206.99 km for Bighead Carp and Silver Carp, respectively). Among the six individuals that had mean distances above 10 km, all recorded minimum distances <1 km and four had mode movement distances of <5 km. The variability within individual movements indicates the ability to be mobile or sedentary may not be static within the population (Peters et al. 2006; Booth et al. 2014). This contrasts with other studies that found individual carp to have relatively consistent mobile or sedentary characteristics (Coulter et al. 2022b). Successful invasive species typically have highly mobile capabilities which allow them to disperse into new environments and compete with native species (Lockwood et al. 2005; Roy et al. 2013; Prechtel et al. 2018).

Many movement studies show that individual variability is important. Individual variation in fish movement behaviors is assumed to contribute to population-level robustness and adaptability (e.g., gene flow, recolonization, species turnover; Albanese et al. 2004; Radinger and Wolter 2014). It is not uncommon to have a large range of variability in movement studies (Dance and Rooker 2015; Becker et al. 2016; Hughes et al. 2022; Pedaccini et al. 2023). My individual variability accounted for only 9% of deviance in fish movement distance model and 12% of deviance in my movement rate model. Harrison et al. (2019) demonstrated by tracking five species of large-bodied fishes that individual movements within a species were often more variable than movements among species. Other studies on invasive species tend to demonstrate highly variable movements among individuals (Peters et al. 2006; Rasmussen et al. 2012; Juette et al. 2014). Other studies of Bighead Carp and Silver carp have shown large variations in individual movement tendencies. For example, most individual Silver Carp had consistent total home range sizes of <26 km or >102 km in the Wabash River (Prechtel et al. 201 8). Also on the

Wabash River, Coulter et al. (2022) found mobile individuals consistently moved at greater distances than sedentary individuals. They found that mobile individual's movements were more related to environmental conditions compared to sedentary individuals. In addition to low individual variability among my tagged fish, there were also only a few that made larger movements.

The spatial patterns of tagged carp in my study indicated minimal large-scale migrations by individuals, especially upriver. The positioning of my SUR array allowed me to detect possible large-scale migration to the outer extents of my study area. SUR gates at both boundaries of my study area recorded zero or few detections. Varying detection efficiency and range of SURs due to different environmental conditions and mooring designs could explain the lack of detection at these gates (Winter et al. 2021; Carlson et al. 2023). However, given the duration that my gates were deployed and the detection of 82% of my tagged carp within the study area, it is unlikely that large numbers of tagged fish went undetected at these gates. My SUR gate 18 rkm below Denison Dam recorded no detections throughout the study period. Carp have the capacity to travel large distances especially when making spawning migrations (Lubejko et al. 2017; Whitledge et al. 2019) meaning this SUR gate was within a reasonable distance from all tagging locations. Large movements were recorded by some individuals, but I did not record any carp moving further upstream than Bois d'Arc Creek. Past studies in the same study area found both species occupy the entire catchment (Birdsall 2023), and USFWS has tagged carp in the upper part of the basin that we also never detected moving downstream past our SUR gate (USFWS, personal communication). The most upstream fish that my team and I tagged were located in Choctaw Creek, just downriver of our uppermost SUR. Interestingly, we never detected those two fish again and never detected any fish moving upstream of that location. Collectively, this suggests that carp may settle into specific areas and limit their overall home range. Smaller home ranges used by more sedentary individuals likely reflect ideal habitat in a smaller area (Prechtel et al. 2018). Stanton et al (2024) and Coulter et al. (2018a) both found carp were less likely to move from the pools they were originally tagged in within Illinois River. It is common that we find movement dynamics of large river fishes or tributary populations move within a specific extent but often not among different systems (e.g., Flathead Catfish, Vokoun and Rabeni 2005; Silver Carp; Werner et al. 2023; White Perch, McGrath and Austin 2009).

My results contrast with other studies that show intense directional movements during spawning conditions (Lubejko et al. 2017; Vallazza et al. 2021). My SUR gate at the lower extent of my study area (AR-LA bordar) only recorded three detections from two individuals. Although my study area is not biologically meaningful to fishes, it appears that the fish I tagged may have home ranges that are primarily within the study area. The proportions of resident and immigrant fish varies in other populations and is thought be influenced by habitat and limitations to movement. Werner et al. (2023) found 54% of adult Silver Carp were resident fish that were born in and had never left the Kansas River, whereas transient individuals mostly traveled short durations into the Missouri River. Barshinger et al. (2024) found that Silver Carp in the Arkansas River had minimal reproductive contributions to the lower Mississippi River catchment indicating large movements were made from the White River and Mississippi River into the Arkansas River for reasons other than spawning. Although successful hatch has not been documented in the lower Red River (Ramsey et al. 2024), we did determine both Bighead Carp and Silver Carp were successfully spawning (i.e., present of empty follicles in ovaries) in the study area via histological analyses (Brewer et al. Unpublished data). This is supported by the moderate movements during conditions that have been associated with spawning and the minimal emigrations out of the study area; behaviors that suggest both species are likely attempting to spawn within the study area. Future efforts would benefit from tagging carp across a broader range of the Red River to determine population home ranges. Moreover, a longer tracking period may reveal that these fish move under certain environmental conditions outside of what we experienced over our study extent (e.g., following a drought when recolonization would be needed).

My top movement distance and movement rate model contained relationships consistent with my variability hypothesis. My results indicated nonlinear relationships between movement and these abiotic conditions. Discharge and temperature variability has been related to fish movement in other studies (Taylor and Cooke 2012; Coulter et al. 2016; Olden and Naiman 2010; Morash et al. 2021). Discharge variability is a key aspect of the flow regimes for many large river fishes (Reinfelds et al. 2013; Carpenter-Bundhoo et a l. 2023). Within their native ranges, flow is very important for carp to complete their life cycles (Duan et al. 2010; Li et al. 2013; Fang et al. 2022). Specific flow and temperature conditions are needed for both species to spawn in native ranges (Chapman 2006; Chapman et al. 2016). Changes to these thermal and flow regimes have negatively affected their abundances in the Yangte River (Yu et al. 2018). Changes to dam operations on the mainstem Red River and major tributaries could affect flow variations and thus limit carp movement but would also likely negatively affect the native fishes with similar flow relationships (i.e., Cyprinids Worthington et al. 2018; Mollenhauer et al. 2022; or Paddlefish Tripp et al. 2019).

My multi-state analysis results points to important periods when carp transition between major habitats. Carp were more likely to transition into different habitats across time intervals with increasing water temperatures and more variable discharge. Intervals that contained decreasing water temperatures and few instances where discharges rose above the mean for the study period resulted in low probability of transitioning into different habitats. The seasonal association with different habitat and movement magnitude have been seen in other studies (Lubejko et al. 2017; Vallazza et al. 2021; Coulter et al. 2022b). Interestingly, carp transitions to and from mainstem and backwater or tributary habitat were high between the same periods (i.e., t4-t5). This time interval was characteristic of environmental conditions associated with spawning by carp (Lubejko et al. 2017; Erickson et al. 2016; Whitledge et al. 2019). Bighead Carp and Silver Carp typically move into higher velocity habitats such as the mainstem to successfully spawn (Deters et al. 2013; Li et al. 2013). Similar probabilities could be caused by individuals being at different stages in the spawning process resulting in similar transition rates as some individuals are moving into the mainstem to possibly spawn and some are moving into backwater and tributaries to rest and feed (Lubejko et al. 2017; Erickson et al. 2016; Yu et al. 2018). Large individual variations in spawning timing is not uncommon (Coulter et al. 2013; Tucker et al. 2020; Lenaerts et al. 2023a). Carp could also be using backwater and tributary habitats as velocity refugia along their spawning movements (Werner et al. 2023) or while waiting for more suitable spawning conditions in the mainstem (Calkins et al. 2012; Coulter et al. 2016)

Recapture probabilities may be influencing the uncertainty in my model estimates. The lower recapture probabilities within the mainstem translated to higher levels of uncertainty in my estimates of transition probabilities and survival in the mainstem river. The high level of uncertainty in my recapture probabilities within the mainstem was not surprising but must be taken into consideration in my model interpretations and subsequent management recommendations. In the Red River, discrete sampling of carp using electrofishing found similar detection discrepancies between the mainstem and other habitats (Birdsall 2023). Using an occupancy framework, Birdsall (2023) found detection was negatively associated with discharge indicating carp were more likely to be detected in lower-velocity habitats. Conditions including velocity, substrate, vegetation, and receiver orientation can limit the detection range of acoustic receivers (Kessel et al. 2014; Stott et al. 2021; Carlson et al. 2023). The wide channel, increased velocity, and shifting sand substates of the Red River could contribute to low and uncertain detection probabilities within the mainstem state. Stanton et al. (2024) found detection probabilities of tagged fish were lower in larger pools with more complex habitat in the Illinois River. Carlson et al. (2023) found that detection probability was higher for receiver mooring designs that protected the receiver from higher velocities compared to designs that were not protected from flows. Weinz et al (2021) found that submerged vegetation also reduced detection efficiency. A greater number of SURs within backwater and tributary habitats could also be contributing to the differences in recapture probabilities. To offset that possibility, I used active tracking more frequently in the mainstem.

My results indicate that environmental conditions were more important to carp movement patterns than individual traits. My individual trait hypothesis models had less relative support than other models. This is likely due to the low amount of variance explained by my individual random effects. This indicates that all fish movements regardless of individual traits were more related to my environmental covariates. This is in contrast with other studies that found relationships between fish weight and movement magnitude (Mollenhauer et al. 2013; Radinger and Wolter 2014; Cooke et al. 2022). Other studies have also found sex to be a related to fish movement (Hutchings and Gerber 2002; Stiver et al. 2007). Bighead Carp did, on average, move at greater distances and rates than Silver Carp. However, species' interactive effect with discharge was not retained in my top model. This could be a result of both species having very similar life-histories and habitat needs (Li et al. 2013; Yao et al. 2016) and thus moving at similar magnitudes.

My results also indicate apparent survival was higher in backwater and tributary habitats compared to mainstem habitats. Commercial fishing and bowfishing in the mainstem could be influencing the lower survival in my mainstem state. Bow fishers regularly target Bighead Carp and Silver Carp in their invaded range (York et al. 2022). Commercial fishing is only open in the Arkansas portion of the Red River is open year-round and may influence carp survival. Carp may be better protected from fishing mortality in tributaries and backwaters that have more turbid water, complex habitat, and cannot be accessed by boat during parts of the year.

My study results may provide useful direction when determining when and where to attempt carp removal efforts in the lower Red River. Carp removal success can vary greatly on timing and location of these efforts (Norman and Whitledge 2015; Altenritter et al. 2022). Understanding when carp may be in specific habitats can help fine tune removal efforts to slow down invasion or reduce carp biomass (Love et al. 2018; Rytwinski et al. 2019; Ridgway et al. 2023a). I found that carp were more likely to transition into different habitats during increased discharge and warming water temperatures. During these conditions, carp may not be as congregated, resulting in less effective capture. This is especially true given that transitions appeared to be in both directions (i.e., to the mainstem river and into backwater and tributaries) as opposed to movement into one area that could be targeted. Targeting carp during times associated with lower movement magnitudes and lower likelihood of transitions between habitats (i.e., winter months) would increase sampling efficiency. These results should be considered context dependent as managing carp across their invaded range in the same way may not reach management goal. Whereas many have suggested that carp removal in known spawning habitats during the spring and summer months could reduce reproductive success of both species (Tsehaye et al. 2013; Cupp et al. 2021; Glubzinski et al. 2021), it is unlikely to be successful using traditional gears on the Red River. Moreover, not sampling during this time would also be less disruptive to spawning by native large river fishes. Most of my tagged carp appeared to remain in the study area indicating carp may not be emigrating out of the study area in great numbers over the timeline of my study. Future studies evaluating the use of barriers lower in the catchment (i.e., Louisiana reaches of the Red River) could also be a strategy worth exploring to ensure that any removed fish are not simply replaced by new fish immigrating into the middle basin of AR, OK, and TX. However, the behavior of fish can change via a compensatory response to some stressors (Zipkin et al. 2008; Weber et al. 2016; Walsworth et al. 2020). Thus, continued evaluation of carp movements may be warranted if the agencies decide to undergo large-scale removal operations. Given the costs, evaluation of successful change in the non-native populations may be warranted.

Chapter III

Habitat selection by Bighead Carp and Silver Carp within the lower Red River catchment

Introduction

Understanding fish habitat use and selection (i.e., disproportionate use) is important in developing conservation and management plans for native and invasive species. Habitat selection can help explain the variations in a fishes' life-history and ecology (Rice et al. 2005). Environmental factors such as water temperature (Lawson et al. 2004), substrate (Coulombe-Pontbriand et al. 2004), and discharge (Allouche et al. 2001) can influence where and when fish occupy certain habitats. Knowledge of habitats that fish select, particularly during important time periods (e.g., spawning seasons), is important for the conservation of some species. Through use of biotelemetry, researchers found aggregations of adult and juvenile Lemon Sharks *Negaprion brevirostris* off the Florida coast in specific habitats, which were then quantified and given protection (Brooks et al. 2019). Favrot et al. (2018) examined the microhabitat use of juvenile Chinook Salmon *Oncorhynchus tshawytscha* and found deep-low-velocity habitats were being selected for. This information was then used to recommend management plans to increase this microhabitat such as the development of beaver-pond complexes. Knowledge of habitat selection can also be used in the management of invasive species. Habitat selected by invasive species can be instructive in understanding how they will interact with other species and at what locations. Many successful invaders are flexible in their niche use, meaning they can use many different types of habitats and overtake new environments easily (Wright et al. 2010; Bussmann et al. 2022). The flexibility of invasive species poses an issue for researchers and managers as invasive species may not select for the same habitat as in their native distribution (Hintz et al. 2017a; Ibarra et al. 2024), thus creating uncertainty in how invasive species interact with new environments.

Knowledge of habitat selection by invasive species can be useful for understanding how to improve control or eradication efforts of these species. Targeted control efforts could be used in habitats that have higher concentration of invasive carp (Cupp et al. 2021; Glubzinski et al. 2021). Herding techniques in suitable locations and specific habitats (e.g., low-velocity areas) can be effective in removing large quantities of Bighead Carp and Silver Carp (Ridgway et al. 2023a). Bussmann et al. (2022) found Round Gobies *Neogobius melanostomus* used human modified habitats at higher rates indicating management strategies could be targeted at these habitats. Understanding the temporal and environmental patterns associated with invasive species habitat selection can further improve management (Kadye and Booth 2013). In the Potomac River, Lapointe et al. (2010) found Northern Snakehead *Channa argus* were most vulnerable to control efforts during their spawning season when adults were more likely to be in shallower habitats. Telemetry technology can also be used by tagging and tracking a smaller number of fish to locate aggregations of fish, where they can be more effectively removed. Known as the Judas technique, this has been successful in controlling Common Carp *Cyprinus carpio* in Midwestern lakes (Bajer et al. 2011; Bajer et al. 2019). Insights into habitat selection by carp can also improve barrier effectiveness by informing when and where these tools can be implemented (i.e., stopping movement between river pools) (Kallis et al. 2023). Knowledge of habitat selection by carp in each system is important for efficient targeted management.

Bighead Carp and Silver Carp inhabit a variety of habitats under different environmental conditions to complete all life stages. Bighead Carp and Silver Carp are associated with low-velocity habitats (e.g., backwaters, behind wingdikes, and in tributaries) throughout much of their invaded range (e.g., Wabash River, Coulter et al. 2016; Wabash River, Prechtel et al 2018; Illinois River, Glubzinski et al. 2021). These low-velocity areas are more conducive for feeding and conserving energy (Coulter et al 2016). However, when spawning, carp move into higher-velocity habitats presumably to facilitate the downstream drift of their semi-buoyant eggs (Chapman 2006; Erickson et al. 2016). Seasonality can also change how carp select habitat. Glubzinski et al. (2021) found shallow-water habitat with lower water temperatures supported greater numbers of Silver Carp during warmer months in the Illinois River. Although habitat-use trends have been established with carp occurrence, different river systems may require carp to change their habitat selection (Glubzinski et al. 2021).

Carp in the lower Red River could select habitat differently compared to more established carp populations in the United States. Carp appeared to have higher occupancy probability in tributaries compared to the mainstem Red River possibly due to limited availability of backwater habitat (Birdsall 2023). Further knowledge on habitat selection by carp in catchments that differ from other established populations is important for understanding the full range of environments that can be exploited by both species (Harms et al. 2024). Combining acoustic telemetry with habitat selection provides a more detailed view of carp behavior compared to other studies (Haupt et al. 2016; Birdsall 2023). Many studies have described habitat used by carp at fine-scales (DeGrandchamp et al. 2008; MacNamara et al. 2018; Glubzinski et al. 2021), but there remains a knowledge gap as to which habitats carp are selecting for in larger catchments such as the Red River. Using individually tagged carp; I can determine habitat selection across a relatively large study extent over time (Brownscombe et al. 2022). Correspondingly, my study objective was to assess habitat selection by Bighead Carp and Silver Carp in the lower Red River catchment.

Methods

Seasons

I determined carp habitat selection within multiple seasons throughout my study (see Chapter 1). Briefly, I based my season criteria on carp biology and historical water temperature data for the lower Red River using the USGS stream gage near Index AR 07337000 from 1990-2022. Typically, winter (i.e., Dec-Feb) is characterized by low water temperatures (mean temperature of 9.9° C) and lower flows (mean discharge 17.7 m^3/s). During the spring (i.e., March-May), water temperatures are typically warm (mean temperature of 19.9° C) and there is an increase in discharge conditions (mean discharge of 336 m^3/s). The summer season (i.e., June-August) is typically characterized by declining discharges to base flow conditions (mean discharge of 170 m^3/s) and warm water temperatures (mean temperature of 29.9° C). The river tends to begin cooling during autumn (i.e., September-November) (mean water temperature 21.1° C) with typically low to moderate flows (mean discharge of 130 m^3/s).

Used and available habitat sampling

I determined habitat selection by Bighead Carp and Silver Carp using my active tracking data (see Chapter 1). Briefly, I tracked within three seasons: winter (Dec 1st-Feb 28th), spring (Mar 1st-May 31st), and summer (Jun 1st-Aug 31st). I tracked multiple reaches of mainstem river and tributaries within the lower Red River catchment in Arkansas, Oklahoma, and Texas (Figure 5). I actively tracked 3-5 days each week within each season. I used an omni-directional hydrophone to approach a fish's location until decibels read ≥75 (Coulter et al. 2016). I then used a directional hydrophone to triangulate and confirm the fish's location (Calkins et al. 2012). Once a location was determined, I recorded GPS coordinates, date, and several habitat characteristics (see 'habitat covariates' below). Environmental conditions such as water depth, substrate type, and vegetation create variability in location estimates from acoustic transmitters (Stott et al. 2021). Due to this limited fine scale positioning ability, I placed a 50-m linear buffer around each fish’s estimated location, (hereafter used points). This encompassed enough area to ensure that the tagged carp was within the 50-m buffer and still provided a measure of reach-scale habitat selection (Coulter et al. 2016). Before tracking I conducted testing to ensure the proper buffer size. I was able to gain a 67-74 decibel reading from a test tag at approximately 25 meters away and 75-85 decibels from approximately 13 meters away. These buffers were used to define areas of used habitat (Manly et al. 2002).

I measured habitat availability using random GPS coordinate points taken within each tracking reach. I first determined the percentage of primary channel and velocity refuges within each tracking reach. I defined the primary channel as areas which appeared to contain the thalweg and were in direct flow of the river. I defined velocity refuges as areas out of the main flow of the river or tributary (i.e., connected oxbow lakes, behind wing dikes, backwaters, forewaters, and cut-off side channels). I used NAIP satellite imagery and ArcGIS Pro tools to find the area in km^2 of both primary channel and velocity refuge areas. This informed the number of available points that were needed in each area to gain an accurate representation of habitat across the catchment. I assigned random available points using ArcGIS Pro prior to tracking, ensuring that no available points were less than 50-m apart. I used the same 50-m linear buffer to measure all covariates as in my used points. I created enough available points to obtain a 1:5 ratio to ensure adequate available habitat was quantified habitat within the lower Red River (Nad’o and Kaňuch 2018).

Based on previous estimates of carp movement, I designated the entire study area as available to tagged individuals (DeGrandchamp et al. 2008; Coulter et al. 2016). My tracking reaches totaled 291 rkm of the mainstem and several major tributaries. This accounts for 41% of the total rkm mainstem the study area. Tracking reaches encompassed a wide range of habitats across the catchment including braided mainstem, channelized mainstem, free-flowing and dammed tributaries, and backwater areas. Tracking a large area was important in locating tagged carp and gathering a representative sample of available habitat (Barbet-Massin et al. 2012). I quantified the same habitat measurements in both used and available points.

Habitat covariates

Rivers and streams are hierarchically structured, and I used this framework in quantifying my habitat variables. Frissel et al. (1986) classified scales from fine to coarse where microhabitats are nested within channel units (e.g., pools, riffles), which are then nested within reaches. Reaches tend to be investigator defined and correspond to sampling effort associated with the life history of an organism or to meet statistical assumptions of closure, etc. (Wathen et al. 2017). Multiple reaches occur within the same stream segment (i.e., tributary confluence to confluence). Lastly, stream segments make up the network within a catchment. Examining how habitat is selected across both coarse and fine scales can be used to answer different questions depending on the species and life history stage (Fausch et al. 2002). For example, Ramsey et al. (2024) found that nursery habitat for some fishes depended on the location of finer-scale features within the stream network. I examined habitat selection by carp at the reach-scale (i.e., used and available points) and stream segment scale. Investigating multiple scales allows managers to see the influence of selection at a coarser-scale such as segment sinuosity on finer habitat selection such as average reach depth. A knowledge gap persists in habitat selection studies that lack a multiscale analysis (McGarigal et al. 2016).

The habitat characteristics that I hypothesized would relate to habitat selection by carp were water depth, water temperature, average velocity, habitat type (i.e., primary channel or velocity refuge), segment sinuosity, distance to velocity refuge, distance to river bend, and distance to third order or greater tributary confluence. I collected average water depth, water temperature, average velocity, and habitat type within each used and randomly assigned available point (detailed below). I also calculated the segment sinuosity, distance to velocity refuge, distance to river bend, and distance to third order or greater tributary confluence at the segment scale of each used and available point (Table 16). Habitat characteristics were indexed to season, which was a factor (i.e., categorical variable) in my model. This allowed me to model variation in habitat selection across seasons.

I quantified water depth (1.0 m) at each used and available point. Depth relates to many important behavioral factors such as thermal regulation, feeding, and predator avoidance (Allouche et al. 2001; MacNamara et al. 2018; Sullivan et al. 2021). DeGrandchamp et al. (2008) found carp at an average depth of 3.9 m in the Illinois River. I recorded water depth using a boat-mounted depth finder. I located the thalweg within each used and available point and collected three measurements of depth at the top, middle, and bottom of each point, and averaged them to reflect used or available point conditions.

I measured water temperature (1.0°C) because it is an important driver of fish habitat selection due to water temperature’s effect on fish activity levels and reproductive development (Brett and Groves 1979; Myrick et al. 2000; Wang et al. 2010). Prechtel et al. (2018) found Silver Carp selected warmer water temperatures and avoided colder water in the Wabash River. I collected water temperature using a water-quality meter (YSI ProDSS) or (Ultrapen PT1) in the middle of the used or available point in the thalweg.

