Factors related to occupancy and detection and population demographics of adult Bighead Carp and Silver Carp in the lower Red River catchment.

by

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Abstract

North America native fishes have declined throughout the 20th and 21st century for a myriad of reasons, including invasive species. Two emblematic invasive fishes, Bighead Carp *Hypophthalmichthys nobilis,* and Silver Carp *Hypophthalmichthys molitrix* (hereafter carp), were first introduced for management purposes (i.e., algal control in aquaculture ponds and wastewater treatment facilities) but quickly spread throughout the Mississippi River catchment and have continued to invade connected catchments. Carp were first detected in the lower Red River catchment of Texas, Oklahoma, and Arkansas in 2012. My study objectives were to determine the hierarchical factors related to warm-water occupancy and assess population demographics of both species. I sampled the mainstem Red River and several tributaries during the presumed spawning season (April-Sept) of 2021 and 2022 using gill nets and electrofishing across 58 reaches. Carp detection was positively associated with sampling effort and water temperature, and negatively associated with water clarity and discharge. Both species occupancy was positively associated with reaches containing backwater habitats and low sinuous river sections where the channel tended to be narrower and deeper than other parts of the catchment. There were species-specific differences where Silver Carp occupied reaches with higher levels of chlorophyll-a, whereas Bighead Carp had no association with chlorophyll-a concentrations. Growth by both species was positively associated with higher air temperatures and negatively associated with discharge variability; however, Silver Carp growth was also positively associated with higher discharges. Silver Carp grew quickly, had stable recruitment variability, and low mortality. Additionally, both species had relatively high theoretical maximum length. However, I did not sample any carp < age three. My results indicate that carp in the lower Red River catchment use habitats characterized by local disturbances (i.e., low sinuosity and decreased width-to-depth ratio) where mitigation efforts (i.e., experimental flows) could be used to decrease this habitat. Additionally, backwater habitat may be suitable locations for targeted mitigation; however, backwaters are important to many native fishes and may be suitable locations for trapping carp or timing removal efforts when native species survival may be higher (i.e., colder water temperatures). Experimental flows to increase discharge variability may reduce carp growth; however, caution is warranted as carp recruitment in their native range has been positively associated with discharge variability. Future efforts aimed at tracking individuals over time would be useful for assessing the timing of fish habitat use or possible congregations to aid removal efforts while minimizing effects on native fishes.

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List of Abbreviations

AICc	Akaike's information criterion correct for small sample size
BHC	Bighead Carp
BRA	Between-reader-agreement
Chl-a	Chlorophyll-*a*
CV	Coefficient of variation
DIC	Deviance information criterion
HDI	Highest density inverval
JAGS	Just Another Gibbs Sampler
K	Growth-rate
LDI	Landscape Development Index
$L\infty$	Theoretical maximum length
M	Natural mortality
MS-222	Tricaine mesylate
NHDplus	National Hydrology Dataset plus
NLCD	National Land Cover Database
PIT	Passive integrated transponder
Rkm	River kilometer
RVI	Recruitment variability index
SVC	Silver Carp
t0	Time at which length was zero
USGS	United States Geological Survey
vBGM	von Bertalanffy growth model
WAIC	Widely applicable information criterion
YSI	Yellow Springs Instrument
Z	Instantaneous natural mortality
ΔAIC	Akaikes difference

CHAPTER I

Introduction

Native fish populations have declined throughout North America due to several factors, including the introduction of non-native species (Jelks et al. 2008, Sleezer et al. 2022). Non-native species can affect native species richness and distributions via direct and indirect pathways via competition for resources and habitat (Grabowska et al. 2016; Mofu et al. 2019; Sharma et al. 2021). For example, Seller and Keeley (2009) found that Cutthroat Trout *Oncorhynchus clarkii* had decreased growth in the presence of hybrid non-native Rainbow Trout *Oncorhynchus mykiss*. Additionally, the relative abundance and body condition of Bigmouth Buffalo *Ictiobus cyprinellus* and Gizzard Shad *Dorosoma cepedianum* in the upper Mississippi River and Illinois River decreased in the presence of invasive Silver Carp *Hypophthalmichthys molitrix* (Pendleton et al. 2017). In some instances, invasive species presence has been associated with the extirpation of native fishes. For example, 21 of the 169 fishes native to the Great Lakes were extirpated and the introduction of 35 non-native species was considered a contributing factor (Mandrak and Cudmore 2010). Non-native species distributions are hypothesized to increase in the future, as management agencies attempt to improve river connectivity (Cooper et al. 2021; Kerr et al. 2021). Two species emblematic of species invasions are Bighead Carp *Hypophthalmichthys nobilis*, and Silver Carp.