I quantified water velocity (1.0 m/s) because fish may occupy different velocities to avoid predators, feed, or reproduce (Lamouroux et al. 1999; Allouche et al. 2001). Carp are associated with lower-velocity areas to conserve energy or efficiently feed in the Illinois River, DeGrandchamp et al. (2008); Mississippi River, Calkins et al. (2012); and Wabash River, Prechtel et al. (2018) and higher velocities to successfully spawn (Lenaerts et al. 2023a). I measured water velocity using a flowmeter (Hach FH950) at approximately 1 m below the water's surface. I took three measurements of velocity at the bottom, middle, and top of the point and calculated an average to represent the used or available point conditions.

I recorded the habitat type (primary channel or velocity refuge) of both used and available points to determine their relative selection for carp. Bighead Carp and Silver Carp are associated with backwater habitats in the Illinois and Mississippi Rivers (Calkins et al. 2012; MacNamara et al. 2018). I designated each used or available point as a velocity refuge, or primary channel. I made these designations based on definitions above. Briefly, I defined velocity refuges as an area of minimal to no velocity that has little to no flow influence from the main river discharge. This includes connected oxbows, behind wing dikes, and side channels. I defined the primary channel as areas in the mainstem or tributaries which contained the thalweg or primary direction of flow.

I quantified the sinuosity of both used and available segments. Sinuosity is a coarse scale metric associated with finer-scale habitat complexity (Rowe et al. 2009). More complex habitat includes areas with both high and low velocities which would allow carp to spawn or feed (Deters et al. 2013). I calculated sinuosity by dividing the river kilometer distance of the segment (i.e., area between 4th order or greater tributary confluences (Strahler 1957)) by the straight-line distance of the segment using the distance tool in ArcGIS Pro. I measured the sinuosity of a random subset of segments that were actively tracked, which served as the available segments.

I recorded the distance (1.0 rkm) from the center of each used and available point to the nearest velocity refuge. Carp tend to associate with low-velocity habitat within both their invaded and native range (Kolar et al. 2007; MacNamara et al. 2018; Prechtel et al 2018; Glubzinski et al. 2021). These areas provide refuge from the higher-velocity main channel (Coulter et al 2016) and provide important larval and juvenile habitat for both species (George and Chapman 2013). I marked the locations of all velocity refuges in ArcGIS Pro using NAIP satellite imagery and NHDplus Flowlines. I defined velocity refuges as areas out of the main flow of the river or tributary (i.e., connected oxbow lakes, behind wing dikes, and cut-off side channels). I then overlaid the GPS coordinates of each used and available point onto the NHDplus flowlines. Next, I used the distance tool in ArcGIS Pro to measure the distance from each used and available point to the center of the closest velocity refuge point in either upstream or downstream directions. I used the river distance to maintain an accurate measurement.

I recorded distance (1.0 rkm) from the center of each used and available point to the nearest river bend. I hypothesized that the outside bend of the primary channel contains the conditions needed for both species to reproduce. Deters et al. (2013) indicated that carp could be using the outside river bends to spawn in more sinuous segments. The higher velocities of the outside bend could be important for carp to release their semi-buoyant eggs into the main channel flow similar to other pelagic broadcast-spawners (Hoagstrom et al. 2015; Durham and Wilde 2009; Camacho et al. 2023). I marked the locations of the middle of each river bend in ArcGIS Pro using NAIP satellite imagery and NHDplus Flowlines. I then overlaid the GPS coordinates of each used and available point onto the NHDplus flowlines. Next, I used the distance tool in ArcGIS Pro to measure the distance from each used and available point to the center of the closest river bend in either upstream or downstream directions. I used the river distance to maintain an accurate measurement.

Finally, I measured the distance (1.0 rkm) from the center of each used and available point to the nearest third order or greater tributary confluence. I chose tributaries that were third order or greater because I hypothesized carp would inhabit large tributaries and be unbale inhabitat tributaries that were <3rd order. For Bighead Carp and Silver Carp, tributaries can serve as low-velocity areas that are used for feeding or refuge in the Mississippi, Illinois River, and Red River (MacNamara et al. 2018; Glubzinski et al. 2021; Birdsall 2023). Tributary confluences are also key spawning areas in their native ranges and the upper Mississippi River (Chapman 2006; Camacho et al. 2023). I calculated the distance to nearest third order or greater tributary confluence using geospatial imagery and tools. I marked the locations of tributaries with a stream order of three (Strahler 1957) or greater, which flowed into the lower Red River in ArcGIS Pro using NAIP satellite imagery and NHDplus Flowlines. I then overlaid the GPS coordinates of each used and available point onto the NHDplus flowlines. Next, I used the distance tool in ArcGIS Pro to measure the distance from each point to the center of the closest tributary confluence point in either upstream or downstream directions. I used the river distance to maintain an accurate measurement. For used and available points that occurred within tributaries, I measured the distance to the confluence with the Red River.

Data analysis

I made several hypotheses that I believed would explain habitat selection by carp. First, I wanted to investigate if habitat relationships were associated with bioenergetics theory. The need to feed and conserve energy is important for all fish to grow and mature (Brown et al. 1983; Silva et al. 2012; Barneche et al. 2018). I hypothesized that carp would select habitat that would maximize their growth. Bighead Carp and Silver Carp have shown to be associated with low-velocity habitats among their native and invaded ranges (Prechtel et al. 2018; Shuai et al. 2018;

Yu et al. 2018). These areas have higher zooplankton and phytoplankton abundances providing carp with their primary food source (Cooke et al. 2009; Li et al. 2013; Houser et al. 2016). Velocity refugia also allows carp to conserve energy (Calkins et al. 2012; Prechtel et al. 2018). High velocity habitats force fish to expend energy by maintaining station (Hoover et al. 2017; Tan et al. 2019; Xi et al. 2024). Optimal thermal conditions are also an important aspect of fish bioenergetics (Selong et al. 2000; van Rijn et al. 2017; Prechtel et al. 2018). Selecting habitats that provide thermal refuge in warm and cold conditions are important for carp growth (MacNamara et al. 2018; Glubzinski et al. 2021). Additive effects of velocity, depth, habitat type, and distance to velocity refuges allowed me to test these hypotheses. I also hypothesized an interactive effect of water temperature and season because I expected carp would select for warmer water in the winter season and cooler water in the summer season to maintain their thermal optima. I expected carp would be more likely to select habitats with low velocities, which were not in the primary channel, contained deeper water and select areas closer to velocity refuges.

My second hypothesis was that carp would select habitat related to spawning. Carp appear to spawn in habitats that differ from habitats more associated with feeding (Coulter et al. 2013; Hintz et al. 2017a; Yu et al. 2018). As protracted pelagic broadcast spawners, carp release their neutrally buoyant eggs over unprepared unguarded substrates (Chapman 2006; Erickson et al. 2016). Minimal velocities are needed to maintain their neutrally buoyant eggs and larvae in suspension (Lenaerts et al. 2023a). Both species require specific spawning habitats (i.e., turbulent water conditions created by hard structures) in their native ranges (Duan et al. 2010; Fang et al. 2022). These habitat requirements could influence carp habitat selection more than their bioenergetic needs. I hypothesized carp may select higher velocity areas and be in closer proximity to possible spawning habitats (i.e., river bends, tributary confluence, or highly sinuous segments). I hypothesized an interactive effect between season and distance to tributary confluence. I expected carp to select habitat closer to tributary confluences in the spring and have no relationship during the summer due to ideal spawning habitat in tributary confluences Deters et al. 2013; Fang et al. 2022). I also hypothesized an interactive effect of velocity and season as I expected carp would select higher velocities in the spring and lower velocities in the summer and winter due to their spawning habitat association (Duan et al. 2010; Fang et al. 2022).

My third hypothesis was that individual characteristics would influence habitat selection by carp. Individual characteristics (i.e., sex, weight, or species) could determine how carp select habitat. Fish can partition resources based on a variety of characteristics due to differences in individual behavior or habitat needs. (Berner et al. 2015; Buxton et al 2020; Harms et al. 2024). For example, Rodnick et al. (2008) found female Coho Salmon *Oncorhynchus kisutch* selected reaches with colder water temperatures compared to males in the West Fork Smith River in Oregon. Sizes of individuals can also influence selection as larger fish may be more prone to dispersal or have greater endurance in higher velocities (Radinger and Wolter 2014; Cooke et al. 2022) Bighead Carp and Silver Carp have very similar life-history traits (Jayasinghe et al. 2015) but could be selecting habitat differently within the lower Red River catchment. Hoover et al. (2017) found Silver Carp had greater endurance in high-velocities compared to Bighead Carp. I hypothesized that females and larger individuals would be more likely to select high velocity conditions and deeper water compared to smaller males. I also hypothesized that Bighead Carp would be more likely to select velocity refugees compared to Silver Carp due to Silver Carps higher endurance (Hoover et. 2017; Xi et al. 2024).

I modeled the variation in carp habitat selection using a resource selection function (RSF) (Manly et al. 2002). I interpreted predicted probabilities from the RSFs as indicators of relative habitat selection (relative to Manly et al. 2002). RSFs are used to determine species selection or avoidance of habitat. My analysis uses a presence-only logistic regression, where used points are designated as 1s, and available points are designated as 0s. My analysis gives insights on how habitat selection by carp in catchments differs between established populations and populations in the lower Red River and informs managers on habitat that is important to carp (Matthiopoulos et al. 2015; Harms et al. 2024). Locating individually tagged fish gives a detailed view of carp behavior and allows managers make better inferences on population wide characteristics (Brownscombe et al. 2022).

I performed any necessary standardizations and transformation to variables prior to model development. I log transformed depth and velocity due to right-skewness in their distribution. I then tested for multicollinearity among my variables as described in objective one (Table 17). Carp total length was highly correlated with carp weight ($| r | = 0.96$), thus I excluded total length and retained all other variables. I examined all continuous variables to ensure they met the assumptions of continuous data. All retained continuous variables were standardized to have a mean of 0 and standard deviation of 1. This promotes convergence of the model and aids interpretation. I used R (version 4.4.1 R Core Team 2024) to conduct all analysis.

I fit a generalized linear mixed-effects model (glmm) with a binomial distribution and logit link function using the “lme4” package (Bates et al. 2015). I gave used points (i.e., individual carp locations) a coded value of $Y= 1$ and available points (i.e., randomly selected points) a coded value of $Y= 0$ (Boyce et al. 2002) for observation i and fish j assuming a Bernoulli distribution.

$Y_{ij} \sim \text{Bernoulli}(\Psi_{ij})$.

I assigned water depth, water temperature, water velocity, carp weight, distance to tributary confluence, distance to velocity refuge, distance to river bend, and sinuosity as continuous variables in my model. Sex, species, and habitat type were assigned as categorical variables. I assigned individual fish as a random effect for all models (Gillies et al. 2006). The glmm can be expressed as:

$\text{logit}(Y_{ij}) = \beta_0 + \beta_n x_{nij} + \alpha_n + \beta_{nj} x_{nj} + \gamma_{0j}$

Ψ = estimated probability of use

β_0 = the grand intercept

$\beta_n x_{nij}$ = the *n* coefficient for *n* continuous covariates at observation *i* for fish *j*

α_n = the *n* coefficient for *n* categorical covariates at observation *i* for fish *j*

$\beta_{nj} x_{nj}$ = the *n* coefficient for covariate *n* for fish *j*

γ_{0j} = the random fish intercept

I built a series of hypothesis-based models to investigate habitat selection by carp. I built three models per overarching hypothesis (stated above) that examined a unique subset of covariates to evaluate the relative support for each hypothesis (Table 18). Each model contained covariates the represented a broad hypothesis about factors that could be influencing habitat selection. I compared all models using Akaike Information Criterion corrected for small sample size (AICc, Burnham and Anderson 2002) to determine which model had the greatest support. The model with the lowest AICc score was designated as my top model. All models with ΔAICc< 2 were considered to have equal empirical support. If models had ΔAICc< 2, the simpler models with fewer parameters were favored to avoid unnecessary model complexity (Burnham and Anderson 2002). I assessed the top model's fit using a binned residuals plot. Models were considered to fit adequately if approximately 95% of residuals fell between the error bounds (Gelman and Hill 2006). I also assessed model fit using marginal R^2 (i.e., the variance explained by my fixed effects) and conditional R^2 (i.e., the variance explained by fixed and random effects

Results

Use and availability sampling

I tagged carp at an approximately even sex ratio and equal numbers of each species over a range of sizes. I tagged 16 male and 9 female Bighead Carp, and 13 male and 12 female Silver Carp. Bighead Carp had a mean total length (TL) of 1040.12 mm (SD: 104.75, range: 964-1340 mm) and a mean weight of 21698 g (SD: 5952.98, range: 11750-36000). Silver Carp had a mean TL of 871.68 mm (SD: 96.71, range: 609-1052 mm) and a mean weight of 9632 g (SD: 3822.76, range: 2500-16900) (Table 8).

I used active tracking to quantify both habitat used by Bighead Carp and Silver Carp and habitat available. I completed171 tracking events across 12 reaches of the lower Red River catchment during my winter, spring, and summer seasons (Table 19). I recorded 394 used points (i.e., fish locations) from 43 individuals, and 2,526 available points. I attempted to gain at least a 1:5 ratio of used to available points, but I was able to achieve a 1:6 ratio of used to available points.

Habitat covariates

Active tracking across three seasons allowed me to gain a representative representation of the habitats and conditions that were available to carp. Habitat covariates values measured at used points were less variable than measurements at available points (Table 20). Available velocity had a range of 2.36 m/s in mainstem habitats during spring flood pulses to 0.00 m/s in backwater habitats. Used velocity only ranged from 1.76-0.00 m/s. Available depth had a mean of 3.07 m and used depth had a mean of 4.10 m.

Data analyses

My selection model that had the most support contained the additive effects of velocity, distance to velocity refuge, habitat type, water depth, and an interactive effect between water temperature and season (Table 21). This model was had adequate fit according to the binned residual plot and R^2 values (Figure 15 and Table 21). Covariates had varying effects on selection likelihood (Table 22). Carp selected deeper water and were more likely to select velocity refuges compared to the primary channel (Figure 16, Figure 17). Although a weak relationship, carp were slightly more likely to select areas closer to velocity refuges (Figure 18). Both species selected slower velocity conditions (Figure 19). Carp were more likely to select warmer water temperatures during my winter season, however there was a considerable amount of uncertainty around this estimate. Carp were slightly more likely to select warmer water temperatures during my spring and summer seasons, however this relationship was also weak (Figure 20).

Discussion

My top model contained relationships consistent with my bioenergetics hypothesis. Carp selected habitats and conditions that could be used to optimize their bioenergetic needs. These habitats may allow carp to feed more efficiently and conserve energy. The selection by carp of these habitats is common among other populations (Li et al. 2013; MacNamara et al. 2018;

Werner et al. 2023). Selection of these habitats could contribute to carp's capacity for rapid growth and high fecundity (Sass et al. 2010; Lenaerts et al. 2023a; Williams et al. 2023). Both traits make them well suited to invade new environments that have enough forage and refuge habitat (Tsehaye et al. 2013; Anderson et al. 2017; Ivan et al. 2020). Plankton densities can be much higher in lower-velocity habitats (Sampson et al. 2009; Houser et al. 2016; Hintz et al. 2017b). Thus, carp are likely using these areas to feed. Carp are also likely selecting lower velocities to conserve energy. Xi et al. (2024) found Silver Carp and Bighead carp displayed avoidance behaviors when subjected to accelerating velocities. Other large river fishes also use velocity refugia. For example, Alligator Gar *Atractosteus spatula* in the Fourche Lafave River were found to use floodplain habitats that provided reduced velocities compared to the mainstem river (Kluender et al. 2017). Habitat outside of the main flow of large rivers are also important for larval and juvenile fish to forge, grow, and avoid predators (Love et al. 2017; Chick et al. 2020a; Ramsey et al. 2024). This highlights the importance of hydrological conditions on large river fishes ecology and the affects human alterations can have on both native and invasive species. The selection of deeper water is less consistent among other studies. In the Illinois River, Silver Carp abundances were found to be negatively associated with increased water depths (Glubzinski et al. 2021). However, Prechtel et al. (2018) found Silver Carp to select water depths greater than five meters in the Wabash River. My results could be influenced by the deeper waters found in velocity refuge habitats. The braided channel mainstem in large sections of the Red River are shallow and might not be suitable habitat for carp (Matthews and Zimmerman 1990). Human modifications (i.e., wing dikes) to the river in the lower portions of my study area create areas with deeper water and slower flow that are ideal for carp (DeGrandchamp et al. 2008; Glubzinski et al. 2021). The possible selection of warmer water during colder conditions could be related to thermal selection. However, the lack of used and available measurement during my winter season did introduce more uncertainty in this relationship than my spring and summer season. Prechetel et al. (2018) found Silver Carp to positively select for warmer water temperature in both years of their study in the Wabash River. Other studies found relative depth changes under different thermal conditions (MacNamara et al. 2018; Glubzinski et al. 2021). My results indicate carp are selecting low-velocity habitats that contain deeper water and were out of the primary channel.

My results better inform managers of which habitats are being selected by Bighead Carp and Silver Carp. In a unique catchment like the Red River, where the main channel and floodplain are largely disconnected, and dynamic water levels are frequent, carp may be challenged to find suitable habitat (Erickson et al. 2016; Lu et al. 2020). Other parts of their invaded range such as the Illinois River contain large amounts of pool-like habitat (Stuck et al. 2015) which are more conducive to carp feeding (Sass et al. 2010; Calkins et al. 2012) and more closely reflect their native ranges (Chen et al. 2007; Lu et al. 2020). Unlike other catchments, the Red River has relatively few velocity refuges. This may provide a management opportunity given the limited areas that carp seem to select. Management of these species in the Red River would be made more efficient if control efforts were conducted in velocity refuges comprising of deeper water. These selected habitats provide ideal conditions for broad-scale removal efforts (Ridgway et al. 2023a). Along with lower velocity areas, habitats near velocity refuges would be ideal for control efforts. Quantifying the availability of these habitats might be helpful in determining a threat assessment for other regions in the catchment not yet invaded (e.g., Millwood Dam, Hugo Dam, or Denison Dam).

Based on efforts to remove other invasive fishes, there are several possible management strategies that may be useful to managers given the characteristics of the Red River catchment. Using telemetry technologies to aid in removal efforts can be especially productive (Brownscombe et al. 2022). Known as the Judas technique, individuals are tagged with transmitters and released back into the environment. These tagged fish are then tracked to find possible congregations of individual where they can be more efficiently captured. The tagged individuals can then be released again, and the process can be repeated (Bajer et al. 2011; Bajer et al. 2019). Hessler et al. (2023) captured more Grass Carp *Ctenopharyngodon idella* in a Missouri reservoir at sites that contained tagged individual compared to sites assumed to contain Grass Carp. This technique may not be well suited in large systems such as the Red River because locating a small number of tagged individuals could prove difficult. Mechanical removal is another common management practice (Rytwinski et al. 2019). Mechanical removal of invasive trout has been successful in smaller streams (Shepard et al. 2014; Bosch et al. 2019). However, few removal efforts have not demonstrated a successful change in abundance of carp in large rivers (Tsehaye et al. 2013; Rytwinski et al. 2019), and caution should be made to not negatively affect native fishes.

Carp selected habitat that overlap with habitats used by different life stages of several important native fishes; managers might consider options for reducing carp numbers that minimize threats to native fishes. Possible competition between carp and native fishes has been a longstanding concern within their invaded range. (e.g., the 1.2-billion-dollar fishing industry fishing industry in the Great Lakes could be affected through competition for resources between carp and native species (Lauber et al 2016; Ivan et al. 2020; Ibarra et al. 2024). Carp have the ability to alter zooplankton communities and consume similar zooplankton species as native planktivorous fishes (Sampson et al. 2009; Sass et al. 2014; Pendleton et al. 2017). These negative effects are exacerbated if native fishes and carp occupy similar habitats. Native planktivorous fishes such as the Paddlefish *Polyodon spathula* and Bigmouth Buffalo *Ictiobus cyprinellus* are also associated with low-flow habitat where they can feed more efficiently (Sampson et al. 2009; Hintz et al. 2017b). Many native juvenile fish in the lower Red River catchment were found to be more associated with the major tributaries compared to the mainstem (Ramsey et al. 2024). Native juvenile occupancy was also positively related to discharge indicating at higher water levels more slackwater and backwater habitats may become available to both native juvenile fish and adult carp. Growth and survival of juvenile fishes may suffer given freshwater species feed on zooplankton in early life-stages (Nunn et al. 2012). Increased competition for resources at early life stages can have pronounced negative effects on adult population sizes. For example, Chick et al. (2020b) found declines in abundance in multiple sport fish in the presence of Silver Carp indicating possible competition for resources between juveniles and adult carp. Caution is warranted when conducting removal or other management efforts to avoid unintended consequences on native fishes. Juvenile fishes of long-lived fishes can be relatively plastic, greater concerns may be warranted for adult large river fishes during sensitive times of the year. Paddlefish spawning cues are related to specific water temperatures during spring flood pulses which are similar to carp’s spawning cues (Coulter et al. 2016; Tripp et al. 2019). These similarities could cause unintentional capture of Paddlefish if removal efforts are conducted during these conditions. Other pelagic broad-cast spawners could seek similar habitats as carp during spawning conditions, putting them at risk of capture and mortality (Hoagstrom et al. 2015). Drought conditions could also stress native species increasing the risk of carp removal efforts causing unwanted mortality in native fishes (Lennox et al. 2019).

Table 1. Variables, scale, unit, and gear or source used for determining movement trends of Bighead Carp and Silver Carp in the lower Red River. SVC = Silver Carp, BHC = Bighead Carp. M = male, and F =female, and SURs = Submersible ultrasonic receivers.

Variable	Scale	Unit	Gear/Source
Average water temperature	Catchment	°C	SURs
Three days before average water temperature	Catchment	°C	SURs
CV of average water temperature	Catchment	-	SURs
Average water temperature squared	Catchment	°C	SURs
Average photoperiod	Catchment	min	https://aa.usno.navy.mil/
Average discharge	Catchment	m^3/S	USGS stream gage
CV of discharge	Catchment	-	USGS stream gage
Three days before average discharge	Catchment	m^3/S	USGS stream gage
Day of study	NA	1 Day	Fish movement
Direction	Individual	1/0	Fish movement
Species	Individual	SVC/BHC	Morphology
Sex	Individual	M/F	Morphology
Weight	Individual	g	Scale
Total Length	Individual	mm	Measuring board

Table 2. Pearson's Correlation matrix for movement distance and rate model covariates. Values > |0.6| were considered multicollinear. Only one of each multicollinear pair was retained in future model building. MQ = mean discharge (m^3/s), MT = mean water temperature (°C), MPP = Mean photo period (Min), DOS = day of study, CVT= coefficient of variation of water temperature, CVD = coefficient of variation discharge, MT3db = mean water temperature of the three days before a movement (°C), MQ3db = mean discharge of the three days before a movement (m^3/s), W = weight of individual carp (g), and L = total length of individual carp (mm).

Covariates	MQ	MT	MPP	DOS	CVT	CVD	MT3db	MQ3db	W	L
MQ	1.00									
MT	0.06	1.00								
MPP	0.18	0.90	1.00							
DOS	0.11	0.78	0.70	1.00						
CVT	0.03	-0.49	-0.42	-0.32	1.00					
CVD	0.25	-0.11	-0.06	-0.13	0.23	1.00				
MT3db	0.05	0.99	0.88	0.78	-0.50	-0.13	1.00			
MQ3db	0.91	0.07	0.19	0.12	-0.03	0.17	0.06	1.00		
W	-0.02	-0.02	0.01	-0.01	0.08	0.03	-0.03	-0.02	1.00	

L	-0.10	-0.02	0.00	0.00	0.07	0.01	-0.02	-0.09	0.93	1.00

Table 3. Hypothesized movement distance and rate models. DOS = day of study, MT = mean water temperature (°C), MQ = mean discharge (m^3/s), CVT= coefficient of variation of water temperature, CVD = coefficient of variation discharge, W = weight of individual carp (g), Species = Bighead Carp or Silver Carp, Sex = sex of individual, Season = my three season labels (Winter, Spring, and Summer), Direction = upstream or downstream movement based on the previous detection, Hypothesis = overarching hypothesis that may relate to carp movement patterns. s() denotes smoothed terms. The random effect of individual was included in all models. Preliminary models to assess temporal autocorrelation are denoted with "*".

Model description	Hypothesis
~s(DOS)*	Exploratory
~s(DOS) + corARMA(~1|DOS)*	Exploratory
~s(W) + s(MQ) + Sex	Individual traits
~s(W) + s(MT) + Sex	Individual traits
~s(W) + s(MQ x Species)	Individual traits
~s(MQ x Season)	Season and direction
~s(MT x Season)	Season and direction
~s(MQ x Direction)	Season and direction
~s(MT x Direction)	Season and direction
~s(CVT) + s(CVD)	Variability
~s(CVD x Temp)	Variability
~s(CVT x MQ)	Variability

Table 4. Description of environmental conditions for each open period interval (i.e., time between each closed period) based on water temperature and discharge in (Figure 7).

Period intervals	Environmental conditions
t1 to t2	Discharges were highly variable with four increases above the mean discharge for the study period (170 m^3/s). Water temperatures increased between these two periods.
t2 to t3	Discharges were lower than average between these periods with one increase in discharge magnitude above mean. Water temperatures decreased from the maximum for the year.
t3 to t4	Discharges were below the mean with one increase in magnitude above the mean. Water temperatures reached the minimum for the study period between these two periods.
t4 to t5	Discharges were highly variable with four increases in magnitude above the mean. Water temperatures steadily increased with moderate variability.
t5 to t6	Discharges were highly variable with extended periods above the mean and a decline below the mean. Water temperatures increased and reached the maximum for the year between these periods.

Table 5. SUR array deployment, final download of data, and the number of detections that each SUR recorded throughout its deployment. These detections were filtered into one detection per fish per day.

Serial number	Deployed	Final download	Detections
489658	3/3/2023	8/26/2024	1869
489657	3/6/2023	8/22/2024	0
489659	3/6/2023	8/22/2024	0
489651	3/15/2023	8/26/2024	61
489653	3/15/2023	8/26/2024	294
489650	3/20/2023	8/26/2024	340
489654	3/20/2023	8/26/2024	211
489652	3/31/2023	8/27/2024	0
489656	3/31/2023	8/27/2024	0
490126	4/4/2023	8/26/2024	520
489655	4/19/2023	8/7/2024	2
490127	4/19/2023	8/31/2023	1
491275	1/12/2024	8/26/2024	0
491276	1/12/2024	8/26/2024	0
491273	1/17/2024	NA	-
491269	1/24/2024	3/6/2024	22
491274	1/24/2024	3/6/2024	20
491268	1/28/2024	8/14/2024	301
491267	2/7/2024	4/23/2024	7

491270	2/7/2024	8/27/2024	129
491271	2/7/2024	8/27/2024	29
491272	2/7/2024	4/23/2024	0

Table 6. Detection history for all tagged individuals for all six periods. t1-t6 indicate each discrete time period in which estimates of transition probability were made across. Tag ID indicates individual tagged fish. Each letter indicates one of the three states that carp could occupy T (tributary), M (mainstem), B (backwater). A zero indicates an individual was not found during that period. “.” Indicate individuals that were estimated to have died or shed their tag. * indicates instances where a detection was moved from an open period to capture a transition.

Tag ID	t1	t2	t3	t4	t5	t6
A69-1604-24204	B	B	B	B	M*	B
A69-1604-24205	T	0	0	0	0	0
A69-1604-24206	T	M*	0	0	M	0
A69-1604-24207	T	T	T*	T	T	T
A69-1604-24208	T	0	0	0	M	0
A69-1604-24209	T	0	0	0	M*	0
A69-1604-24210	M	0	0	0	0	0
A69-1604-24211	M	T	0	T	·	·
A69-1604-24212	T	T*	T	T	T	T
A69-1604-24213	B	·	·	·	·	·
A69-1604-24214	T	T	0	T	T	T
A69-1604-24215	B	0	0	0	0	0
A69-1604-24216	T	0	0	0	T	0
A69-1604-24217	T	M*	0	0	0	0
A69-1604-24218	T	0	0	0	0	0

A69-1604-24219	B	0	0	0	0	M
A69-1604-24220	T	0	0	0	T*	0
A69-1604-24221	T	M	0	0	0	0
A69-1604-24222	B	B	0	0	B	·
A69-1604-24223	B	B	B	B	B	B
A69-1604-24224	B	B	B	B	B	B
A69-1604-24225	B	B	B	B	B	B
A69-1604-24226	B	·	·	·	·	·
A69-1604-24227	B	·	·	·	·	·
A69-1604-24228	B	0	0	0	0	0
A69-1604-24229	B	B	B	B	M	B
A69-1604-24230	B	B	B	B	M	B
A69-1604-24231	B	T	B	B	M*	B
A69-1604-24232	B	B	B	B	M	B
A69-1604-24233	B	M	0	0	0	M
A69-1604-24234	B	M	M	M	B*	B
A69-1604-24235	B	0	0	0	0	0
A69-1604-24236	B	·	·	·	·	·
A69-1604-24237	B	B	B	B	0	B*
A69-1604-24238	B	B	B	B	B	0
A69-1604-24239	B	0	0	0	0	0
A69-1604-24240	T	0	0	0	B*	0

A69-1604-24241	T	T*	0	0	0	0
A69-1604-24242	T	B*	B	0	B	0
A69-1604-24243	B	0	T*	0	M	0
A69-1604-24244	T	T	T	T	T	0
A69-1604-24245	T	·	·	·	·	·
A69-1604-24246	B	B	B	B	B*	0
A69-1604-24247	T	T	T	T	T	T
A69-1604-24248	B	B	B	B	M	B
A69-1604-24249	T	B	B	B	M	0
A69-1604-24250	T	M*	0	0	M	0
A69-1604-24251	T	0	T	T	T	0
A69-1604-24252	B	·	·	·	·	·
A69-1604-24253	B	T	T*	T	M	T

Table 7. Recapture probability estimates (p) for time periods (t) and time-constant average survival probability estimate (s) from the three-state transition model. Parameters = each estimated parameter where B is backwater, M is mainstem, and T is tributary, Mode = most likely value, C.I. = 95% credibility interval.

Parameter	Mode	C.I.
p(B,t2)	0.92	(0.69, 0.99)
p(B,t3)	0.93	(0.73, 0.99)
p(B,t4)	0.88	(0.64, 0.99)
p(B,t5)	0.82	(0.53, 0.98)
p(B,t6)	0.82	(0.54, 0.98)
p(M,t2)	0.56	(0.25, 0.92)
p(M,t3)	0.13	(0.02, 0.44)
p(M,t4)	0.13	(0.02, 0.44)
p(M,t5)	0.83	(0.56, 0.99)
p(M,t6)	0.26	(0.07, 0.62)
p(T,t2)	0.62	(0.35, 0.87)
p(T,t3)	0.59	(0.30, 0.89)
p(T,t4)	0.77	(0.41, 0.98)
p(T,t5)	0.82	(0.46, 0.98)
p(T,t6)	0.73	(0.33, 0.98)
s(B,.)	0.95	(0.95, 1)
s(M,.)	0.86	(0.67, 0.97)
s(T,.)	0.96	(0.87, 1)

Table 8. Summary of tagged fish demographics, tagging dates, shed tag or death, and number of detections. Tag Identification, date tagged, species (Silver Carp (SVC) or Bighead Carp (BHC)), length (total length mm), weight (g), sex (male (M) or female (F)), number of detections of tagged carp, and shed tag or death are included. Shed tag or death column indicates the date that a fish is estimated to have died or shed their tag. Individuals with no date were believed to be alive throughout the study.

Tag ID	Date Tagged	Species	Length (mm)	Weight (g)	Sex	Number of detections	Shed tag or death
A69-1604-24204	3/14/23	SVC	900	8000	M	286	
A69-1604-24205	3/13/23	SVC	1052	15900	F	0	
A69-1604-24206	3/10/23	SVC	798	6000	M	6	
A69-1604-24207	3/22/23	BHC	974	14500	M	10	
A69-1604-24208	3/17/23	BHC	1055	16500	M	16	
A69-1604-24209	3/17/23	SVC	835	11000	F	1	
A69-1604-24210	3/24/23	SVC	682	5000	F	0	
A69-1604-24211	3/24/23	SVC	856	7500	M	10	2/12/2024
A69-1604-24212	3/22/23	BHC	1005	15000	M	315	
A69-1604-24213	4/4/23	SVC	991	16900	F	13	6/23/2023
A69-1604-24214	3/29/23	SVC	786	6750	M	42	
A69-1604-24215	3/24/23	SVC	838	7000	M	0	
A69-1604-24216	4/6/23	SVC	850	9000	F	3	
A69-1604-24217	4/6/23	SVC	795	6000	F	3	
A69-1604-24218	4/5/23	SVC	881	7000	M	0	
A69-1604-24219	4/26/23	BHC	1200	21800	F	1	

A69-1604-24220	4/18/23	BHC	1025	17000	F	3	
A69-1604-24221	4/27/23	BHC	1289	27000	M	3	
A69-1604-24222	3/3/23	SVC	850	7450	M	64	5/23/2024
A69-1604-24223	3/3/23	SVC	929	15000	F	365	
A69-1604-24224	3/3/23	SVC	1000	15500	F	401	
A69-1604-24225	3/3/23	SVC	882	9450	M	267	
A69-1604-24226	3/3/23	SVC	959	12750	M	5	5/27/2023
A69-1604-24227	3/3/23	SVC	978	15100	F	92	7/4/2023
A69-1604-24228	3/3/23	BHC	1221	24450	M	0	
A69-1604-24229	3/3/23	SVC	901	10000	M	313	
A69-1604-24230	3/3/23	SVC	892	9500	M	338	
A69-1604-24231	3/3/23	SVC	903	10500	M	238	
A69-1604-24232	3/3/23	BHC	1155	20750	M	138	
A69-1604-24233	3/9/23	BHC	1245	30750	F	9	
A69-1604-24234	3/9/23	BHC	1105	22000	M	24	
A69-1604-24235	3/9/23	BHC	1212	24500	M	1	
A69-1604-24236	3/9/23	BHC	1155	24500	M	5	7/31/2023
A69-1604-24237	3/9/23	BHC	1071	23600	F	38	
A69-1604-24238	3/9/23	BHC	1010	13500	M	94	
A69-1604-24239	3/9/23	BHC	1186	25000	M	2	
A69-1604-24240	4/11/23	BHC	1340	36000	F	18	
A69-1604-24241	4/18/23	SVC	800	5500	F	2	
A69-1604-24242	4/27/23	BHC	1279	26200	M	7	

A69-1604-24243	4/12/23	SVC	913	11000	F	9	
A69-1604-24244	4/24/23	BHC	1061	18500	M	214	
A69-1604-24245	4/11/23	SVC	609	2500	M	1	4/25/2023
A69-1604-24246	4/26/23	BHC	1158	20500	F	85	
A69-1604-24247	4/11/23	BHC	964	11750	M	270	
A69-1604-24248	4/26/23	BHC	1171	23300	F	124	
A69-1604-24249	4/27/23	BHC	1086	25000	M	52	
A69-1604-24250	4/18/23	BHC	1220	29500	F	5	
A69-1604-24251	4/24/23	BHC	1040	15750	F	85	
A69-1604-24252	4/26/23	BHC	1051	15100	M	3	8/10/2023
A69-1604-24253	4/12/23	SVC	912	10500	F	139	

Table 9. Summary statistics of movement for Silver Carp (male (M) or female (F)) and Bighead Carp (male (M) or female (F)). Movement distances were calculated as the distance moved between consecutive detections. Movement rates were calculated as the movement distance divided by the duration of time between consecutive detections. Means, standard deviations (±), maximum distance, and maximum rate are reported.

Species	Sex	Mean distance (km)	Mean rate (km/d)	Maximum distance (km)	Maximum rate (km/d)
Silver	M	1.43 ± 0.31	0.40 ± 0.03	206.99	18.02
Silver	F	0.37 ± .03	0.29 ± 0.02	26.39	3.73
Bighead	M	1.87 ± 0.43	0.46 ± .04	319.19	25.70
Bighead	F	3.96 ± 1.35	0.45 ± 0.13	336.57	37.89

Table 10. Exploratory movement distance and rate models investigating linear and smooth terms for each covariate. MT = mean water temperature (°C), MQ = mean discharge (m^3/s), CVT = CV of water temperature, CVD = CV of discharge, W = weight of individual carp (g), and s() denotes smoothed terms. A random effect of individual was included in all models.

Model description
~s(MT) + s(MQ) + s(CVT) + s(CVD) + s(W)
~ MT + s(MQ) + s(CVT) + s(CVD) + s(W)
~s(MT) + MQ + s(CVT) + s(CVD) + s(W)
~s(MT) + s(MQ) + CVT + s(CVD) + s(W)
~s(MT) + s(MQ) + s(CVT) + CVD + s(W)
~s(MT) + s(MQ) + s(CVT) + s(CVD) + W

Table 11. Summary of top movement distance model. Model = response variable, Covariates = covariates included in the model, CVD = coefficient of variation discharge, CVT= coefficient of variation of water temperature MQ = mean discharge (m^3/s), Individual = random effect of individual fish, and edf = effective degrees of freedom. s() denotes smoothed terms. X denotes an interactive effect.

Model	Covariate	edf
Distance	s(CVD)	7.9
	s(CVT x MQ)	27.39
	s(Individual)	35.55

Table 12. Summary of top movement distance and movement rate models. Model = response variable for each model, Model description = covariates included either additive (+) or interactive (x), CVD = coefficient of variation discharge, CVT= coefficient of variation of water temperature MQ = mean discharge (m^3/s). s() denotes smoothed terms. The random effect of individual was included in all models. df = degrees of freedom, logLik = log-likelihood AICc = AIC corrected for small sample size, ΔAICc = the difference between each model and the top ranked model, w_i = Akaike weight, and Deviance explained = proportion of the deviance in residuals that is explained by fixed and random effects.

Model	Model description	df	logLik	AICc	ΔAICc	w_i	Deviance explained
Distance	~s(CVD) + s(CVT x MQ)	73	-3338.524	6825.8	0	1	71%
Rate	~s(CVD) + s(CVT x MQ)	68	- 1153.404	2446.2	0	1	39.2%

Table 13. Summary of top movement rate model. Model = response variable, Covariates = covariates included in the model, CVD = coefficient of variation discharge, CVT= coefficient of variation of water temperature MQ = mean discharge (m^3/s), Individual = the random effect of individual, and edf = effective degrees of freedom, s() denotes smoothed terms. X denotes an interactive effect.

Model	Covariate	edf
Rate	s(CVD)	5.45
	s(CVT x MQ)	26.3
	s(Individual)	34.27

Table 14. Probability of remaining in a given state (Ψ) and time constant average survival probability for each state (s) from my two-state model. Parameters = Probabilities of remaining in each state (A = backwater/tributary state, M = mainstem state) across each time period and time constant survival estimates for each state. Mode = most likely value, C.I. = 95% credibility intervals.

Parameter	Mode	C.I.
Ψ(A-A,t1)	0.62	(0.45, 0.77)
Ψ(A-A,t2)	0.95	(0.76, 1)
Ψ(A-A,t3)	0.95	(0.77, 1)
Ψ(A-A,t4)	0.63	(0.40, 0.79)
Ψ(A-A,t5)	0.89	(0.53, 1)
Ψ(M-M,t1)	0.41	(0.0, 0.94)
Ψ(M-M,t2)	0.96	(0.732, 1)
Ψ(M-M,t3)	0.97	(0.71, 1)
Ψ(M-M,t4)	0.61	(0.22, 0.9)
Ψ(M-M,t5)	0.23	(0.0, 0.61)
s(A,.)	0.98	(0.92, 1)
s(M,.)	0.85	(.72, 0.95)

Table 15. Recapture probability estimates (p) from the two-state model. Parameters = detection probabilities for each state (A = backwater/tributary state, M = mainstem state) within each time period (t2-t6), Mode = Most likely value, C.I. = 95% credibility intervals.

Parameter	Estimate	C.I.
p(A,t2)	0.90	(0.73, 0.99)
p(A,t3)	0.86	(0.68, 0.97)
p(A,t4)	0.89	(0.70, 0.99)
p(A,t5)	0.88	(0.62, 0.99)
p(A,t6)	0.67	(0.45, 0.95)
p(M,t2)	0.37	(0.17, 0.6)
p(M,t3)	0.10	(0.02, 0.3)
p(M,t4)	0.12	(0.02, 0.34)
p(M,t5)	0.79	(0.52, 0.96)
p(M,t6)	0.45	(0.09, 0.95)

Table 16. Variables collected, scale, unit, and gear or sources of the variables for determining the habitat selection by Bighead Carp and Silver Carp in the lower Red River.

Variable	Scale	Unit	Gear/Source
Sinuosity	Segment	km	NAIP imagery
Distance to velocity refuge	Segment	km	NAIP imagery
Distance to river bend	Segment	km	NAIP imagery
Distance to tributary confluence	Segment	km	NAIP imagery
Water temperature	Reach	°C	YSI
Thalweg depth	Reach	m	Boat mounted sonar
Average velocity	Reach	m/s	Portable Velocity Meter
Habitat type	Reach	PC/VR	Visual inspection
Sex	Individual	M/F	Visual Inspection
Weight	Individual	g	Scale
Total length	Individual	mm	Measuring board

Table 17. Pearson's correlation matrix for habitat selection covariates. Temp = water temperature (°C), Depth = water depth (m), Velocity = water velocity (m/s), Dis_trib = distance in km to closest 3rd order or greater tributary confluence, Dis_RB = distance in km to the closest river bend, Dis_VR = distance in km to the closest velocity refuge, L = total length of individual in mm, W = weight of individual in grams Sinuosity = Sinuosity of segment.

Covarites	Temp	Depth	Velocity	Dis_trib	Dis_RB	Dis_VR	L	W	Sinuosity
Temp	1.00								
Depth	-0.20	1.00							
Velocity	-0.19	-0.01	1.00						
Dis_trib	-0.06	0.12	0.06	1.00					
Dis_RB	0.05	-0.14	-0.32	-0.14	1.00				
Dis_VR	-0.07	0.05	0.15	0.53	-0.21	1.00			
L	0.01	-0.02	0.02	0.01	0.05	0.02	1.00		
W	0.01	-0.02	0.01	0.01	0.05	0.02	0.96	1.00	
Sinuosity	-0.04	0.28	-0.17	0.23	-0.03	0.09	-0.03	-0.03	1.00

Table 18. Hypothesized resource selection models. (+) indicate additive effects and (x) indicate interactive effects. Hab = primary channel (PC) or velocity refuge (VR), Temp = water temperature (°C), D = water depth (m), V= water velocity (m/s), Dis_trib = distance in km to closest 3^{rd} order or greater tributary confluence, Dis_RB = distance in km to the closest river bend, Dis_VR = distance in km to the closest velocity refuge, Sin = Sinuosity of segment, Species = Bighead Carp or Silver Carp, Sex = male or female, and Season = (winter, spring, and summer). A random effect of individual was included in all models. Main effects were included in models with interaction.

Model description	Hypothesis
~D + V + Temp x Season	Bioenergetics
~V + Hab*D + Temp x Season	Bioenergetics
~ V + Dis_VR + Hab + D + Temp x Season	Bioenergetics
~V + Dis_trib + Dis_RB + Sin	Spawning
~Dis_trib + Dis_RB + V x Season	Spawning
~V + Dis_RB + Dis_trib x Season	Spawning
~Hab + D + V x W	Individual traits
~D + Hab x Species + V x Sex	Individual traits
~D + V + Hab x Species	Individual traits

Table 19. Summary of all tracking reaches that were used to actively track tagged Bighead Carp and Silver Carp. Reach identification letter (Figure 5), length of the river reach in kilometers, the number of tracking events conducted per reach, and the total number of river kilometers actively tracked within each tracking reach are included.

Reach	Length of reach	Number of tracking events	River km
J	24	21	504
G	23	24	552
F	31	22	682
K	48	12	576
A	25	1	25
I	35	11	385
C	22	16	352
E	33	15	495
H	21	27	567
D	37	10	370
B	20	12	240
Total	319	171	4748

Table 20. Summary of used and available habitat within the lower Red River. Temp = water temperature (°C), Depth = water depth (m), Velocity = water velocity (m/s), Dis_trib = distance in km to closest 3rd order or greater tributary confluence, Dis_RB = distance in km to the closest river bend, Dis_VR = distance in km to the closest velocity refuge, L = total length of individual in mm, Sinuosity = sinuosity of segment.

Covariates	Available Mean	Available SD	Available Min	Available Max	Used Mean	Used SD	Used Min	Used Max
Temp	24.89	6.98	4.60	37.7	25.24	7.07	8.10	36.00
Depth	3.07	1.75	0.22	10.79	4.10	1.69	0.50	10.59
Velocity	0.62	0.38	0.00	2.36	0.24	0.36	0.00	1.76
Dis_trib	8.61	6.70	0.00	28.74	5.05	2.78	0.03	16.59
Dis_RB	1.01	0.88	0.00	6.26	3.74	5.71	0.00	22.16
Dis_VR	8.83	7.28	0.00	26.22	1.68	1.22	0.01	6.00
Sinuosity	1.73	0.22	1.21	1.95	1.80	0.16	1.26	1.93

Table 21. Summary of my top ranked habitat selection model. A random effect of individual was added to the model. Model description = covariates included either additive (+) or interactive (x), df = degrees of freedom, LogLink = the log-likelihood, AICc = AIC corrected for small sample size, ΔAICc = the difference between each model and the top ranked model, wi = wi = Akaike weight, R^2c = variance explained by fixed and random effects, and R^2m = the variance explained by only the fixed effects.

Model description	df	LogLik	AICc	ΔAICc	wi	R^2c	R^2m
~ V + Dis_VR + Hab + D + Temp x Season	11	-717	1456.10	0	0.99	0.26	0.25

Table 22. Coefficient estimates and their associated standard errors, 95% confidence intervals (C.I), from my top ranked habitat selection model. V = water velocity (m/s), Dis_VR = distance in km to the closest velocity refuge, Hab = habitat type where primary channel was the reference, D = water depth (m), Temp x Winter = the interaction between water temperature and my winter season, Temp x Spring = the interaction between water temperature and my spring season, Temp x Summer = the interaction between water temperature and my summer season.