Bighead Carp and Silver Carp (hereafter carp), were introduced into the United States as biological controls but their unintended spread led to ecological consequences that were amplified by actions to restore native fish habitats. Carp were introduced with the goal of plankton control in aquaculture and wastewater treatment facilities (Kolar et al. 2007). Following their introduction, high-water events permitted expansion by these species into the Mississippi River basin where they established populations (Chick and Pegg 2001; Kolar et al. 2007). Subsequently, carp expanded into the Illinois River and Missouri River. Stakeholders have become concerned about the possible implications carp pose to native fishes. Carp presence is related to a decrease in abundance and body condition for multiple fishes (e.g., sportfish, Paddlefish *Polyodon spathula*, Gizzard Shad, and Bigmouth Buffalo, Schrank et al. 2003; Irons et al. 2007; Chick et al. 2020). Actions to recover native fishes via improvements to backwater and shallow-water habitats and the release of more natural river discharges has increased habitat availability for carp populations. For example, following the effort to restore the Swan Lake backwater habitat of the Illinois River, carp benefited by using backwater habitat during higher discharge events (Coulter et al. 2017). Carp are opportunistic invaders, who may benefit from their feeding and life-history strategies (i.e., pelagic broadcast spawning) in novel environments.

Carp have specific traits and associated plasticity that appear to facilitate their successful introduction into non-native habitats. The feeding strategy of carp has led to perceived competition with many native planktivores. Pyron et al. (2017) found carp in the Wabash River, Indiana became the dominant planktivore after the decline of Gizzard Shad. In addition to competition with adult planktivores (Irons et al. 2007; Pendleton et al. 2017), carp can limit resources available for many juvenile fishes. For example, declines in the abundance of species with planktivorous juvenile life stages (e.g., White Crappie *Pomoxis annularis*, Sauger *Sander canadensis*) followed the establishment of carp in the Illinois River (Solomon et al. 2016). The spawning strategy of carp is also thought to help them successfully invade new ecosystems. Carp are pelagic broadcast spawners which may be one reason they can successfully exploit new environments (Lenaerts et al. 2021). Pelagic broadcast spawning is a hedge betting strategy where populations experience relatively high recruitment under proper environmental conditions (Hoagstrom and Turner 2015). Successful spawning by carp can be highly dependent on discharge, with large cohorts often associated with flood events (Kolar et al. 2007; Gibson-Reinemer et al. 2017). However, there is evidence that some successful spawning occurs independent of flood events (Coulter et al. 2016). Carp spawning can vary both spatially and temporally throughout a basin (Deters et al. 2013; Hintz et al. 2017). In the lower Missouri River, both carp species spawned between May and July with little to no spawning occurring in tributaries (Deters et al. 2013). However, Williams et al. (2021) found that Silver Carp in the upper Mississippi River spawned in mainstem tributaries. In the Wabash River, carp spawning occurred in the mainstem through September (Coulter et al. 2016b). Both carp species can reach sexual maturity at age two (Santiago et al. 2004, Williamson and Garvey 2005), with Silver Carp and Bighead Carp producing up to 5 million eggs (Nico et al. 2022a) and 1.6 million eggs (Nico et al. 2022b), respectively. The ecological concerns resulting from the successful invasion by carp has led managers to develop strategies to attempt to reduce population numbers.