Covariate	Estimate	SE	C.I
V	-0.74	0.10	(-0.94, -0.53)
Dis_VR	-0.31	0.09	(-0.49, -0.14)
Hab	2.14	0.32	(1.52, 2.77)
D	0.90	0.09	(0.73, 1.08)
Temp x Winter	0.72	1.05	(-1.18, 2.79)
Temp x Spring	-0.14	1.03	(-2.79, 1.18)
Temp x Summer	-0.72	1.05	(-0.51, 0.78)

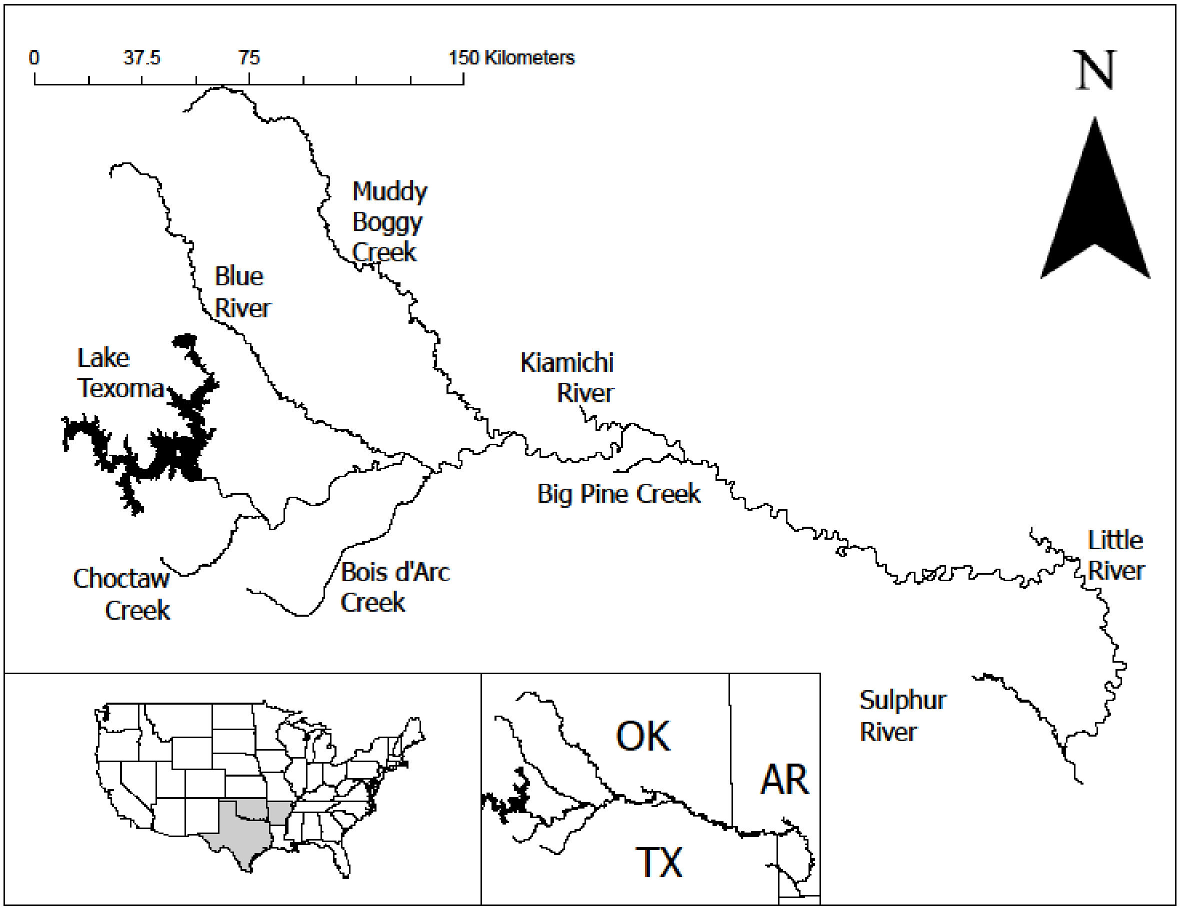

Figure 1. My study area in the mainstem Red River catchment including the lower portions of the major tributaries from Lake Texoma to the Arkansas-Louisiana border. The uppermost extent of my study area in the tributaries was an impoundment in several cases (e.g., Little River and Kiamichi River), limited by boat access (e.g., Blue River and Choctaw Creek), or determined by examining SUR data (e.g., Muddy Boggy Creek, Big Pine Creek, and Sulphur River).

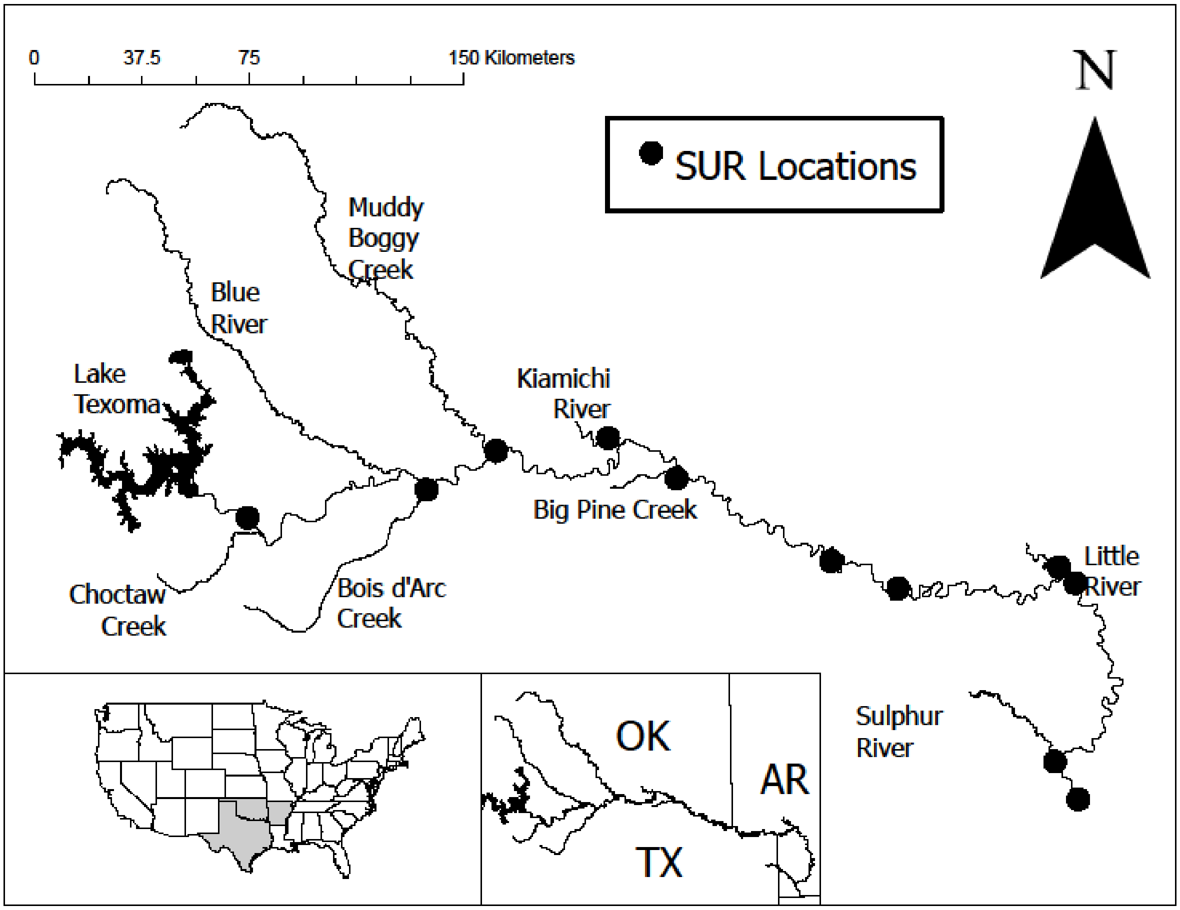

Figure 2. Locations of deployed SUR gates in the lower Red River catchment. Black dots indicate the locations of each SUR gate. Gates consisted of two SURs that were placed approximately 0.5-3 km apart.

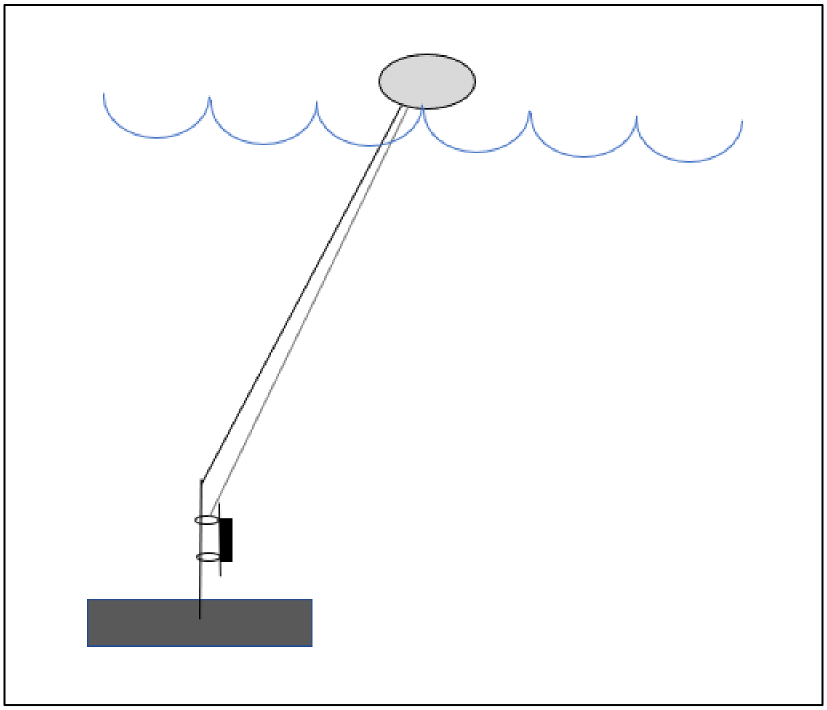

Figure 3. Receiver mooring design used to hold SURs in the Red River catchment to passively detect carp movements at a coarse scale. The black rectangle indicates the receiver that was attached to the mooring system. I used a 72-kg concrete anchor with a 0.6-meter rebar post placed in the middle of the anchor. The rebar post was attached to a near-surface buoy by a 6.3-millimeter stainless steel cable. The SUR was attached to a rebar bracket and threaded onto the rebar anchor post, and a secondary rope was attached from the SUR bracket to the near-surface buoy.

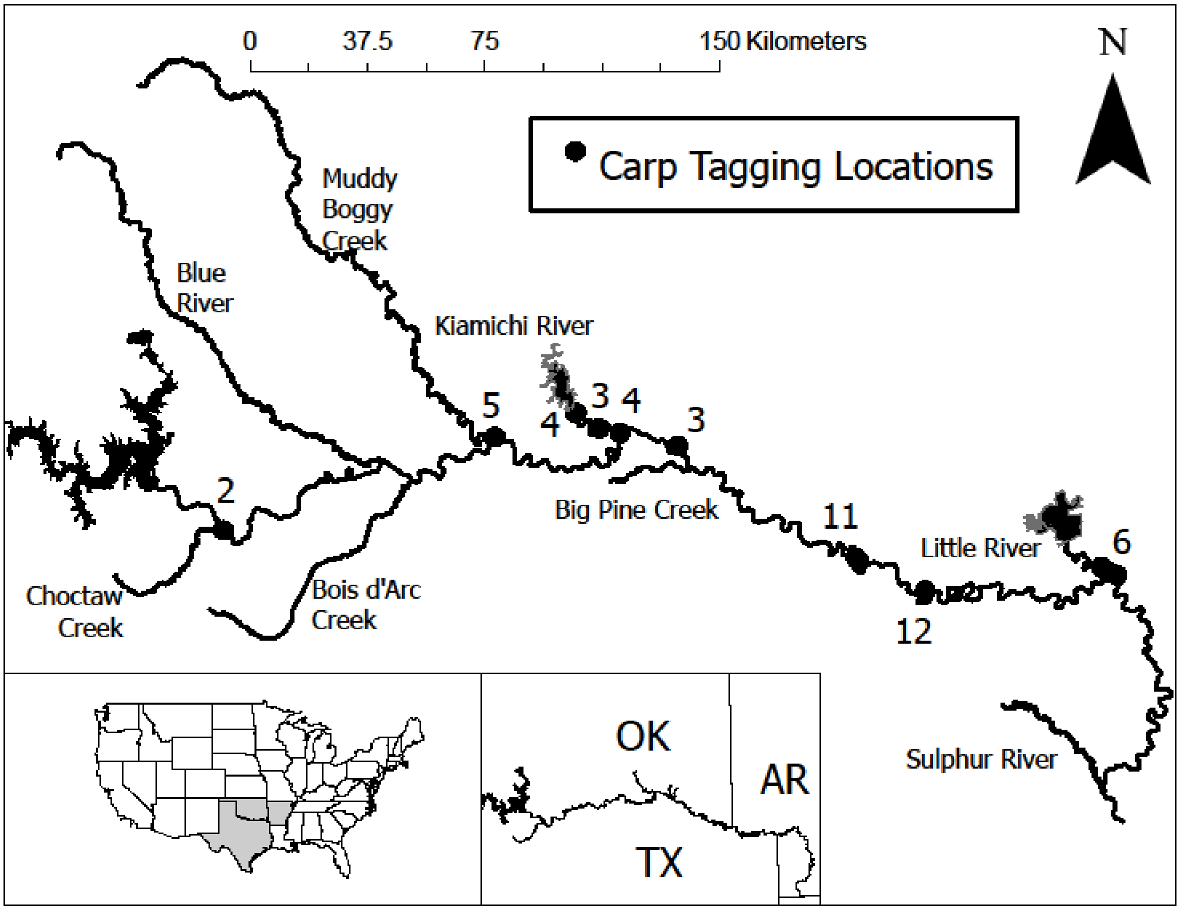

Figure 4. The locations where tagged carp were surgically implanted with acoustic transmitters across the lower Red River catchment. Black dots indicate each tagging site, and the associated number indicates the total number of carp tagged in that location.

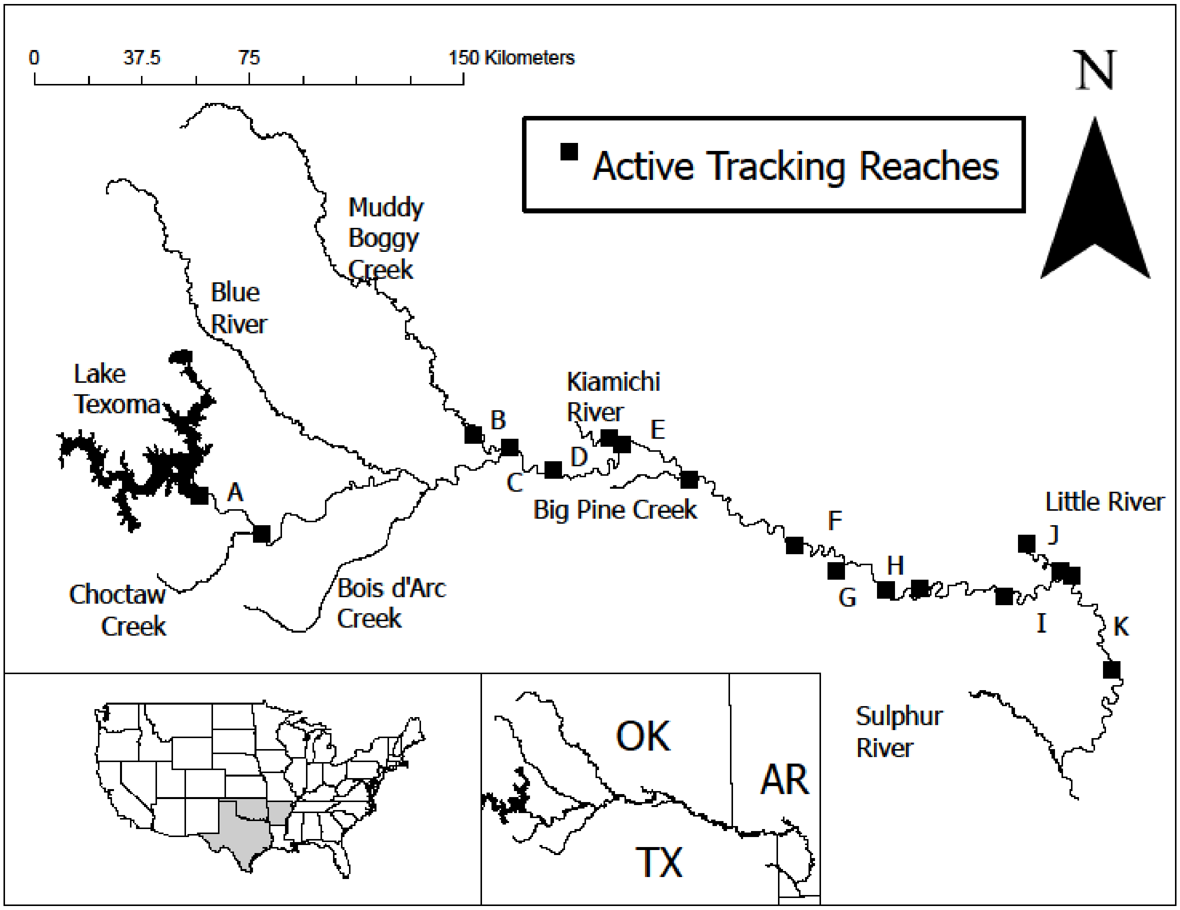

Figure 5. Active tracking reaches across the lower Red River catchment. Black squares indicate the beginning and end of tracking reaches. Letters between corresponding squares indicate individual tracking reaches.

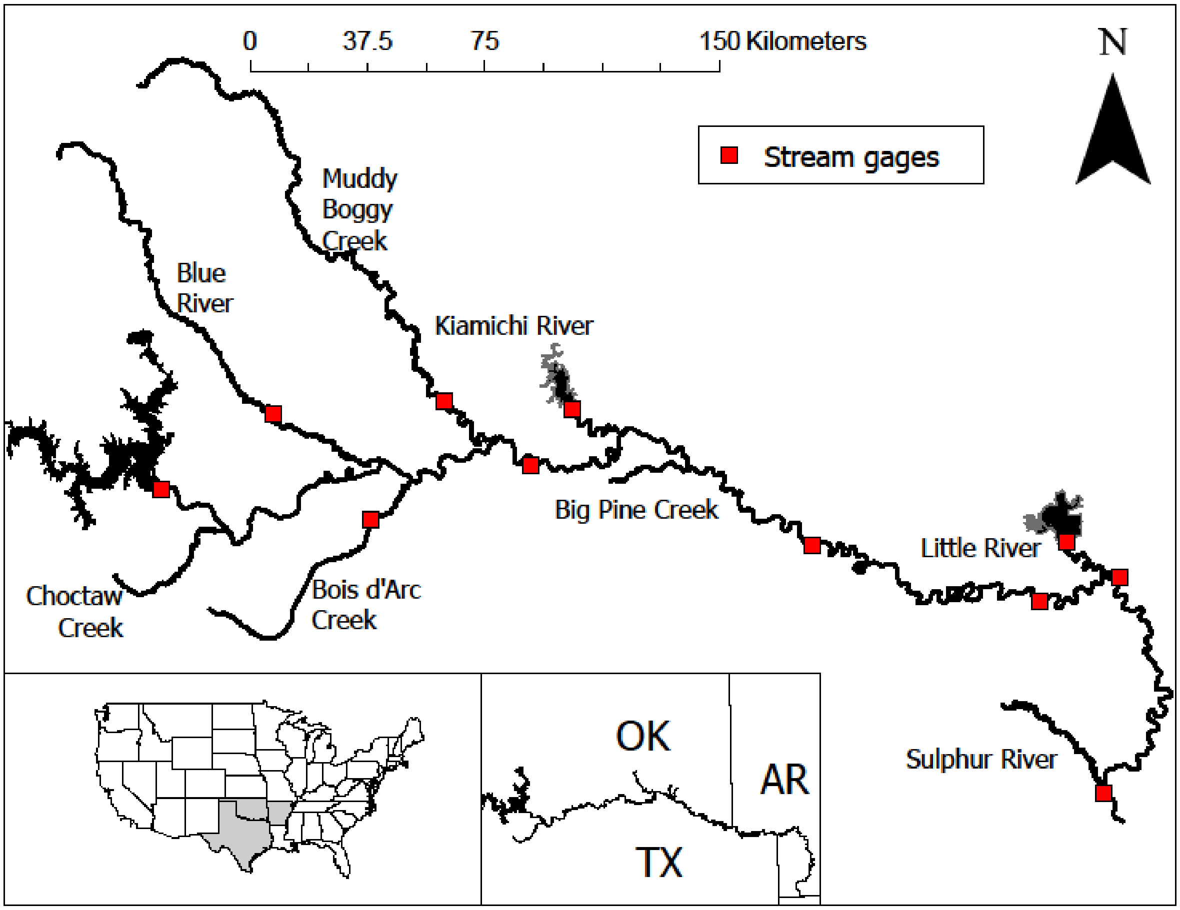

Figure 6. USGS stream gages within the lower Red River catchment. The red squares indicate each stream gage location from which discharge data were collected for my movement pattern analysis.

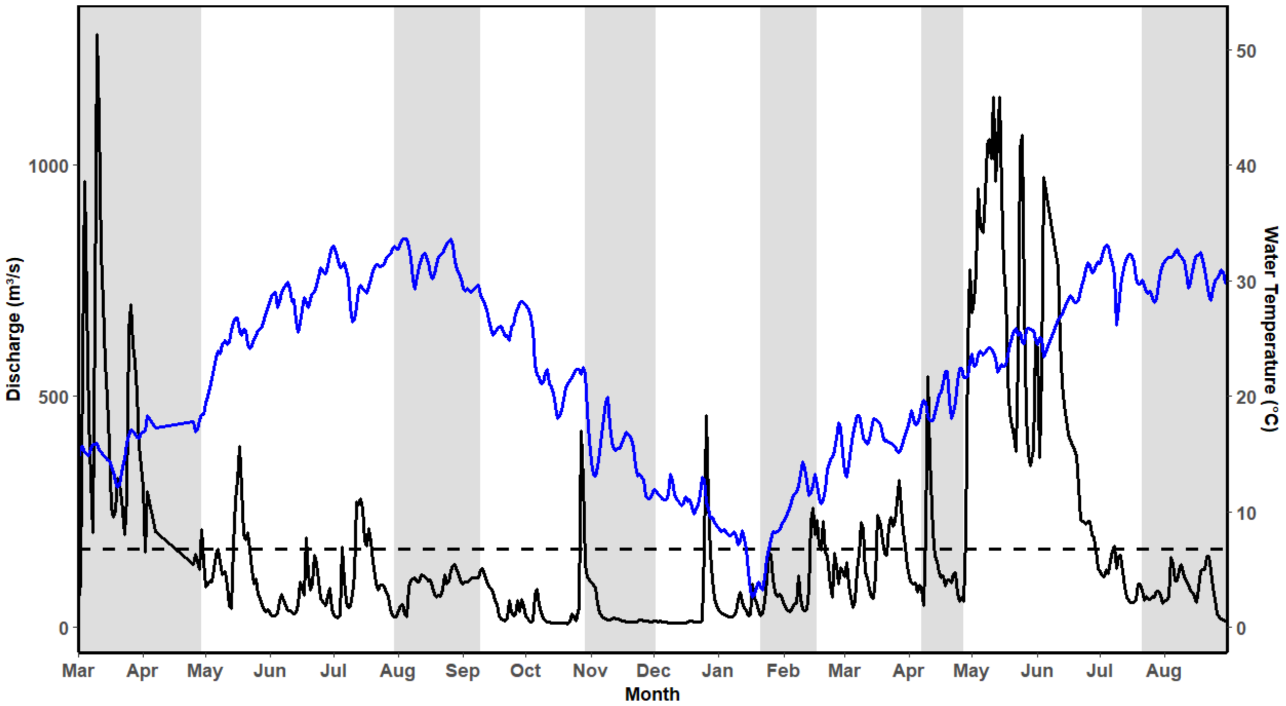

Figure 7. Environmental conditions for the lower Red River catchment during the study period. Discharge measurements (black line) were collected from the USGS stream gage near Arthur City TX 07335500. The dashed line represents mean discharge for the study period (170 m^3/s). Water temperature measurements (blue line) were collected from the USGS stream gage near Index AR 07337000. Shaded bars indicate closed periods which were condensed to create the six time periods of my multistate model.