Developing mitigation efforts to reduce carp populations has been difficult, and in some cases, actually led to improved condition of the carp. Commercial harvest of carp is a method managers use to control invasive carp populations (Tsehaye et al. 2013). To collapse a population, it is estimated that 70 percent of individuals within all size classes need to be removed (Tsehaye et al. 2013). Sub-adult fish are especially difficult to capture (Tsehaye et al. 2013), making the task of exploitive collapse challenging. In addition, commercial harvest may increase the invasive expansion of carp into new catchments. For example, Coulter et. al (2018) found that carp populations in the Illinois River that experienced commercial harvest had increased body condition. Fish with higher body condition display increased movement, larger ranges, and in the case of carp are more likely to expand the invasive front (Minns et al. 1995; Li et al. 2017; Coulter et al. 2018; Kanno et al. 2023).

Over time, carp have expanded beyond the Mississippi River leading to uncertainty in how to best manage these populations. Some of the new populations occur in rivers with vastly different physicochemical conditions when compared to the Mississippi River and Missouri River. For example, Hayer et al. (2013) found that Silver Carp in the Big Sioux, Vermillion, and James rivers, South Dakota had different population demographics compared to populations in the Missouri and Mississippi rivers. Relying on research conducted in a few locations fails to recognize the full potential of these invaders to exploit new environments that have a different assemblage structure (Sakai et al. 2001). Bighead Carp and Silver Carp were first detected in the lower Red River in 2012 (Patton and Tacket 2012). The Red River catchment differs from other areas where carp have invaded. The catchment has relatively long low-gradient, free-flowing river segments, where discharge patterns tend to fluctuate between extreme droughts and floods (Mollenhauer et al. 2021). The catchment has several major tributaries that drain upland areas, and a braided Red River mainstem with high conductivity fluctuations (622 – 5667 μ/S, Hargrave and Taylor 2010). Understanding how carp populations grow, reproduce, and use habitat within the Red River catchment may provide possible insight into additional control methods that may be useful for limiting carp expansion and reducing their abundance.

The overall goal of my thesis was to describe the spatial and temporal dynamics of Bighead Carp and Silver Carp in the lower Red River catchment of Texas, Oklahoma, and Arkansas. To achieve my goal, I had two thesis objectives: 1) to determine factors related to occupancy by adult Bighead Carp and Silver Carp within the lower Red River catchment, and 2) assess the population demographics of Bighead Carp and Silver Carp. Completion of my first objective is useful to agencies as it provides a complete picture of the current range of Silver Carp and Bighead Carp populations in the Red River catchment and describes the physicochemical attributes that drive reach-scale occupancy. My study design accounts for incomplete gear detection which is important because both species are known to be difficult to capture (Norman and Whitledge 2015: Butler et al. 2019). My second objective builds on the first by examining how physicochemical attributes relate to carp growth, and I establish baseline population dynamic rates that are needed for managers to both monitor these populations over time and explore the benefits of certain management actions through the use of population models (i.e., where these data are useful for developing models).

Study Area

The Red River catchment is primarily located in the southern Great Plains and is emblematic of relatively extreme physicochemical conditions. The Red River begins in the semi-arid portion of eastern New Mexico and flows eastward through Texas, Oklahoma, Arkansas, and meets the confluence of the Atchafalaya River in Louisiana (Figure 1) (Longing and Haggard, 2012). The Red River catchment is the second largest in the Great Plains and is susceptible to extended drought and high-discharge events (Mollenhauer et al. 2021), with mean yearly rainfall ranging from 500 to 1300-mm (Benke 2005; Bertrand and McPherson 2018). Extensive droughts, with periodic heavy rain events, are anticipated to become more common throughout the catchment (Bertrand and McPherson 2018). The mainstem river forms the border of Texas and Oklahoma. The upper river was impounded by Dennison Dam in 1944. The river below the dam (hereafter lower Red River) has a landscape largely dominated by pasture, with some agriculture and forested regions (Benke et al. 2005). The lower Red River catchment encompasses multiple Level IV ecoregions, including the San Antonio Prairie, Pleistocene Fluvial Terraces, Tertiary Uplands, Blackland Prairie, Floodplains and Low Terraces, and the Red River Bottomlands (US EPA 2015). The major tributaries in the catchment drain upland regions that vary quite substantially from the Red River (i.e., some spring flow, much lower conductivity, and a larger proportion of underlying limestone lithology, Woods et al. 2005), but these areas are unpassable by fishes via major impoundments.