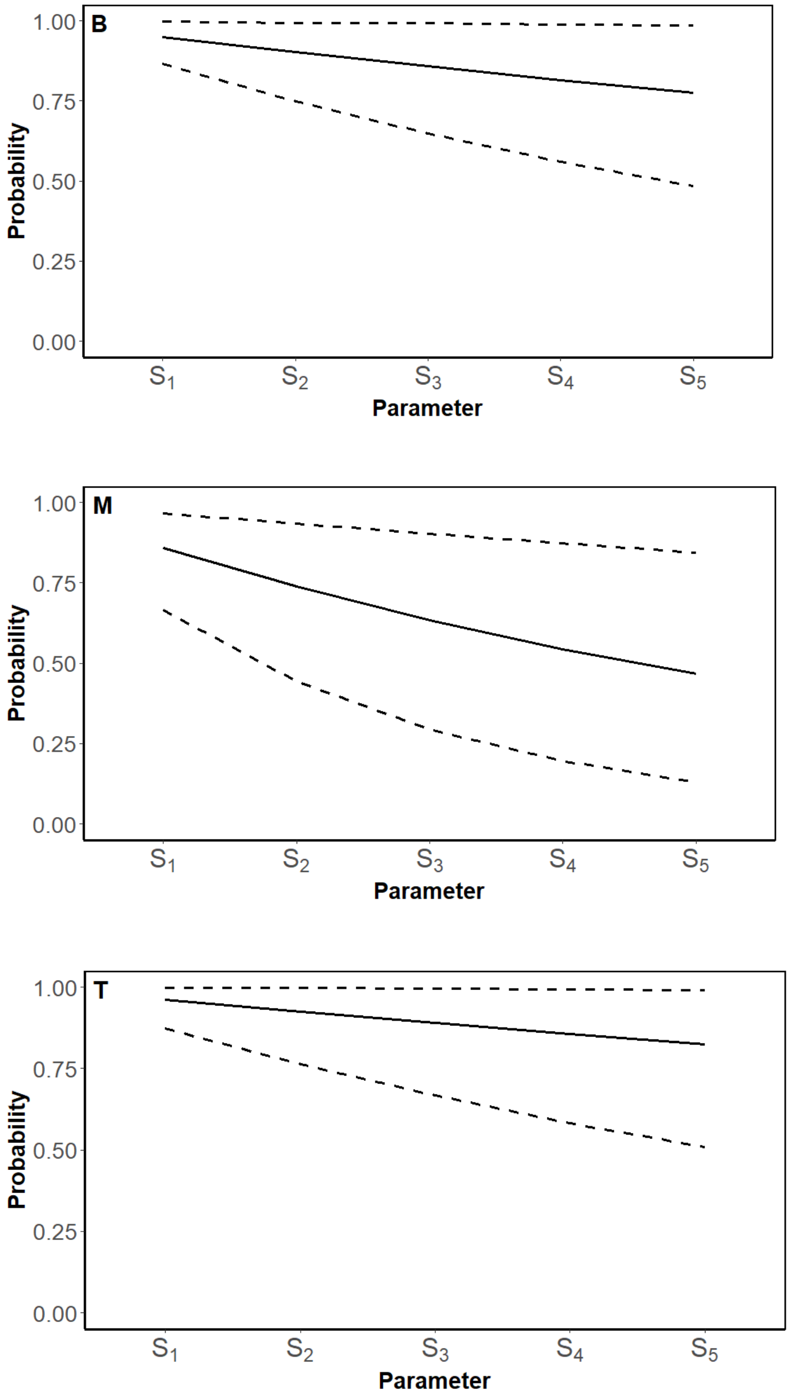

Figure 8. Cumulative apparent survival estimates for my three-state model. Panel B shows survival estimates in the backwater state, panel M shows the survival estimates in the mainstem

state, and panel T shows survival estimates in the tributary state. The y-axis shows the probability of survival. The x-axis shows the survival notation (S) of each time period. The black dots indicate the mode estimate, and the black lines indicate the 95% credibility intervals.

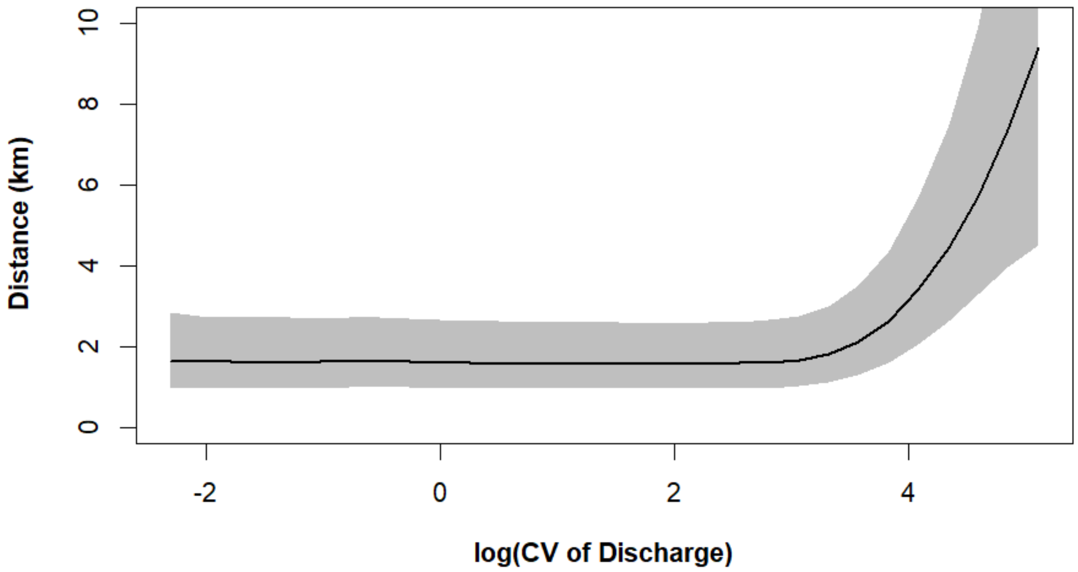

Figure 9. Relationship between CV of discharge and movement distance. Shaded areas around the line indicate the 95% confidence intervals. The y-axis shows the model-predicted distance traveled in river-kilometers between consecutive detections by tagged individuals. The x-axis shows natural-logged-transformed coefficient of variation of discharge.

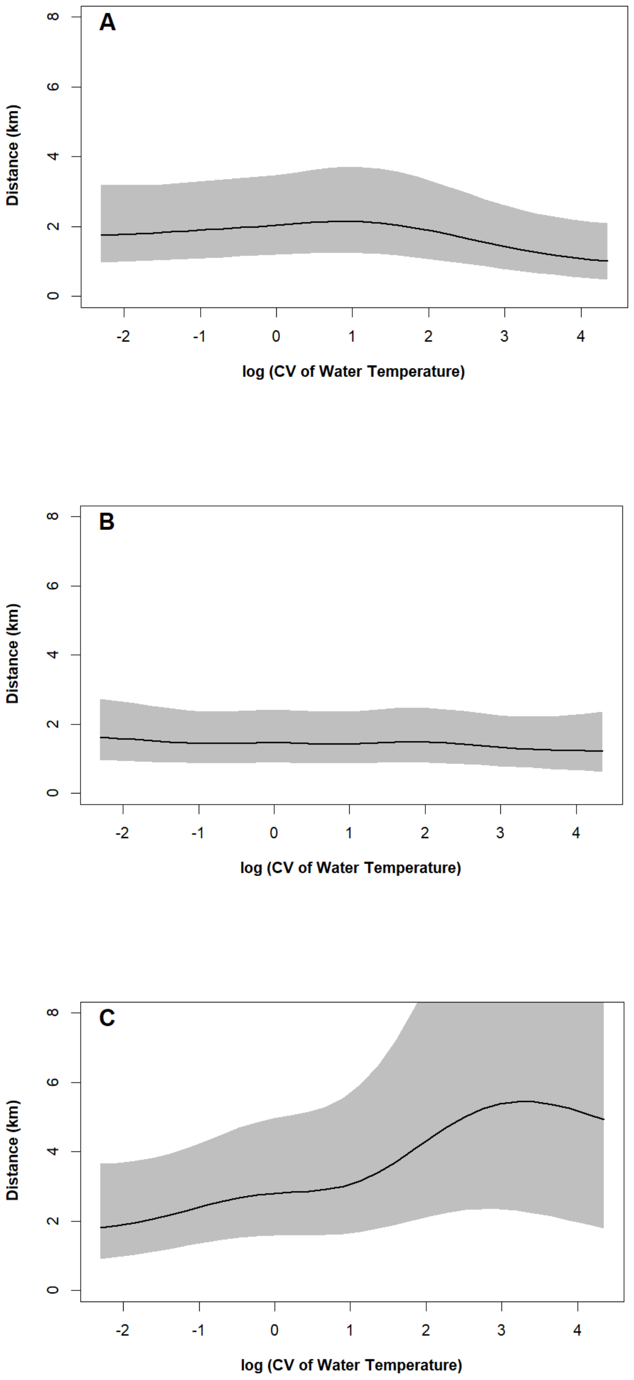

Figure 10. The relationship between CV of water temperature and movement distance at three levels of discharge. Shaded areas around the line indicate the 95 % confidence intervals. Panel A

shows the relationship while holding discharge two standard deviations below the mean. Panel B shows the relationship while holding discharge at the mean value. Panel C shows the relationship while holding discharge two standard deviations above the mean. The y-axis shows the model-predicted river-kilometers traveled between consecutive detections by tagged individuals. The x-axis shows the natural-logged-transformed coefficient of variation of water temperature.

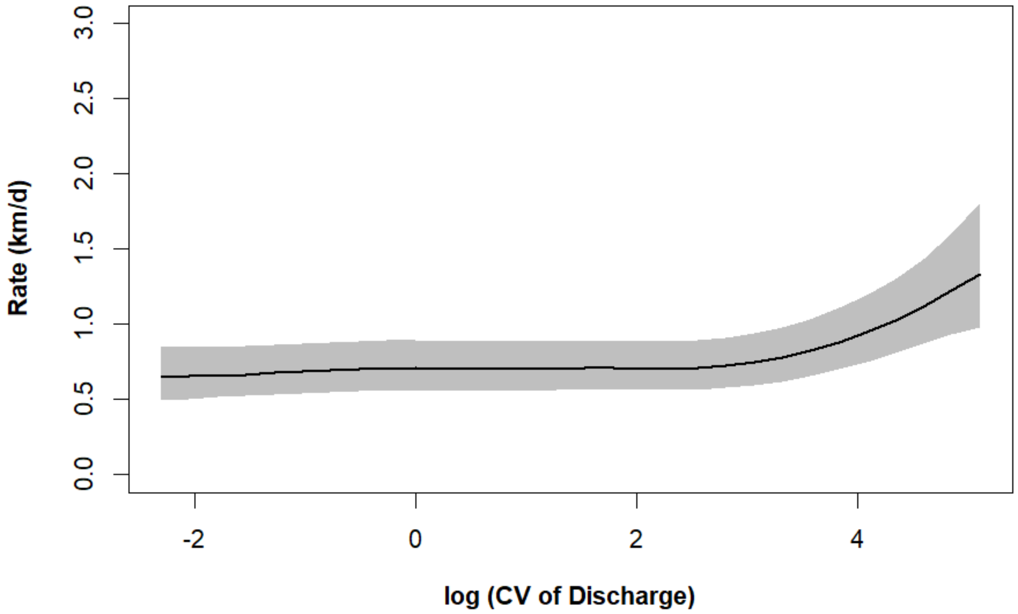

Figure 11. Relationship between CV of discharge and movement rate. Shaded areas around the line indicate the 95% confidence intervals. The y-axis shows the model-predicted river-kilometers traveled per day between consecutive detections by tagged individuals. The x-axis shows the natural-logged-transformed coefficient of variation of discharge.

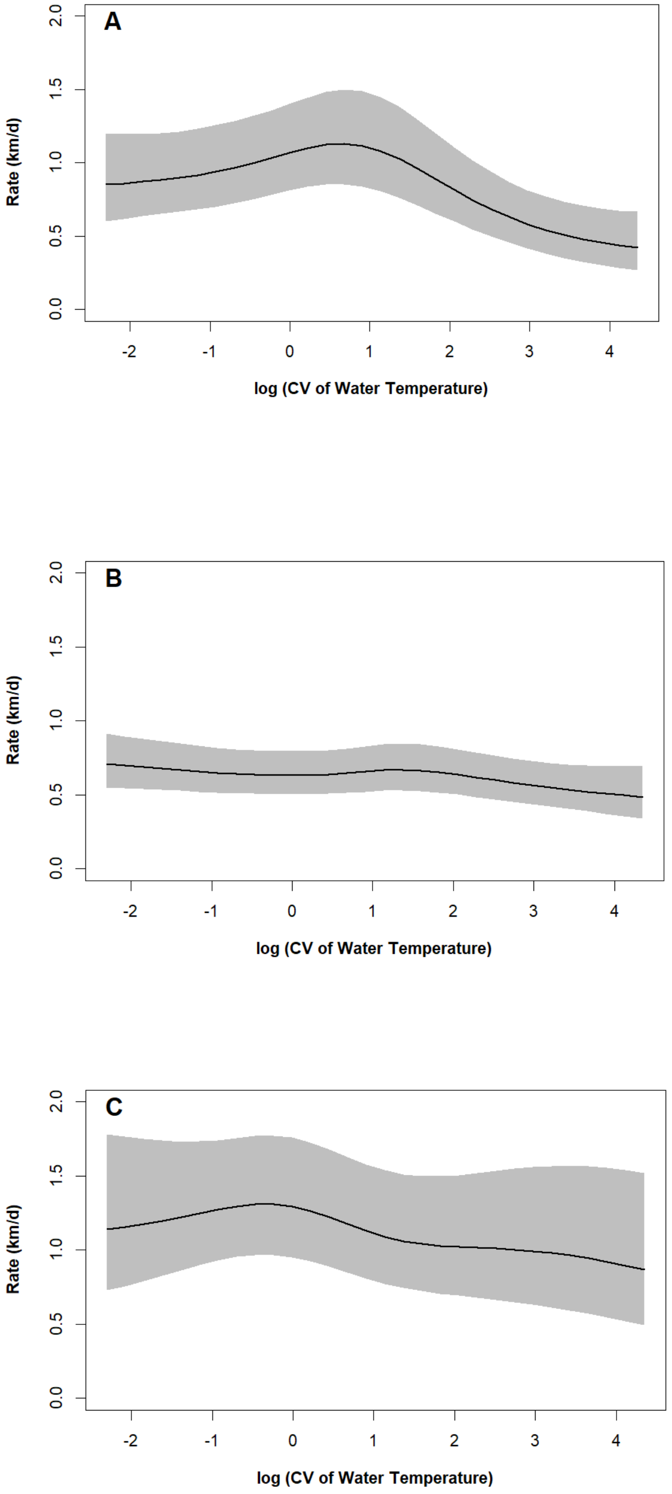

Figure 12. The relationship between CV of water temperature and movement rate at three levels of discharge. Shaded areas around the line indicate the 95 % confidence intervals. Panel A shows

the relationship while holding discharge two standard deviations below the mean. Panel B shows the relationship while holding discharge at the mean value. Panel C shows the relationship while holding discharge two standard deviations above the mean. The y-axis shows the model-predicted river-kilometers traveled per day between consecutive detections by tagged individuals. The x-axis shows the natural-logged-transformed coefficient of variation of water temperature.

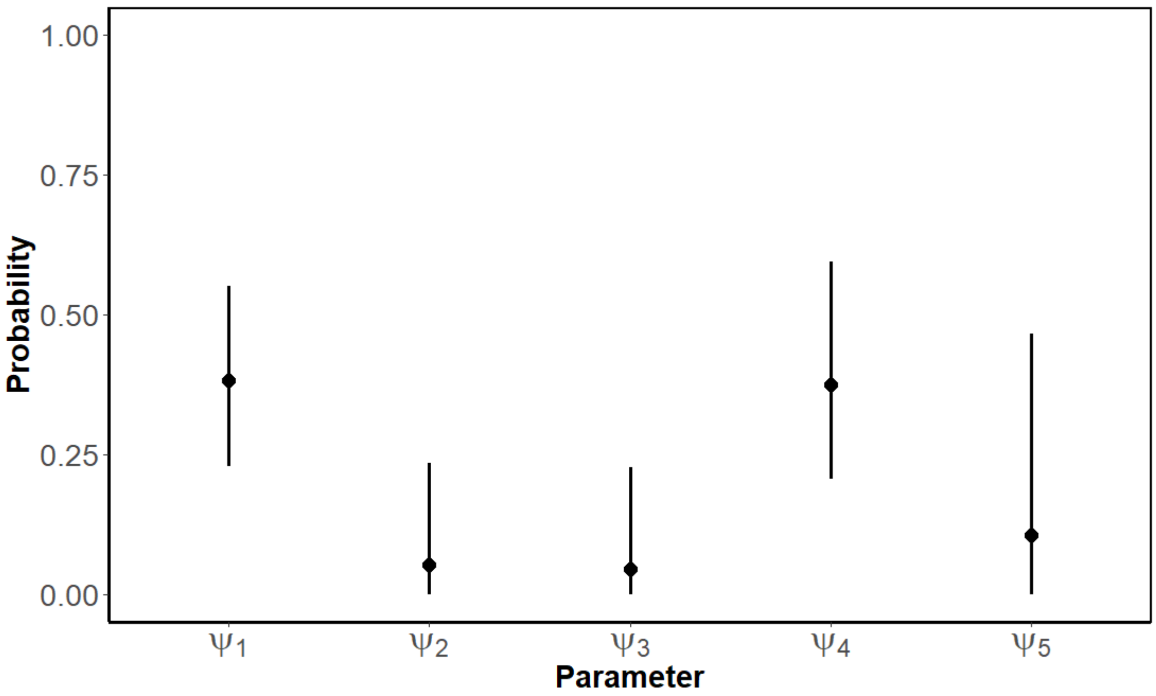

Figure 13. Transition probability estimates from state A to state M from the MCMC simulation for the two-state model. The y-axis shows the probability of transitioning. The x-axis shows transition notation (ψ) between each time period. The black dots indicate the mode estimate, and the black lines indicate the 95% credibility intervals.

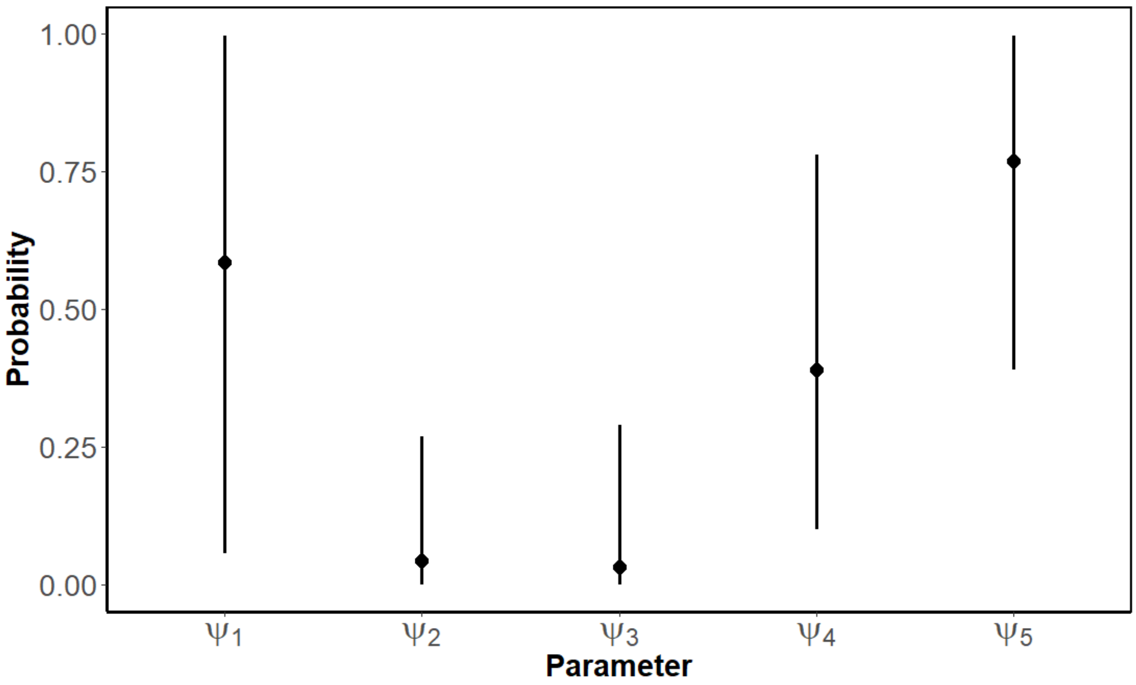

Figure 14. Transition probability estimates from state M to state A from the MCMC simulation for the two-state model. The y-axis shows the probability of transitioning. The x-axis shows transition notation (ψ) between each time period. The black dots indicate the mode estimate, and the black lines indicate the 95% credibility intervals.

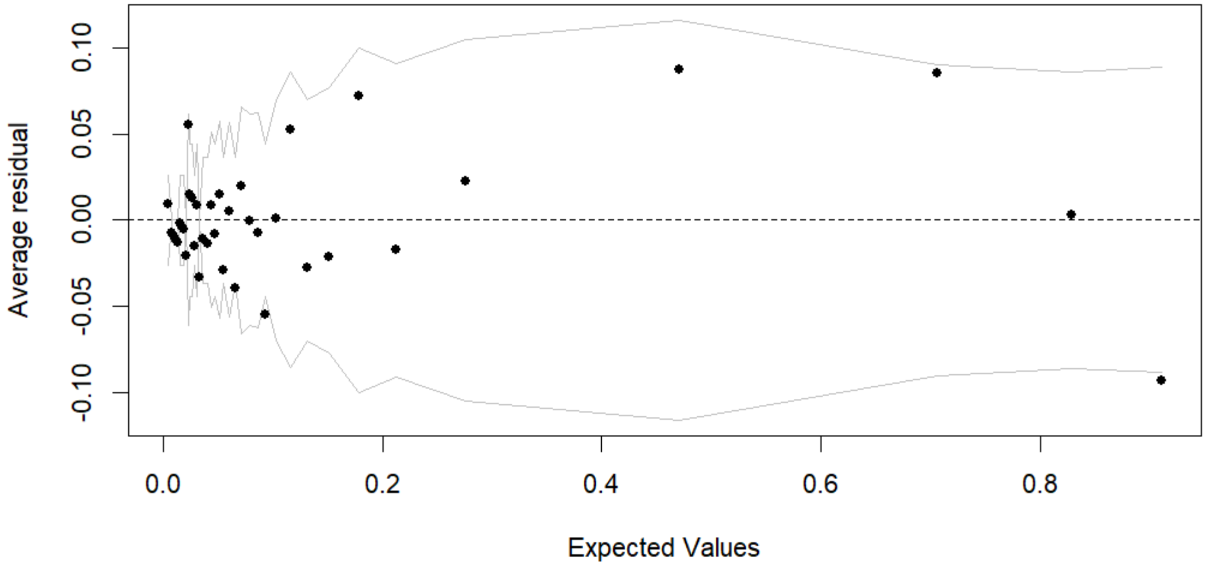

Figure 15. Binned residuals plot for my top ranked habitat selection model showing adequate fit. Gray lines are the theoretical error bounds and black points are the binned residuals.

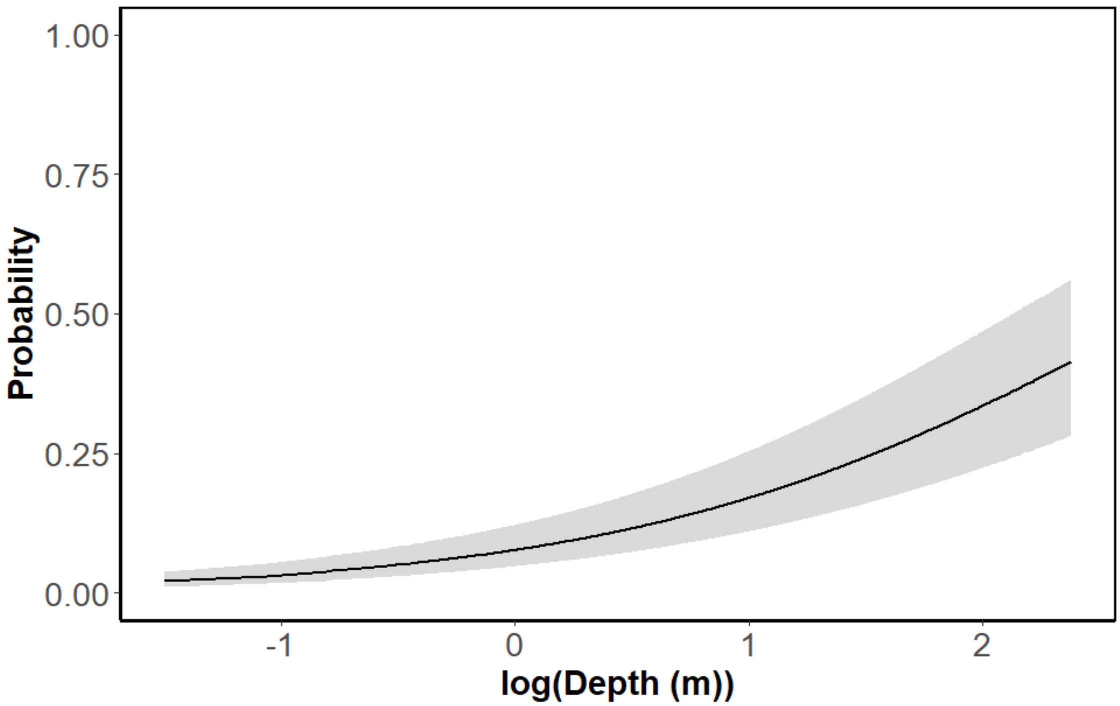

Figure 16. Model predicted probability of selection of water depth (m) by Bighead Carp and Silver Carp. The solid line shows the predicted probability of selection. The shaded areas around the line indicates the 95% confidence intervals. The y-axis shows the probability of selection. The x-axis shows the natural-log-transformed water depths in meters.

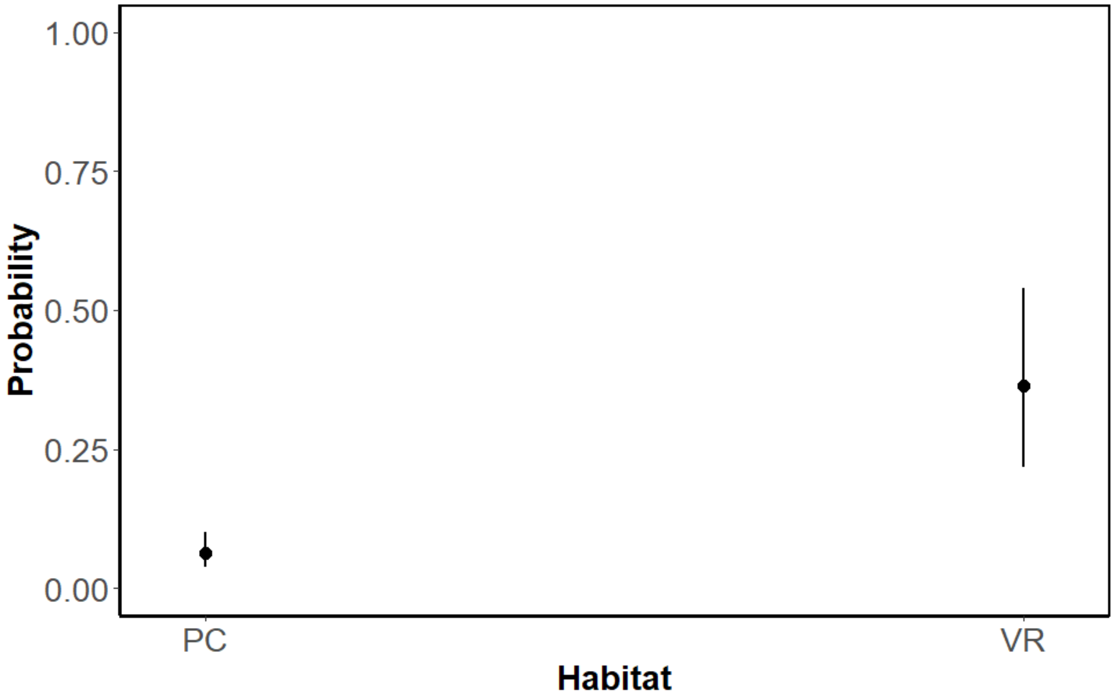

Figure 17. Model predicted probability of selection of habitat type by Bighead Carp and Silver Carp. The black dots show the point estimate of selection. The lines around each point indicate the 95% confidence intervals. The y-axis shows the probability of selection. The x-axis shows my two habitat distinctions, primary channel (PC) or velocity refuge (VR).

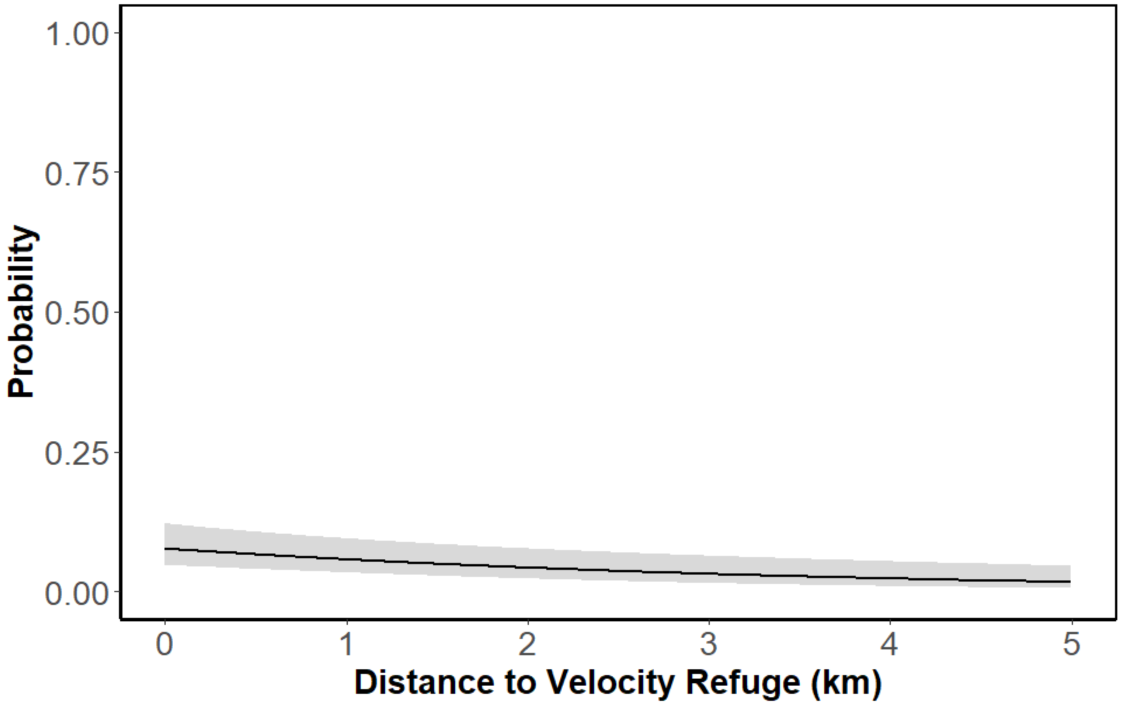

Figure 18. Model predicted probability of selection of distance to the closest velocity refuge by Bighead Carp and Silver Carp. The shaded area around the line indicates the 95% confidence intervals. The y-axis shows the probability of selection. The x-axis shows the distance to the closest velocity refuge in kilometers.

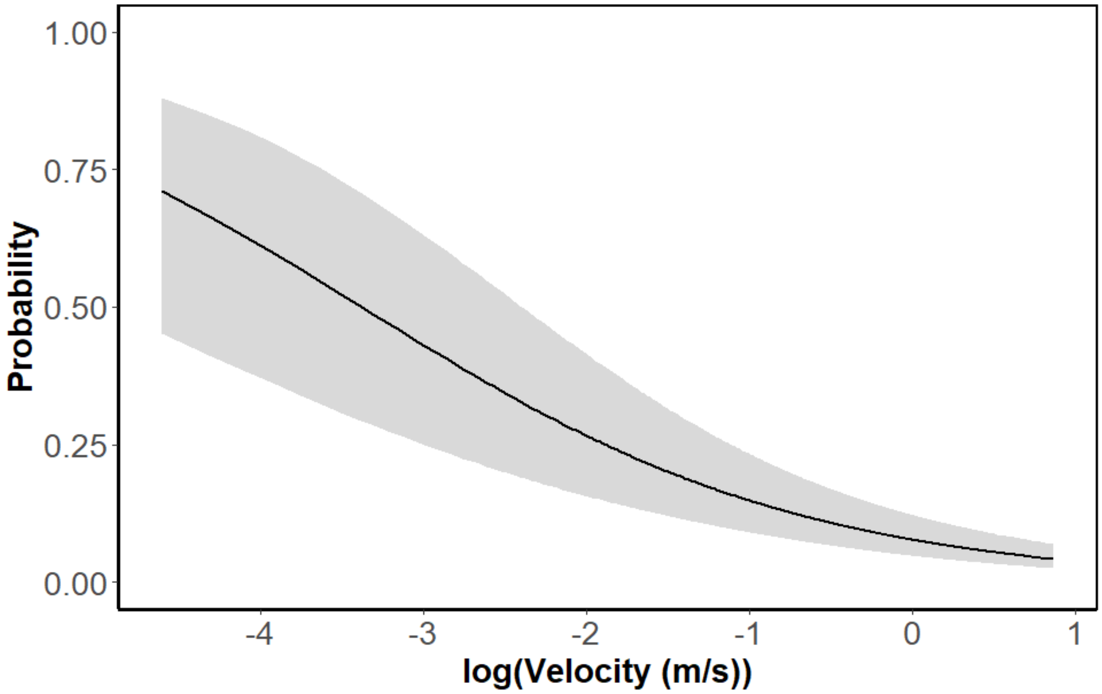

Figure 19. Model predicted probability of selection of water velocity (m/s) by Bighead Carp and Silver Carp. The solid line shows the predicted probability of selection. The shaded areas around the line indicates the 95% confidence intervals. The y-axis shows the probability of selection. The x-axis shows the natural-log-transformed water velocity in meters per second.

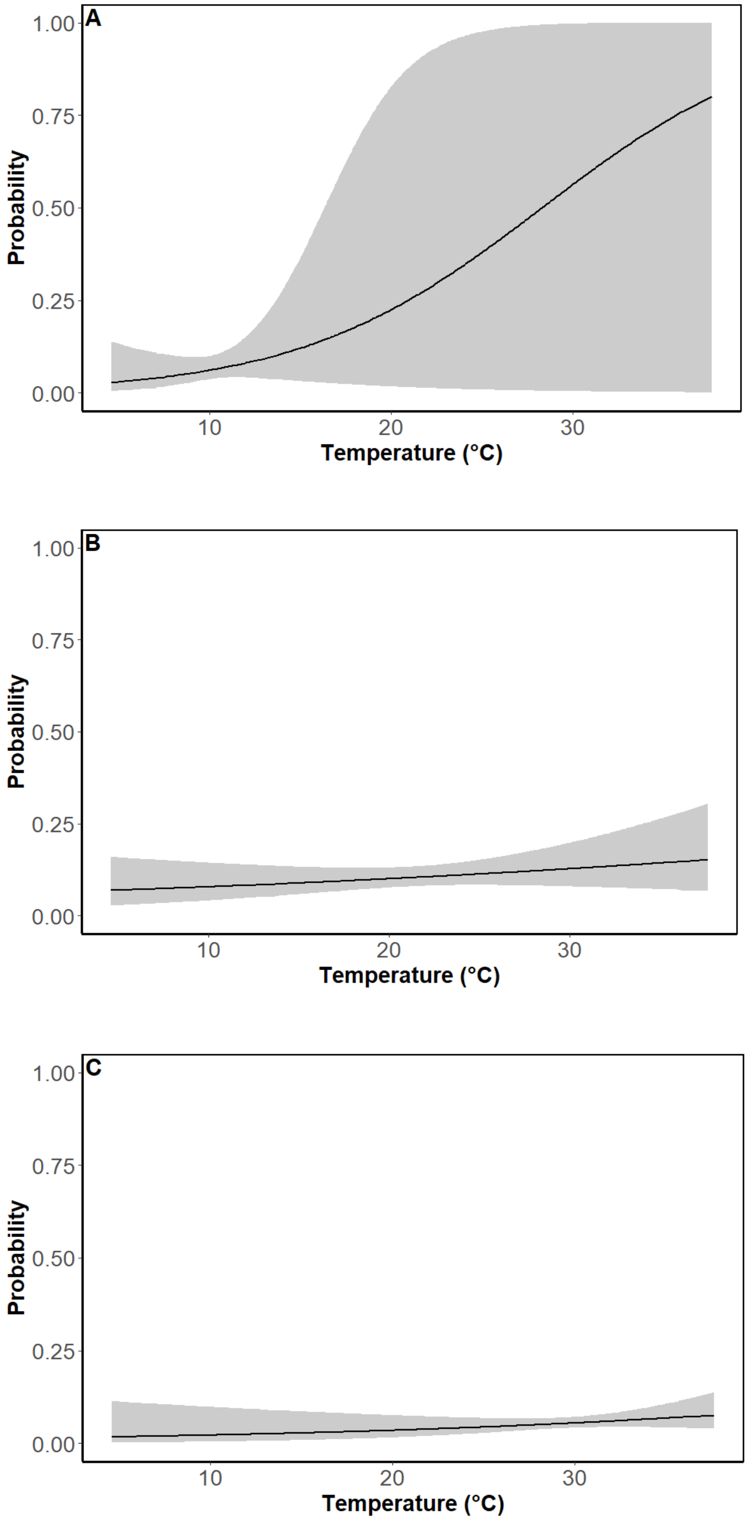

Figure 20. Model predicted probability of selection of water temperature (°C) within my winter, spring, and summer seasons by Bighead Carp and Silver Carp. Panel A shows the relationship

during my winter season (Dec 1st to Feb 29th). Panel B shows the relationship during my spring season (March 1st to May 31st). Panel C shows the relationship during my summer season (June 1st to Aug 31st). The shaded area around the line indicates the 95% confidence intervals. The y-axis shows the probability of selection. The x-axis shows water temperatures in degrees Celsius.

References

Albanese, B., P. L. Angermeier, and S. Dorai-Raj. 2004. Ecological correlates of fish movement in a network of Virginia streams. Canadian Journal of Fisheries and Aquatic Sciences 61(6): 857-869

Alexandre, C. M., P. R. Almeida, T. Neves, C. S. Mateus, J. L. Costa, and B. R. Quintella. 2016. Effects of flow regulation on the movement patterns and habitat use of a potamodromous cyprinid species. Ecohydrology 9(2): 326-340.

Allouche, S., and Gaudin, P. 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by Chub, *Leuciscus cephalus*, in an experimental stream. Oikos 94(3): 481-492.

Altenritter, M. E., DeBoer, J. A., Maxson, K. A., Casper, A. F., and Lamer, J. T. 2022. Ecosystem responses to aquatic invasive species management: A synthesis of two decades of Bigheaded Carp suppression in a large river. Journal of Environmental Management 305: 114354.

Anderson, K. R., Chapman, D. C., Wynne, T. T., and Paukert, C. P. 2017. Assessment of phytoplankton resources suitable for Bigheaded carps in Lake Michigan derived from remote sensing and bioenergetics. Journal of Great Lakes Research 43(3): 90-99.

Bajer, P. G., Chizinski, C. J., and Sorensen, P. W. 2011. Using the Judas technique to locate and remove wintertime aggregations of invasive Common Carp. Fisheries Management and Ecology 18(6): 497-505.

Bajer, P. G., Ghosal, R., Maselko, M., Smanski, M. J., Lechelt, J. D., Hansen, G., and Kornis, M. S. 2019. Biological control of invasive fish and aquatic invertebrates: a brief review with case studies. Management of Biological Invasions 10(2): 227-254.

Barbet-Massin, M., Jiguet, F., Albert, C. H., and Thuiller, W. 2012. Selecting pseudo-absences for species distribution models: How, where and how many? Methods in Ecology and Evolution 3(2): 327-338

Barneche, D. R., and Allen, A. P. 2018. The energetics of fish growth and how it constrains food-web trophic structure. Ecology letters. 21(6): 836-844.

Barshinger, C. E., Eggleton, M. A., and Spurgeon, J. J. 2024. Use of otolith microchemistry to determine natal origin for Silver Carp *Hypophthalmichthys molitrix* in the lower Mississippi River basin. Biological Invasions 26(9): 3091-3106.

Bates, D., M. Mächler, and B. Bolker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67(1):1-48.

Becker, A., Holland, M., Smith, J. A., and Suthers, I. M. 2016. Fish movement through an estuary mouth is related to tidal flow. Estuaries and Coasts 39: 1199-1207.

Berner, D., and Thibert-Plante, X. 2015. How mechanisms of habitat preference evolve and promote divergence with gene flow. Journal of evolutionary biology, 28(9): 1641-1655.

Bertrand, D., and McPherson, R. A. 2018. Future hydrologic extremes of the Red River basin. Journal of Applied Meteorology and Climatology 57(6): 1321-1336.

Birdsall, B. 2023. Factors related to occupancy and detection and population demographics of adult Bighead Carp and Silver Carp in the lower Red River catchment (Master's Thesis, Auburn University).

Booth, M. T., Flecker, A. S., and Hairston Jr, N. G. 2014. Is mobility a fixed trait? Summer movement patterns of catostomids using PIT telemetry. Transactions of the American Fisheries Society 143(4): 1098-1111.

Bosch, J., Bielby, J., Martin-Beyer, B., Rincon, P., Correa-Araneda, F., and Boyero, L. 2019. Eradication of introduced fish allows successful recovery of a stream-dwelling amphibian. PloS one 14(4): e0216204.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. 2002. Evaluating resource selection functions. Ecological Modelling 157(2-3): 281-300.

Brett, J. R., and Groves, T. D. D. 1979. Physiological energetics. Fish physiology 8(6): 1-786.

Brewer, S.K., J. Dattilo, P. Ramsey, and B. Birdsall. 2023. Evaluating the spatial and temporal distribution and ecology of Bighead and Silver Carp and native fishes of the lower Red River basin. U.S. Department of Interior, Fish and Wildlife Service, Cooperator Science Series FWS/CSS-153-2023, Washington, D.C.

Britton, J. R., Gozlan, R. E., and Copp, G. H. 2011. Managing non-native fish in the environment. Fish and Fisheries 12(3): 256-274.

Brooks, S.P. and Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7(4): 434-455.

Brooks, J. L., Chapman, J. M., Barkley, A. N., Kessel, S. T., Hussey, N. E., Hinch, S. G., Patterson, D. A., Hedges, K. J., Cooke, S. J., Fisk, A. T., Gruber, S. H., and Nguyen, V. M. 2019. Biotelemetry informing management: case studies exploring successful integration of biotelemetry data into fisheries and habitat management. Canadian Journal of Fisheries and Aquatic Sciences 76(7): 1238-1252.

Brown, J. H., Marquet, P. A., and Taper, M. L. 1983. Evolution of body size: consequences of an energetic definition of fitness. The American Naturalist 142(4): 573-584.

Brownscombe, J. W., Griffin, L. P., Brooks, J. L., Danylchuk, A. J., Cooke, S. J., and Midwood, J. D. 2022. Applications of telemetry to fish habitat science and management. Canadian Journal of Fisheries and Aquatic Sciences 79(8): 1347-1359.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference, 2nd edition. Springer-Verlag, New York.

Bussmann, K., Hirsch, P. E., Lehmann, M. F., and Burkhardt-Holm, P. 2022. Differential habitat use of a notorious invasive fish, the Round Goby, in a translocation-relevant system. Ecology and Evolution 12(8): e9202.

Buxton, V. L., Enos, J. K., Sperry, J. H., and Ward, M. P. 2020. A review of conspecific attraction for habitat selection across taxa. Ecology and Evolution 10(23): 12690-12699.

Byrd, C. G., Chapman, D. C., Pherigo, E. K., and Jolley, J. C. 2019. Tag retention and survival of juvenile Bighead Carp implanted with a dummy acoustic tag at three temperatures. Journal of Applied Ichthyology 35(3): 763-768

Calkins, H. A., Tripp, S. J., and Garvey, J. E. 2012. Linking Silver Carp habitat selection to flow and phytoplankton in the Mississippi River. Biological Invasions 14(5): 949-958.

Camacho, C. A., Sullivan, C. J., Weber, M. J., and Pierce, C. L. 2023. Invasive carp reproduction phenology in tributaries of the upper Mississippi River. North American Journal of Fisheries Management 43(1): 61-80.

Carlson, T. L., LaBrie, L. A., Wesner, J. S., Chipps, S. R., Coulter, A. A., and Schall, B. J. 2023. Receiver mount design, transmitter depth, and wind speed affect detection probability of acoustic telemetry transmitters in a Missouri River tributary. Animal Biotelemetry 11(1): 6.

Carpenter-Bundhoo, L., Butler, G. L., Bond, N. R., Thiem, J. D., Bunn, S. E., and Kennard, M. J. 2023. Fish movements in response to environmental flow releases in intermittent rivers. Freshwater Biology 68(2): 260-273.

Chase, N. M., Caldwell, C. A., Carleton, S. A., Gould, W. R., and Hobbs, J. A. 2015. Movement patterns and dispersal potential of Pecos Bluntnose Shiner (*Notropis simus pecosensis*) revealed using otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 72(10): 1575-1583.

Chapman, Duane. (2006). Early Development of Four Cyprinids Native to the Yangtze River, China. USGS professional paper 239: 1-51.

Chen, Y., D. Chapman, J. Jackson, D. Chen, Z. Li, J. Kilgore, Q. Phelps, and M. Eggleton, 2016. Fishery resources, environment, and conservation in the Mississippi and Yangtze (Changjiang) River Basins. American Fisheries Society, Bethesda, Maryland.

Chen, P., Wiley, E. O., and Mcnyset, K. M. 2007. Ecological niche modeling as a predictive tool: silver and bighead carps in North America. Biological Invasions 9: 43-51.