The lower Red River has several attributes that distinguish the catchment from other large rivers where carp have been introduced. The catchment is characterized by relatively high salinity due to upper basin salt springs, salt seeps, and brine from oil fields (Laughlin and Lacewell, 1981; Hargrave and Taylor 2010). Immediately downriver of Denison Dam, the river is relatively clear but quickly progresses to a highly turbid state due to suspended red clay sediment (Christman et al. 2018). It is a low-gradient river, characterized by a large flood plain with oxbow lakes and backwater connections (Benke et al. 2005). The water temperatures can reach extremes as high as 39 °C due to high air temperatures, the lack of riparian cover caused by meandering and braided alluvial channels (Benke et al. 2005), and the limited groundwater influence during dry seasons and also related groundwater pumping (Krueger et al. 2017; Smith et al. 2021).

Methods

Site selection and fish sampling

I sampled 58 reaches throughout the lower Red River catchment using an occupancy modeling framework (see Chapter 2 methods for more details). Each reach was approximately 1.5 to 2 river km (rkm) to meet the closure assumption (hereafter sites, see methods Chapter 2). Because access is somewhat limited on the Red River, my sites were selected based on access to private lands, conditions conducive to boat launching, and spatial coverage of the catchment (Figure 1). Each site was surveyed 1-3 times during 2021 and 2022. My sampling (i.e., surveys) each year occurred during the season of April through September, defined by historical water-temperature patterns deemed important for carp reproduction (Cooke et al. 2012; Nico et al. 2022a) (Figure 2). My season was chosen to meet the closure assumption where my study design assumed Silver Carp and Bighead Carp (i.e., the species) either occupied or were absent from each site during the season (MacKenzie et al. 2005).

I surveyed fishes using a combination of gillnets and electrofishing because they have been shown useful for sampling carp in perceived low-density environments (Butler et al. 2019; Norman and Whitledge 2015). Three experimental sinking gillnets were placed throughout each site. Gillnets were 54.8-m long for the mainstem Red River and 30.5-m long for the tributaries by 3.65-m tall with 8.9, 10.16, and 10.8-cm bar-length mesh panels Gillnets were deployed perpendicular to the shoreline, with one placed near the upstream and downstream end of the reach and the third net placed near the middle at the narrowest location to restrict carp movement. After net placement, I sampled the entirety of the reach using an 80-amp Midwest Lakes Electrofishing Systems shocking unit using DC electrofishing (Midwest Lakes; Polo, Missouri). I used standard AFS electrofishing settings based on conductivity, adjusting the settings to reach a target power (Miranda 2009). Preliminary sampling efforts indicated that standard electrofishing settings were as effective as low and high frequencies. Water conductivity in the tributaries was much lower than the mainstem Red River. I used a high conductivity Infinity HC-80 (Midwest lakes; Polo, Missouri) shock box with voltage set to high range (pulsed DC current, >300 volts, 60Hz) for the tributaries and low range (pulsed DC current, <300 volts, 60Hz) for the mainstem Red River. Beginning at the upstream end of the site, I slowly motored the boat downstream in a cloverleaf pattern with electrical current applied for 10-sec with 5-sec "off peddle" intervals to increase the effectiveness of capturing carp and to drive fish into the nets and shoreline (Bouska et al. 2017). Electrofishing continued until the entirety of the reach was sampled. Gillnets were removed after a six-hour soak.

The carp I sampled were euthanized for later age-and-growth analyses (see Chapter 3 methods). All carp collected during a survey were euthanized with a lethal dose of tricaine mesylate (MS-222) (300 mg/L). I measured total length (mm, +/- 1 mm) and weighed each fish (g, +/- 10 g) using a Pesola scale (80035).