Chick, J. H., Colaninno, C. E., Beyer, A. M., Brown, K. B., Dopson, C. T., Enzerink, A. O., Goesmann, S. R., Higgins, T., Knutzen N. Q., Laute, E. N., Long P. M., Ottenfeld P. L., Uehling, A. T., Ward L. C., Maxson, K. A., Ratcliff, E. N., Lubinski B. J., and Gittinger, E. J. 2020a. Following the edge of the flood: use of shallow-water habitat by larval Silver Carp *Hypophthalmichthys molitrix* in the upper Mississippi river system. Journal of Freshwater Ecology 35(1): 95-104.

Chick, J. H., Gibson-Reinemer, D. K., Soeken-Gittinger, L., and Casper, A. F. 2020b. Invasive Silver Carp is empirically linked to declines of native sport fish in the Upper Mississippi River System. Biological Invasions 22(2): 723-734.

Cooke, S. L., Hill, W. R., and Meyer, K. P. 2009. Feeding at different plankton densities alters invasive Bighead Carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition. Hydrobiologia 625(1): 185-193.

Cooke, S. J., Paukert, C., and Hogan, Z. 2012. Endangered river fish: factors hindering conservation and restoration. Endangered Species Research 17(2): 179-191.

Cooke, S. J., Martins, E. G., Struthers, D. P., Gutowsky, L. F., Power, M., Doka, S. E., Dettmers, J. M., Crooke D. A., Lucas M. C., Holbrook C. M., and Krueger, C. C. 2016. A moving target—incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. Environmental Monitoring and Assessment, 188: 1-18.

Cooke, S. J., Bergman, J. N., Twardek, W. M., Piczak, M. L., Casselberry, G. A., Lutek, K., Dahlmo, L. S., Birnie-Gauvin, K., Griffin, L. P., Brownscombe, J. W., Raby, G. D., Standen, E. M., Horodysky, A. Z., Johnsen, S., Danylchuk, A. J., Furey, N. B., Gallagher, A. J., Lédée, E. J.I., Midwood, J. D., Gutowsky, L. F.G., Jacoby D. M.P., Matley, J. K., and Lennox, R. J. 2022. The movement ecology of fishes. Journal of Fish Biology 101(4): 756-779.

Cooper, A. R., Infante, D. M., O'Hanley, J. R., Yu, H., Neeson, T. M., and Brumm, K. J. 2021. Prioritizing native migratory fish passage restoration while limiting the spread of invasive species: a case study in the Upper Mississippi River. Science of the Total Environment 791: 148317.

Copeland, R. R. 2002. Red River Below Denison Dam, Texas, Oklahoma, Arkansas, and Louisiana. Engineer research and development center Vicksburg MS coastal and hydraulics lab.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51(3/4): 429-438.

Coulombe-Pontbriand, M., and Lapointe, M. 2004. Landscape controls on boulder-rich, winter habitat availability and their effects on Atlantic Salmon (*Salmo salar*) parr abundance in two fifth-order mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 61(4): 648-658.

Coulter, A. A., Keller, D., Amberg, J. J., Bailey, E. J., and Goforth, R. R. 2013. Phenotypic plasticity in the spawning traits of Bigheaded carp (Hypophthalmichthys spp.) in novel ecosystems. Freshwater Biology 58(5): 1029-1037.

Coulter, A. A., Bailey, E. J., Keller, D., and Goforth, R. R. 2016. Invasive Silver Carps movement patterns in the predominantly free-flowing Wabash River (Indiana, USA). Biological Invasions 18(2): 471-485.

Coulter, A. A., Brey, M. K., Lubejko, M., Kallis, J. L., Coulter, D. P., Glover, D. C., Whitledge, G. W., and Garvey, J. E. 2018a. Multistate models of Bigheaded carps in the Illinois River reveal spatial dynamics of invasive species. Biological Invasions 20: 3255-3270.

Coulter, D. P., Tristano, E. P., Coulter, A. A., Seibert, J. R., and Garvey, J. E. 2018b. Role of winter severity on juvenile Bighead Carp and Silver Carp growth and survival across latitudes. Biological Invasions 20: 3357-3371.

Coulter, A. A., Coulter, D. P., Lark, E., Fritts, M. W., Davis, C., Glover, D., and Goforth, R. 2022a. Sublethal effects of acoustic dummy tag implantation and external tags in Silver Carp. North American Journal of Fisheries Management 42(6): 1502-1512.

Coulter, A. A., Prechtel, A. R., and Goforth, R. R. 2022b. Consistency of mobile and sedentary movement extremes exhibited by an invasive fish, Silver Carp Hypophthalmichthys molitrix. Biological Invasions 24(8): 2581-2596.

Cucherousset, J., and Olden, J. D. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36(5): 215-230.

Cuddington, K., Currie, W. J. S., and Koops, M. A. 2014. Could an Asian carp population establish in the Great Lakes from a small introduction? Biological Invasions 16(4): 903-917.

Cupp, A. R., Brey, M. K., Calfee, R. D., Chapman, D. C., Erickson, R., Fischer, J., Fritts, A. K., George, A. E., Jackson, P. R., Knights, B. C., Saari, G. N., Kočovský, P. M. 2021. Emerging control strategies for integrated pest management of invasive carps. Journal of Vertebrate Biology 70(4): 21057-1.

Dance, M. A., and Rooker, J. R. 2015. Habitat-and bay-scale connectivity of sympatric fishes in an estuarine nursery. Estuarine Coastal and Shelf Science 167: 447-457.

DeBoer, J. A., Anderson, A. M., and Casper, A. F. 2018. Multi-trophic response to invasive Silver Carp (*Hypophthalmichthys molitrix*) in a large floodplain river. Freshwater Biology 63(6): 597-611.

DeGrandchamp, K. L., Garvey, J. E., and Colombo, R. E. 2008. Movement and habitat selection by invasive Asian carps in a large river. Transactions of the American Fisheries Society 137(1): 45-56.

Dennis, C. E., Zielinski, D., and Sorensen, P. W. 2019. A complex sound coupled with an air curtain blocks invasive carp passage without habituation in a laboratory flume. Biological Invasions 21: 2837-2855.

Deters, J. E., Chapman, D. C., and McElroy, B. 2013. Location and timing of Asian carp spawning in the lower Missouri River. Environmental Biology of Fishes 96: 617-629.

Duan, X., Liu, S., Huang, M., Qiu, S., Li, Z., Wang, K., and Chen, D. 2010. Changes in abundance of larvae of the four domestic Chinese carps in the middle reach of the Yangtze River, China, before and after closing of the Three Gorges Dam. Chinese Fishes 13-22.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews of the Cambridge Philosophical Society 81(2):163-182.

Durham, B. W., and Wilde, G. R. 2009. Effects of streamflow and intermittency on the reproductive success of two broadcast-spawning cyprinid fishes. Copeia 2009(1): 21-28.

Erickson, R. A., Rees, C. B., Coulter, A. A., Merkes, C. M., McCalla, S. G., Touzinsky, K. F., Walleser L., Goforth R. R., and Amberg, J. J. 2016. Detecting the movement and spawning activity of Bigheaded Carps with environmental DNA. Molecular Ecology Resources 16(4): 957-965.

Fang, D. A., Zhou, Y. F., Ren, P., Peng, Y. X., Xue, X. P., Ren, L., and Xu, D. P. 2022. The status of Silver Carp resources and their complementary mechanism in the Yangtze River. Frontiers in Marine Science 8: 790614.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., and Li, H. W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes: a continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. BioScience 52(6): 483-498.

Favrot, S. D., Jonasson, B. C., and Peterson, J. T. 2018. Fall and winter microhabitat use and suitability for Spring Chinook Salmon Parr in a US Pacific Northwest River. Transactions of the American Fisheries Society 147(1): 151-170.

Ferguson, A., Reed, T. E., Cross, T. F., McGinnity, P., and Prodöhl, P. A. 2019. Anadromy, potamodromy and residency in Brown Trout *Salmo trutta*: the role of genes and the environment. Journal of Fish Biology 95(3): 692-718.

Forsythe, P. S., Scribner, K. T., Crossman, J. A., Ragavendran, A., Baker, E. A., Davis, C., and Smith, K. K. 2012. Environmental and lunar cues are predictive of the timing of river entry and spawning-site arrival in Lake Sturgeon *Acipenser fulvescens*. Journal of Fish Biology 81(1): 35-53.

Frank, H. J., Mather, M. E., Smith, J. M., Muth, R. M., Finn, J. T., and McCormick, S. D. 2009. What is "fallback"?: metrics needed to assess telemetry tag effects on anadromous fish behavior. Hydrobiologia 635(1): 237-249.

Frissell, C. A., Liss, W. J., Warren, C. E., and Hurley, M. D. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10(2): 199-214.

Fritts, A. K., Knights, B. C., Stanton, J. C., Milde, A. S., Vallazza, J. M., Brey, M. K., Trip, S. J., Devine, T. E., Sleeper, W., Lamer, J. T., and Mosel, K. J. 2021. Lock operations influence upstream passages of invasive and native fishes at a Mississippi River high-head dam. Biological Invasions 23(3): 771-794.

Garcia, T., Murphy, E. A., Jackson, P. R., and Garcia, M. H. 2015. Application of the FluEgg model to predict transport of Asian carp eggs in the Saint Joseph River (Great Lakes tributary). Journal of Great Lakes Research 41(2): 374-386.

Gatz Jr, A. J., and Adams, S. M. 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. Ecology of Freshwater Fish 3(1): 35-48.

Gerber, K. M., Mather, M. E., and Smith, J. M. 2017. A suite of standard post-tagging evaluation metrics can help assess tag retention for field-based fish telemetry research. Reviews in Fish Biology and Fisheries 27: 651-664.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C.E., and Jerde, C. L. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75(4): 887-898.

Glubzinski, M. A., Coulter, D. P., and Whitledge, G. W. 2021. Environmental factors associated with Silver Carp presence and relative abundance near an invasion front to inform removal efforts. Hydrobiologia 848(15): 3571-3585.

Gosset, C., Rives, J., & Labonne, J. 2006. Effect of habitat fragmentation on spawning migration of Brown Trout (*Salmo trutta L*.). Ecology of Freshwater Fish 15(3): 247-254.

Haggard, B. E., Scott, J. T., and Longing, S. D. 2013. Sestonic chlorophyll-a shows hierarchical structure and thresholds with nutrients across the Red River Basin, USA. Journal of Environmental Quality 42(2): 437-445.

Harms, J. D., Jimerson, K. R., Schmidt, J. M., Lucchesi, D. O., Schall, B. J., and Coulter, A. A. 2024. Progression along the invasion curve: Silver Carp growth slows temporally in two Missouri River tributaries. Aquatic Invasions 19(1): 109-120.

Harrison, P. M., Keeler, R. A., Robichaud, D., Mossop, B., Power, M., and Cooke, S. J. 2019. Individual differences exceed species differences in the movements of a river fish community. Behavioral Ecology 30(5): 1289-1297.

Haupt, K. J., and Phelps, Q. E. 2016. Mesohabitat associations in the Mississippi River Basin: a long-term study on the catch rates and physical habitat associations of juvenile Silver Carp and two native planktivores. Aquatic Invasions 11(1): 93-99.

Heer, T., Wells, M. G., and Mandrak, N. E. 2019. Assessment of Asian carps spawning potential in tributaries to the Canadian Lake Ontario basin. Journal of Great Lakes Research 45(6): 1332-1339.

Herborg, L. M., Mandrak, N. E., Cudmore, B. C., and MacIsaac, H. J. 2007. Comparative distribution and invasion risk of Snakehead (*Channidae*) and Asian carp (*Cyprinidae*) species in North America. Canadian Journal of Fisheries and Aquatic Sciences 64(12): 1723-1735.

Hessler, T. M., Chapman, D. C., Paukert, C. P., Jolley, J. C., and Byrne, M. E. 2023. Winter habitat selection and efficacy of telemetry to aid Grass Carp removal efforts in a large reservoir. North American Journal of Fisheries Management 43(1): 189-202.

Hintz, W. D., Glover, D. C., Szynkowski, B. C., and Garvey, J. E. 2017a. Spatiotemporal reproduction and larval habitat associations of nonnative Silver Carp and Bighead Carp. Transactions of the American Fisheries Society 146(3): 422-431.

Hintz, W. D., MacVey, N. K., Asher, A. M., Porreca, A. P., and Garvey, J. E. 2017b. Variation in prey selection and foraging success associated with early-life ontogeny and habitat use of American paddlefish (Polyodon spathula). Ecology of Freshwater Fish 26(2): 181-189.

Hitt, N. P., Frissell, C. A., Muhlfeld, C. C., and Allendorf, F. W. 2003. Spread of hybridization between native westslope Cutthroat Trout, *Oncorhynchus clarki lewisi*, and nonnative

Rainbow Trout, *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Sciences 60(12): 1440-1451.

Hoagstrom, C. W., and Turner, T. F. 2015. Recruitment ecology of pelagic-broadcast spawning minnows: paradigms from the ocean advance science and conservation of an imperilled freshwater fauna. Fish and Fisheries 16(2): 282-299.

Hoover, J. J., Zielinski, D. P., and Sorensen, P. W. 2017. Swimming performance of adult Bighead Carp *Hypophthalmichthys nobilis* (Richardson, 1845) and Silver Carp *H. molitrix* (Valenciennes, 1844). Journal of Applied Ichthyology 33(1): 54-62.

Houser, J. N. 2016. Contrasts between channels and backwaters in a large, floodplain river: testing our understanding of nutrient cycling, phytoplankton abundance, and suspended solids dynamics. Freshwater Science 35(2): 457-473.

Hughes, J. M., Meadows, N. M., Stewart, J., Booth, D. J., and Fowler, A. M. 2022. Movement patterns of an iconic recreational fish species, Mulloway (*Argyrosomus japonicus*), revealed by cooperative citizen-science tagging programs in coastal eastern Australia. Fisheries Research 247: 106179.

Hunsicker, M. E., Kappel, C. V., Selkoe, K. A., Halpern, B. S., Scarborough, C., Mease, L., and Amrhein, A. 2016. Characterizing driver–response relationships in marine pelagic ecosystems for improved ocean management. Ecological Applications 26(3): 651-663.

Hutchings, J. A., and Gerber, L. 2002. Sex–biased dispersal in a salmonid fish. Proceedings of the Royal Society of London. Series B: Biological Sciences 269(1508): 2487-2493.

Ibarra, J. G., Nelson, E. J., Romy, S. E., and Lash, C. L. 2024. A systematic literature review of the various effects, impacts, and management options regarding Silver and Bighead Carp in the Great Lakes Region. Bios 95(1): 44-51.

Ivan, L. N., Mason, D. M., Zhang, H., Rutherford, E. S., Hunter, T., Sable, S., Adamack, A. T., and Rose, K. 2020. Potential establishment and ecological effects of Bighead and Silver Carp in a productive embayment of the Laurentian Great Lakes. Biological Invasions 22: 2473-2495.

Jayasinghe, U. A. D., García-Berthou, E., Li, Z., Li, W., Zhang, T., and Liu, J. 2015. Co-occurring bighead and silver carps show similar food preference but different isotopic niche overlap in different lakes. Environmental Biology of Fishes 98: 1185-1199.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren. 2008. Conservation status of imperiled North American freshwater and diadromous Fishes. Fisheries 33(8):372-407.

Jennings, D. P. 1988. Bighead carp (Hypophthalmichthys nobilis): biological synopsis. Fish and Wildlife Service 88(29): 35

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52(1/2): 225-247.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research, 66(1991): 20-35.

Juette, T., Cucherousset, J., and Cote, J. 2014. Animal personality and the ecological impacts of freshwater non-native species. Current Zoology 60(3): 417-427.

Kadye, W. T., and Booth, A. J. 2013. Movement patterns and habitat selection of invasive African Sharptooth Catfish. Journal of Zoology 289(1): 41-51.

Kallis, J., Erickson, R., Coulter, D. P., Coulter, A. A., Brey, M. K., Catalano, M., Dettmers, J., Garvey, J., Irons, K., Marschall, E., Rose, K., Wildhaber, M., and Glover, D. 2023. Incorporating metapopulation dynamics to inform invasive species management: Evaluating Bighead and Silver Carp control strategies in the Illinois River. Journal of Applied Ecology 60(9): 1841.

Kellner, K. 2015. jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version 1(1).

Kessel, S. T., Cooke, S. J., Heupel, M. R., Hussey, N. E., Simpfendorfer, C. A., Vagle, S., and Fisk, A. T. 2014. A review of detection range testing in aquatic passive acoustic telemetry studies. Reviews in Fish Biology and Fisheries 24(1): 199-218.

Kéry, M., and Schaub, M. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic press.

Khan, J. A., Welsh, J. Q., and Bellwood, D. R. 2016. Using passive acoustic telemetry to infer mortality events in adult herbivorous coral reef fishes. Coral Reefs 35: 411-420.

Kim, J., Doyle, B., and Mandrak, N. E. 2017. Electrosedation of freshwater fishes for the surgical implantation of transmitters. Canadian Journal of Zoology 95(8): 575-580.

Klinard, N. V., and Matley, J. K. 2020. Living until proven dead: addressing mortality in acoustic telemetry research. Reviews in Fish Biology and Fisheries 30(3): 485-499.

Kluender, E. R., Adams, R., and Lewis, L. 2017. Seasonal habitat use of Alligator Gar in a river–floodplain ecosystem at multiple spatial scales. Ecology of Freshwater Fish 26(2): 233-246.

Kolar, C. S., D. C. Chapman, W. R. C. Jr, C. M. Housel, J. D. Williams, and D. P. Jennings. 2007. Bigheaded Carps: a biological synopsis and environmental risk assessment.

LaBrie, L. A., and Wesner, J. S. 2023. Using passive telemetry and environmental variables to predict Silver Carp (*Hypophthalmichthys molitrix*) movement cues on the northwestern edge of their invasion front. bioRxiv 2023-12.

Labuzzetta, C. J., Coulter, A. A., and Erickson, R. A. 2024. Comparing maximum likelihood and Bayesian methods for fitting hidden Markov models to multi-state capture-recapture data of invasive carp in the Illinois River. Movement Ecology 12(1): 2.

Laake, J., and Rexstad, E. 2008. RMark–an alternative approach to building linear models in MARK. Program MARK: a gentle introduction C1-C113.

Lamarins, A., Hugon, F., Piou, C., Papaïx, J., Prévost, E., Carlson, S. M., and Buoro, M. 2022. Implications of dispersal in Atlantic Salmon: lessons from a demo-genetic agent-based model. Canadian Journal of Fisheries and Aquatic Sciences 79(12): 2025-2042.

Lamouroux, N., Olivier, J. M., Persat, H., PouilLy, M., Souchon, Y., and Statzner, B. 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. Freshwater Biology 42(2): 275-299.

Lapointe, N. W. R., Thorson, J. T., and Angermeier, P. L. 2010. Seasonal meso-and microhabitat selection by the Northern Snakehead (*Channa argus*) in the Potomac river system. Ecology of Freshwater Fish 19(4): 566-577.

Lauber, T. B., Stedman, R. C., Connelly, N. A., Rudstam, L. G., Ready, R. C., Poe, G. L., Bunnell, D. B., Hook, T. O., Koops, M. A., Ludsin, S. A., and Rutherford, E. S. 2016. Using scenarios to assess possible future impacts of invasive species in the Laurentian Great Lakes. North American Journal of Fisheries Management 36(6): 1292-1307.

Laughlin, D. H., and Lacewell, R. D. 1981. Agricultural benefits of salinity control on the Red River. Western Journal of Agricultural Economics 6(2): 195-206.

Lawrence, M. J., Wilson, B. M., Reid, G. K., Hawthorn, C., English, G., Black, M., Leadbeater, S., McKindsey, C. W., Trudel, M. 2023. The fate of intracoelomic acoustic transmitters in Atlantic Salmon (*Salmo salar*) post-smolts and wider considerations for causal factors driving tag retention and mortality in fishes. Animal Biotelemetry 11(1): 40.

Lawson, P. W., Logerwell, E. A., Mantua, N. J., Francis, R. C., and Agostini, V. N. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest Coho Salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 61(3): 360-373.

Lebreton, J. D., Nichols, J. D., Barker, R. J., Pradel, R., and Spendelow, J. A. 2009. Modeling individual animal histories with multistate capture–recapture models. Advances in ecological research 41: 87-173.

Lenaerts, A. W., Coulter, A. A., Irons, K. S., and Lamer, J. T. 2023a. Examination of Bigheaded Carp ovaries indicates batch spawning. North American Journal of Fisheries Management 43(1): 25-34.

Lenaerts, A. W., Coulter, A. A., Irons, K. S., and Lamer, J. T. 2023b. A quick method for estimating batch fecundity in bigheaded carp. North American Journal of Fisheries Management 43(1): 3-11.

Lennox, R. J., Crook, D. A., Moyle, P. B., Struthers, D. P., and Cooke, S. J. 2019. Toward a better understanding of freshwater fish responses to an increasingly drought-stricken world. Reviews in Fish Biology and Fisheries, 29: 71-92.

Li, M., Gao, X., Yang, S., Duan, Z., Cao, W., and Liu, H. 2013. Effects of environmental factors on natural reproduction of the four major Chinese carps in the Yangtze River, China. Zoological Science 30(4): 296-303.

Lockwood, J. L., Cassey, P., and Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution, 20(5): 223-228.

Lohmeyer, A. M., and Garvey, J. E. 2009. Placing the North American invasion of Asian carp in a spatially explicit context. Biological Invasions 11(4): 905-916.

Longing, S. D., and Haggard, B. E. 2010. Distributions of median nutrient and chlorophyll concentrations across the Red River basin, USA. Journal of Environmental Quality 39(6): 1966-1974.

Love, S. A., Lederman, N. J., Anderson, R. L., DeBoer, J. A., and Casper, A. F. 2018. Does aquatic invasive species removal benefit native fish? The response of Gizzard Shad

(*Dorosoma cepedianum*) to commercial harvest of Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*). Hydrobiologia 817: 403-412.

Love, S. A., Phelps, Q. E., Tripp, S. J., and Herzog, D. P. 2017. The importance of shallow-low velocity habitats to juvenile fish in the middle Mississippi River. River Research and Applications 33(3): 321-327.

Lubejko, M. V., Whitledge, G. W., Coulter, A. A., Brey, M. K., Oliver, D. C., and Garvey, J. E. 2017. Evaluating upstream passage and timing of approach by adult Bigheaded Carps at a gated dam on the Illinois River. River Research and Applications 33(8): 1268-1278.

Lu, G., Wang, C., Zhao, J., Liao, X., Wang, J., Luo, M., Zhu, L., Bernatzhez, L., Li, S. 2020. Evolution and genetics of bighead and Silver Carps: Native population conservation versus invasive species control. Evolutionary Applications 13(6): 1351-1362.

MacNamara, R., Coulter, D. P., Glover, D. C., Lubejko, A. E., and Garvey, J. E. 2018. Acoustically derived habitat associations of sympatric invasive bigheaded carps in a large river ecosystem. River Research and Applications 34(6): 555-564.

Maindonald, M. J. 2023. Package ‘gamclass’.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. and Erickson, W.P. 2002 Resource Selection by Animals: Statistical Analysis and Design for Field Studies. Chapman and Hall, London

Marjoram, P., J. Molitor, V. Plagnol, and S. Tavaré. 2003. Markov chain Monte Carlo without likelihoods. Proceedings of the National Academy of Sciences of the United States of America 100(26):15324-15328.

Matthews, W. J. (1988). North American prairie streams as systems for ecological study. Journal of the North American Benthological Society 7(4): 387-409.

Matthews, W. J., and Zimmerman, E. G. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the Southwest. Fisheries 15(6): 26-32.

Matthiopoulos, J., Fieberg, J., Aarts, G., Beyer, H. L., Morales, J. M., and Haydon, D. T. 2015. Establishing the link between habitat selection and animal population dynamics. Ecological Monographs 85(3): 413-436.

Mazziotta, A., Lindén, A., Eyvindson, K., Bianchi, S., Kangas, A., Melin, M., Ruha, L., and Forsman, J. T. 2024. Unraveling the characteristic spatial scale of habitat selection for forest grouse species in the boreal landscape. Forest Ecology and Management 563: 122008.

McDonald, D. B., Parchman, T. L., Bower, M. R., Hubert, W. A., and Rahel, F. J. 2008. An introduced and a native vertebrate hybridize to form a genetic bridge to a second native species. Proceedings of the National Academy of Sciences 105(31): 10837-10842.

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., and Cushman, S. A. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape ecology 31: 1161-1175.

McGrath, P., and Austin, H. A. 2009. Site fidelity, home range, and tidal movements of White Perch during the summer in two small tributaries of the York River, Virginia. Transactions of the American Fisheries Society 138(5): 966-974.

Melnychuk, M. C., Dunton, K. J., Jordaan, A., McKown, K. A., and Frisk, M. G. 2017. Informing conservation strategies for the endangered Atlantic Sturgeon using acoustic telemetry and multi-state mark–recapture models. Journal of Applied Ecology 54(3): 914-925.

Miller, S. E., and Scarnecchia, D. L. 2011. Sex-specific differences in migratory movements of adult Paddlefish above Fort Peck Reservoir, Montana, USA. Folia Zoologica 60(3): 181-188.

Miranda, L. E. 2009. Standardizing electrofishing power for boat electrofishing. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland, 223-230.

Mollenhauer, R., Wagner, T., Kepler, M. V., and Sweka, J. A. 2013. Fall and early winter movement and habitat use of wild Brook Trout. Transactions of the American Fisheries Society 142(5): 1167-1178.

Mollenhauer, R., Zhou, Y., and Brewer, S. K. 2019. Multiscale habitat factors explain variability in stream fish occurrence in the Ozark Highlands ecoregion, USA. Copeia 107(2): 219-231.

Mollenhauer, R., Brewer, S. K., Perkin, J. S., Swedberg, D., Wedgeworth, M., and Steffensmeier, Z. D. 2021. Connectivity and flow regime direct conservation priorities for pelagophil fishes. Aquatic Conservation: Marine and Freshwater Ecosystems 31(11): 3215-3227.

Mollenhauer, R., Mouser, J. B., Roland, V. L., and Brewer, S. K. 2022. Increased landscape disturbance and streamflow variability threaten fish biodiversity in the Red River catchment, USA. Diversity and Distributions 28(9): 1934-1950.

Moore, S. L., and Thorp, J. H. 2008. Coping with hydrogeomorphic variations in a prairie river: resiliency in young-of-the-year fishes. River Research and Applications 24(3): 267-278.

Morash, A. J., Speers-Roesch, B., Andrew, S., and Currie, S. 2021. The physiological ups and downs of thermal variability in temperate freshwater ecosystems. Journal of Fish Biology 98(6): 1524-1535.

Munz, J. T., and Higgins, C. L. 2013. The influence of discharge, photoperiod, and temperature on the reproductive ecology of cyprinids in the Paluxy River, Texas. Aquatic Ecology 47(1): 67-74.

Myrick, C. A., and Cech, J. J. 2000. Temperature influences on California rainbow trout physiological performance. Fish Physiology and Biochemistry 22(3): 245-254.

Nad'o, L., and Kaňuch, P. 2018. Why sampling ratio matters: Logistic regression and studies of habitat use. PLoS One 13(7): e0200742.

Nico, L. G., Williams, J. D., and Jelks, H. L. 2005. Black Carp: Biological synopsis and risk assessment of an introduced fish. vol. 32. American Fisheries Society Special Publication, Bethesda, MD.

Norberg, B., Brown, C. L., Halldorsson, O., Stensland, K., and Björnsson, B. T. 2004. Photoperiod regulates the timing of sexual maturation, spawning, sex steroid and thyroid hormone profiles in the Atlantic Cod (*Gadus morhua*). Aquaculture 229(1-4): 451-467.

Norman, J. D., and Whitledge, G. W. 2015. Recruitment sources of invasive Bighead Carp (*Hypopthalmichthys nobilis*) and Silver Carp (*H. molitrix*) inhabiting the Illinois River. Biological Invasions 17: 2999-3014.

Nunn, A. D., Tewson, L. H., and Cowx, I. G. 2012. The foraging ecology of larval and juvenile fishes. Reviews in Fish Biology and Fisheries 22: 377-408.

Okamura, H., McAllister, M. K., Ichinokawa, M., Yamanaka, L., and Holt, K. 2014. Evaluation of the sensitivity of biological reference points to the spatio-temporal distribution of fishing effort when seasonal migrations are sex-specific. Fisheries Research 158: 116-123.

Olden, J. D., and Naiman, R. J. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology 55(1): 86-107.

Otis, D. L., and White, G. C. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. The Journal of Wildlife Management 63(3): 1039-1044.

Pavlov, D. S., and Mikheev, V. N. 2017. Downstream migration and mechanisms of dispersal of young fish in rivers. Canadian Journal of Fisheries and Aquatic Sciences 74(8): 1312-1323.

Parker, A. D., Glover, D. C., Finney, S. T., Rogers, P. B., Stewart, J. G., and Simmonds Jr, R. L. 2016. Fish distribution, abundance, and behavioral interactions within a large electric dispersal barrier designed to prevent Asian carp movement. Canadian Journal of Fisheries and Aquatic Sciences 73(7): 1060-1071.

Patton, T., and C. T. Tacket. 2012. Status of Silver Carp (*Hypophthalmichthys molitrix*) and Bighead Carps (*Hypophthalmichthys nobilis*) in Southeastern Oklahoma. Proceedings of the Oklahoma Academy of Science 53-58.

Pedaccini, M., Sousa, I., Bentes, L., DeBenito-Abelló, C., Lino, P. G., Moland, E., Gonçalves, J. M. S., and e Costa, B. H. 2023. Spawning-related fish movement synchrony of White Seabream *Diplodus sargus* in a no-take zone. Marine Ecology Progress Series 707: 99-113.

Perry, R. W., Skalski, J. R., Brandes, P. L., Sandstrom, P. T., Klimley, A. P., Ammann, A., and MacFarlane, B. 2010. Estimating survival and migration route probabilities of juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta. North American Journal of Fisheries Management 30(1): 142-156.

Peters, L. M., Pegg, M. A., and Reinhardt, U. G. 2006. Movements of adult radio-tagged Bighead Carp in the Illinois River. Transactions of the American Fisheries Society 135(5): 1205-1212.

Plummer, M. 2003. JAGS: A program for analysis of bayesian graphical models using gibbs sampling JAGS : Just Another Gibbs Sampler (Dsc).

Prechtel, A. R., Coulter, A. A., Etchison, L., Jackson, P. R., and Goforth, R. R. 2018. Range estimates and habitat use of invasive Silver Carp (*Hypophthalmichthys molitrix*): evidence of sedentary and mobile individuals. Hydrobiologia 805(1): 203-218.

Radinger, J., and Wolter, C. 2014. Patterns and predictors of fish dispersal in rivers. Fish and Fisheries 15(3): 456-473.

Ramsey, P. Q., Dattilo, J., DeVries, D. R., and Brewer, S. K. 2024. Evaluating the context dependency of large river nursery habitats for fishes in the lower Red River catchment. River Research and Applications 40(5): 761-779.

Rasmussen, J. E., and Belk, M. C. 2012. Dispersal behavior correlates with personality of a North American fish. Current Zoology 58(2): 260-270.

Reinfelds, I. V., Walsh, C. T., Van Der Meulen, D. E., Growns, I. O., and Gray, C. A. 2013. Magnitude, frequency and duration of instream flows to stimulate and facilitate catadromous fish migrations: Australian Bass (*Macquaria novemaculeata Perciformes, Percichthyidae*). River Research and Applications 29(4): 512-527.

Rhymer, J. M., and Simberloff, D. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27(1): 83-109.

Rice, J. C. 2005. Understanding fish habitat ecology to achieve conservation. Journal of Fish Biology 67: 1-22.

Riggs, C. D., and Bonn, E. W. 1959. An annotated list of the fishes of Lake Texoma, Oklahoma and Texas. The Southwestern Naturalist 4(4): 157-168.

Ridgway, J. L., Lawson, K. M., Shier, S. A., Calfee, R. D., and Chapman, D. C. 2023a. An assessment of fish herding techniques: management implications for mass removal and control of Silver Carp. North American Journal of Fisheries Management 43(1): 176-188.

Ridgway, J. L., Acre, M. R., Hessler, T. M., Broaddus, D. W., Morris, J., and Calfee, R. D. 2023b. Silver Carp herding: A telemetry evaluation of efficacy and implications for design and application. North American Journal of Fisheries Management 43(6): 1750-1764.

Robertson, B. P., Gardner, J. P., and Savage, C. 2015. Macrobenthic–mud relations strengthen the foundation for benthic index development: A case study from shallow, temperate New Zealand estuaries. Ecological Indicators 58: 161-174.

Rodnick, K. J., St.-Hilaire, S., Battiprolu, P. K., Seiler, S. M., Kent, M. L., Powell, M. S., and Ebersole, J. L. 2008. Habitat selection influences sex distribution, morphology, tissue biochemistry, and parasite load of juvenile Coho Salmon in the West Fork Smith River, Oregon. Transactions of the American Fisheries Society 137(6): 1571-1590.

Roever, C. L., H. L. Beyer, M. J. Chase, and R. J. Van Aarde. 2014. The pitfalls of ignoring behavior when quantifying habitat selection. Diversity and Distributions 20(3): 322-333.

Rowe, D. C., C. L. Pierce, and T. F. Wilton. 2009. Physical Habitat and Fish Assemblage Relationships with Landscape Variables at Multiple Spatial Scales in Wadeable Iowa Streams. North American Journal of Fisheries Management 29(5): 1333-1351.

Roy, M. L., Roy, A. G., Grant, J. W., and Bergeron, N. E. 2013. Individual variability in the movement behaviour of juvenile Atlantic Salmon. Canadian Journal of Fisheries and Aquatic Sciences 70(2): 339-347.

Rytwinski, T., Taylor, J. J., Donaldson, L. A., Britton, J. R., Browne, D. R., Gresswell, R. E., Lintermans, M., Prior, K. A., Pellatt, M. G., Vis, C., and Cooke, S. J. 2019. The effectiveness of non-native fish removal techniques in freshwater ecosystems: a systematic review. Environmental Reviews 27(1): 71-94.

Sampson, S. J., Chick, J. H., and Pegg, M. A. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions 11(3): 483-496.

Sánchez-González, J. R., and Nicieza, A. G. 2021. Individual differences in dominance-related traits drive dispersal and settlement in hatchery-reared juvenile Brown Trout. Scientific Reports 11(1): 7277.

Sass, G. G., Cook, T. R., Irons, K. S., McClelland, M. A., Michaels, N. N., Matthew O'Hara, T., and Stroub, M. R. 2010. A mark-recapture population estimate for invasive Silver Carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. Biological Invasions 12: 433-436.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41(10): 704-712.

Schrank, S. J., Braaten, P. J., and Guy, C. S. 2001. Spatiotemporal variation in density of larval Bighead Carps in the lower Missouri River. Transactions of the American Fisheries Society 130(5): 809-814.

Seber, G. A. 1965. A note on the multiple-recapture census. Biometrika 52(1/2): 249-259.

Selong, J. H., McMahon, T. E., Zale, A. V., and Barrows, F. T. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130(6): 1026-1037.

Shepard, B. B., Nelson, L. M., Taper, M. L., and Zale, A. V. 2014. Factors influencing successful eradication of nonnative Brook Trout from four small Rocky Mountain streams using electrofishing. North American Journal of Fisheries Management 34(5): 988-997.

Shuai, F., Lek, S., Baehr, C., Park, Y. S., Li, Y., and Li, X. 2018. Silver Carp larva abundance in response to river flow rate revealed by cross-wavelet modelling. Ecological Modelling 383: 98-105.

Silva, A. T., Katopodis, C., Santos, J. M., Ferreira, M. T., and Pinheiro, A. N. 2012. Cyprinid swimming behaviour in response to turbulent flow. Ecological Engineering 44: 314-328.

Sleezer, L. J., P. L. Angermeier, E. A. Frimpong, B. L. Brown, and X. Liu. 2021. A new composite abundance metric detects stream fish declines and community homogenization during six decades of invasions. Diversity and Distributions 27(11): 2136-2156.

Solomon, L. E., Pendleton, R. M., Chick, J. H., and Casper, A. F. 2016. Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. Biological Invasions 18(10): 2883-2895.

Stanton, J. C., Brey, M. K., Coulter, A. A., Stewart, D. R., and Knights, B. 2024. Bayesian multistate models for measuring invasive carp movement and evaluating telemetry array performance. PeerJ 12: e17834.

Stiver, K. A., Desjardins, J. K., Fitzpatrick, J. L., Neff, B., Quinn, J. S., and Balshine, S. 2007. Evidence for size and sex-specific dispersal in a cooperatively breeding Cichlid fish. Molecular Ecology 16(14): 2974-2984.

Stott, N. D., Faust, M. D., Vandergoot, C. S., and Miner, J. G. 2021. Acoustic telemetry detection probability and location accuracy in a freshwater wetland embayment. Animal Biotelemetry 9(1): 19

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Eos, Transactions American Geophysical Union 38(6): 913-920.

Stuck, J. G., Porreca, A. P., Wahl, D. H., and Colombo, R. E. 2015. Contrasting population demographics of invasive Silver Carp between an impounded and free-flowing river. North American Journal of Fisheries Management 35(1): 114-122.

Sullivan, C. J., Vokoun, J. C., Helton, A. M., Briggs, M. A., and Kurylyk, B. L. 2021. An ecohydrological typology for thermal refuges in streams and rivers. Ecohydrology 14(5): e2295.

Summerfelt, R. C., and L. S. Smith. 1990. Anesthesia, surgery, and related techniques. Pages 213–272 in C. B. Shreck and P. B. Moyle, editors. Methods for Fish Biology. American Fisheries Society, Bethesda, Maryland.

Tan, J., Gao, Z., Dai, H., Yang, Z., Shi, X. 2019. Effects of turbulence and velocity on the movement behaviour of Bighead Carp (*Hypophthalmichthys nobilis*) in an experimental vertical slot fishway. Ecological engineering 127: 363-374.

Taylor, M. K., and Cooke, S. J. 2012. Meta-analyses of the effects of river flow on fish movement and activity. Environmental Reviews 20(4): 211-219.

Tillotson, N. A., Weber, M. J., and Pierce, C. L. 2022. Zooplankton community dynamics along the bigheaded carp invasion front in the Upper Mississippi River. Hydrobiologia 849(7): 1659-1675.

Tillotson, N. A., Weber, M. J., and Pierce, C. L. 2023. Effects of bigheaded carp on larval Freshwater Drum diets. Transactions of the American Fisheries Society 152(5): 530-549.

Tripp, S. J., Phelps, Q. E., Hupfeld, R. N., Herzog, D. P., Ostendorf, D. E., Moore, T. L., Brooks, R. C., and Garvey, J. E. 2019. Sturgeon and Paddlefish migration: evidence to support the need for interjurisdictional management. Fisheries 44(4): 183-193.

Tsehaye, I., Catalano, M., Sass, G., Glover, D., and Roth, B. 2013. Prospects for fishery-induced collapse of invasive Asian carp in the Illinois River. Fisheries 38(10): 445-454.

Tucker, E. K., Zurliene, M. E., Suski, C. D., and Nowak, R. A. 2020. Gonad development and reproductive hormones of invasive Silver Carp (*Hypophthalmichthys molitrix*) in the Illinois River. Biology of Reproduction 102(3): 647-659.

US EPA, O. 2015, November 25. Level III and IV Ecoregions of the Continental United

States. Data and Tools.

Vallazza, J. M., Mosel, K. J., Reineke, D. M., Runstrom, A. L., Larson, J. H., and Knights, B. C. 2021. Timing and hydrological conditions associated with Bigheaded Carp movement past navigation dams on the upper Mississippi River. Biological Invasions 23(11): 3409-3425.

Vander Zanden, M., Casselman, J. and Rasmussen, J. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464-467.

van Rijn, I., Buba, Y., DeLong, J., Kiflawi, M., and Belmaker, J. 2017. Large but uneven reduction in fish size across species in relation to changing sea temperatures. Global Change Biology 23(9): 3667-3674.

Van Vleet, N. P., Ward, D. M., Som, N. A., Barton, D. C., Anderson, C., and Henderson, M. J. 2024. It's about time: A multistate semicontinuous time mark–recapture model to evaluate seasonal survival and movement rates of juvenile Coho Salmon in a small coastal watershed. Transactions of the American Fisheries Society 153(5): 541-558.

Vine, J. R., Holbrook, S. C., Post, W. C., and Peoples, B. K. 2019. Identifying environmental cues for Atlantic Sturgeon and Shortnose Sturgeon spawning migrations in the Savannah River. Transactions of the American Fisheries Society 148(3): 671-681.

Vokoun, J. C., and Rabeni, C. F. 2005. Home range and space use patterns of Flathead Catfish during the summer–fall period in two Missouri streams. Transactions of the American Fisheries Society 134(2): 509-517.

Wagner, T., Hayes, D. B., and Bremigan, M. T. 2006. Accounting for multilevel data structures in fisheries data using mixed models. Fisheries 31(4): 180-187.

Walsworth, T. E., Landom, K., and Gaeta, J. W. 2020. Compensatory recruitment, dynamic habitat, and selective gear present challenges to large-scale invasive species control. Ecosphere 11(6): e03158.

Wang, N., Teletchea, F., Kestemont, P., Milla, S., and Fontaine, P. 2010. Photothermal control of the reproductive cycle in temperate fishes. Reviews in Aquaculture 2(4): 209-222.

Wang, J., Chapman, D., Xu, J., Wang, Y., and Gu, B. 2018. Isotope niche dimension and trophic overlap between Bigheaded Carp and native filter-feeding fish in the lower Missouri River, USA. PloS one 13(5): e0197584.

Waters, D. S., and R. L. Noble. 2004. Spawning Season and Nest Fidelity of Largemouth Bass in a Tropical Reservoir. North American Journal of Fisheries Management 24(4): 1240-1251.

Wathen, G., Weber, N., Bennett, S., Bouwes, N., and Jordan, C. E. 2017. An assessment of the geographic closure assumption in mark–recapture abundance estimates of anadromous steelhead populations. North American Journal of Fisheries Management 37(5): 951-961

Weber, M. J., Hennen, M. J., Brown, M. L., Lucchesi, D. O., and Sauver, T. R. S. 2016. Compensatory response of invasive Common Carp *Cyprinus carpio* to harvest. Fisheries Research 179: 168-178.

Wedgeworth, M., Mollenhauer, R., and Brewer, S. K. 2023. Variation in Prairie Chub hatch relationships across wet and dry years in the upper Red River basin. North American Journal of Fisheries Management 43(5): 1246-1259.

Weinz, A. A., Matley, J. K., Klinard, N. V., Fisk, A. T., and Colborne, S. F. 2021. Performance of acoustic telemetry in relation to submerged aquatic vegetation in a nearshore freshwater habitat. Marine and Freshwater Research 72(7): 1033-1044.

Werner, J. P., Dean, Q. J., Pegg, M. A., and Hamel, M. J. 2023. Patterns in spatial use and movement of Silver Carp among tributaries and main-stem rivers: insight from otolith microchemistry analysis. Biological Invasions 25(2): 471-484.

White, G. C., Kendall, W. L., and Barker, R. J. 2006. Multistate survival models and their extensions in Program MARK. The Journal of Wildlife Management 70(6): 1521-1529.

Whitledge, G. W., Knights, B., Vallazza, J., Larson, J., Weber, M. J., Lamer, J. T., Phelps Q. E., and Norman, J. D. 2019. Identification of Bighead Carp and Silver Carp early-life environments and inferring Lock and Dam 19 passage in the Upper Mississippi River: insights from otolith chemistry. Biological Invasions 21: 1007-1020.

Williamson, C. J., and Garvey, J. E. 2005. Growth, fecundity, and diets of newly established Silver Carp in the middle Mississippi River. Transactions of the American Fisheries Society 134(6): 1423-1430.

Williams, J. A., Whitledge, G. W., Knights, B. C., Bloomfield, N. C., and Lamer, J. T. 2023. Age-0 Silver Carp otolith microchemistry and microstructure reveal multiple early life environments and protracted spawning in the upper Mississippi River. North American Journal of Fisheries Management 43(1): 141-153.

Winemiller, K. O., and Jepsen, D. B. 1998. Effects of seasonality and fish movement on tropical river food webs. Journal of fish Biology 53: 267-296.

Winter JD. 1996. Underwater biotelemetry. In: Murphy BR, Willis DW (eds) Fisheries Techniques, 2nd edn. American Fisheries Society 371-395

Winter, E. R., Hindes, A. M., Lane, S., and Britton, J. R. 2021. Detection range and efficiency of acoustic telemetry receivers in a connected wetland system. Hydrobiologia 848: 1825-1836.

Wood, S. N. 2017. Generalized additive models: An introduction with R, second edition. page Generalized Additive Models: An Introduction with R, Second Edition. CRC Press.

Wood, S. N. 2023. December 21. Package “mgcv.” CRAN.

Worthington, T. A., Echelle, A. A., Perkin, J. S., Mollenhauer, R., Farless, N., Dyer, J. J., Logue, D. and Brewer, S. K. 2018. The emblematic minnows of the North American Great Plains: a synthesis of threats and conservation opportunities. Fish and Fisheries 19(2): 271-307.

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., and Russello, M. A. 2010. Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. Ethology Ecology and Evolution 22(4): 393-404.

Xi, Y., Cao, C., Liu, S., Li, P., Xiao, L., and Yao, W. 2024. Swimming behaviour of downstream migrating carp in accelerating flows. Journal of Hydraulic Research 62(3): 253-266.

Yao, X., Huang, G., Xie, P., and Xu, J. 2016. Trophic niche differences between coexisting omnivores Silver Carp and Bighead Carp in a pelagic food web. Ecological Research 31: 831-839.

York, B., Schooley, J. D., and Scarnecchia, D. L. 2022. Oklahoma bowfishing values and perspectives toward nongame fishes and their management. North American Journal of Fisheries Management 42(4): 1020-1040.

Yu, L., Lin, J., Chen, D., Duan, X., Peng, Q., and Liu, S. 2018. Ecological flow assessment to improve the spawning habitat for the four major species of carp of the Yangtze River: a study on habitat suitability based on ultrasonic telemetry. Water 10(5): 600.

Zemeckis, D. R., Dean, M. J., DeAngelis, A. I., Van Parijs, S. M., Hoffman, W. S., Baumgartner, M. F., Hatch, L. T., Cadrin, S. X., McGuire, C. H. 2019. Identifying the distribution of Atlantic Cod spawning using multiple fixed and glider-mounted acoustic technologies. ICES Journal of Marine Science 76(6): 1610-1625.

Zipkin, E. F., Sullivan, P. J., Cooch, E. G., Kraft, C. E., Shuter, B. J., and Weidel, B. C. 2008. Overcompensatory response of a Smallmouth Bass (*Micropterus dolomieu*) population to harvest: release from competition? Canadian Journal of Fisheries and Aquatic Sciences 65(10): 2279-2292.