CHAPTER II

FACTORS RELATED TO OCCUPANCY AND DETECTION OF BIGHEAD CARP AND SILVER CARP IN THE LOWER RED RIVER CATCHMENT

Introduction

The importance of multi-scale habitat use by fishes is well recognized, and important to the development of meaningful fisheries management strategies. The distribution of fishes relies on structural features (i.e., appropriate climate and geology) that set the physicochemical conditions tolerated by many species. For example, the pH of a river is dictated, in part, by the underlying lithology of the region (Sarkar et al. 2007), and fishes have specific pH tolerances that regulate a variety of attributes (e.g., successful egg hatching, Buckler et al. 1995). Within the appropriate coarse-scale structural features, a combination of other physicochemical factors at the stream segment or reach scale (i.e., finer scales) contribute to a heterogeneous riverscape (Fausche et al. 2002) where aquatic organisms use a set of variables that are assumed to maximize fitness (Bailey et al. 2022). The habitat needs of fishes are often used as the foundation of conservation and recovery plans (Peterson and Rabeni 2001). Priority use areas can be identified, and restoration actions planned for threatened and endangered species. For example, Deoboer et al. (2015) found that after restoration of prioritized, fragmented reaches, Sculpin *Cotus* spp. expanded their suitable habitat unto areas that were previously not available. Moreover, habitat use information is also useful for developing strategies to reduce population numbers or attempt eradication of invasive species (MacNamara et al. 2018).

Large rivers and associated native fishes face a myriad of threats and conservation and management challenges, including the spread of invasive species (Dudgeon et al. 2006; Cooke et al. 2012). In 2008, we recognized the doubling of invasive species within three decades, and fishes were the most common taxa introduced (Gozlan 2008). With these introductions, there were related ecological concerns such as hybridization (Hanfling et al. 2005; Blackwell et al. 2021), predation (Ruzycki et al. 2003; Walrath et al. 2015), competition (Grabowska et al. 2016; Sharma et al. 2021), disease (Shafland 1979; Peeler et al. 2011), and the introduction of novel parasites (Ondračková et al. 2019; Rodriguez et al. 2019). Additionally, the number of native fishes that are threatened or endangered has increased greatly (Jelks et al. 2008). It is difficult for managers to improve river conditions for declining native species when the actions taken also need to consider the effects to invasive species. Re-establishing connectivity with floodplain habitat may benefit many native fishes but may also allow for the proliferation of non-native fishes (Cooke et al. 2012). For example, dam removal in the Great Lakes may improve habitat connectivity for native species while permitting the spread of invasive Sea Lamprey *Petromyzon marinus* and increasing disease transfer (Walter et al. 2021). Consequently, improving riverine conditions for native fishes would benefit from an understanding of the presence of non-native species and how they respond to the physicochemical conditions.

Bighead Carp and Silver Carp habitat use has been documented in portions of the central United States where they were introduced during the 1970s; however, new invasion fronts occur in novel river catchments with different physicochemical conditions. Both species are typically associated with low-velocity habitat and tend to avoid main-channel environments of the Mississippi River and Illinois River (Calkins et al. 2012; MacNamara et al. 2018). Both species are associated with backwater environments, tributaries, and shoreline locations in the Illinois and Wabash rivers (Pretchel et al. 2018, MacNamara et al. 2018; Glubzinski et al. 2021). For example, Coulter et al. (2016a) used acoustic telemetry and found that Silver Carp were associated with backwater environments throughout the summer months in the Wabash River. Carp affinity for low-velocity environments may be due to higher forage potential (Williamson and Garvey 2005), as both Bighead Carp and Silver Carp are obligate planktivorous filter-feeders, where Silver Carp primarily forage on phytoplankton and Bighead Carp on zooplankton (Li et al. 2013; Cooke et al. 2009; Ochs et al. 2019). Unfortunately, most of our current habitat-use knowledge associated with both Bighead Carp and Silver Carp comes from rivers of the central United States. Both species are pushing the invasion fronts into rivers of the south-central Great Plains and the southeast United States where the physicochemical conditions differ from the Midwest (see study area, Chapter 1). Correspondingly, my first thesis objective was to determine the factors related to Bighead Carp and Silver Carp probability of occupancy after accounting for incomplete sampling detection in the lower Red River catchment. This will provide insight into how, if any, changes in carp habitat-use occur relative to these differences in physicochemical conditions.

Methods

I sampled using an occupancy modeling framework. My warm-water season was defined as April through September where I could reasonably assume each site (sampling reach, defined as a 1.5 – 2.0 rkm section) was closed to changes in Silver Carp or

Bighead Carp occupancy (i.e., if the species was present, then it was assumed present for the season, though individuals may move back and forth from the site) (Mackenzie et al. 2005). I defined the season using the species' biology and associated water temperature. Silver Carp remain relatively stationary during the summer months (Coulter et al. 2016a) and are hypothesized to spawn at water temperatures above 18 °C (Cooke 2016, Nico et al. 2022a). Therefore, I established my season as April through September based on historical water temperature trends (Figure 2). I conducted repeated fish surveys (see Chapter I) using multiple gears where my surveys were temporally replicated over each season during my two-year sampling period (2021 – 2022).

Physicochemical Covariates

I quantified the physicochemical factors that I hypothesized were related to carp distributions across multiple spatial scales (i.e., catchment, segment, reach). The habitat factors were collected in the field or obtained using existing geospatial data (Table 1). Habitat factors were used to account for variation in incomplete sampling detection or were related to species occurrence (Table 1).

The habitat factors operating at the catchment scale that may be related to carp occurrence were drainage area, disturbance, and lithology (Table 1). Drainage area (km^2) is a coarse scale habitat factor that influences fish distributions, assemblage structure, and species richness (Newall and Magnuson 1999; Osborne and Wiley 2011; Griffiths 2018). I used the National Hydrography Database Plus (NHDplus) (https://apps.nationalmap.gov/downloader/#/) flow lines in ArcGIS Pro (version 3.0.1, Esri, Redlands, CA) to delineate each catchment (i.e., the entire upstream area that drains to the site) using the watershed tool and quantified the area of each catchment.

Disturbance can affect assemblage structure and distribution by altering nutrient flow and habitat availability, and lead to decreased diversity throughout multiple trophic levels (Scrimgeour et al. 2008; Wang et al. 2008; Johnson and Angeler 2014). I used ArcGIS Pro to quantify the area of each land use type in each catchment using the National Land Cover Database (NLCD) and previously calculated drainage areas. Each land type was assigned the corresponding disturbance value from the Landscape Development Index (LDI) (Brown and Vivas 2005). However, in instances where the land-cover type applied to multiple LDI coefficients (e.g., multiple types of agriculture land), I calculated the average of the relative LDI coefficients. I multiplied the proportion of each land type in the catchment by the assigned LDI value to quantify the overall disturbance factor for each land type. I then summed the coefficients of the disturbance factors within each catchment to characterize the disturbance level for the catchment. For example, if a catchment was 50% woodland pasture and 50% row crop then the pastureland was assigned an LDI coefficient of 2.02 and the row crop was assigned an LDI coefficient of 4.45 resulting in an overall disturbance factor of 3.23. Lastly, lithology is related to sedimentation, pH, and controls the macro and micronutrient cycling load within a catchment (Sarkar et al. 2007; Zeng et al. 2007; McDowell et al. 2013; Glaus et al. 2019). Sandstone contains high quantities of silica which leads to predominately neutral or slightly acidic environments because soluble silica forms orthosilicate acid (Worden and Morad 2000; Belton et al. 2012). Catchments with lower percentages of sandstone will likely have higher pH than those with higher percentages of sandstone. I quantified the percentage of sandstone for the drainage area of the catchment using the United States

Geological Survey's (USGS) National Geologic Map Database (https://mrdata.usgs.gov/geology/state/) and the identify tool in ArcGIS Pro.

Habitat factors operating at the segment scale that may be related to carp occurrence were sinuosity, slope, and discharge (Table 1). Segments were classified by 5th order tributary confluences. Stream sinuosity, the ratio of the straight-line segment of the river to the channel distance (Rowe et al. 2009), is associated with habitat complexity (e.g., woody debris, canopy cover) and floodplain connection (Nagayama and Nakamura 2018). Sinuous reaches in a river are important for certain species reproduction (e.g., Sakhalin Taimen *Hucho perryi*; Fukushima et al. 2011), and carp in the Missouri River spawned larger quantities of eggs in more sinuous river segments (Deters et al. 2013). Sinuosity was calculated by dividing the river kilometer (rkm) distance by the straight-line distance of the segment using the distance tool in ArcGIS Pro. Slope can affect species distributions by influencing water velocity, channel morphology, and substrate, which are often correlated with the stream gradient (Camana et al. 2016). Stream gradient may alter the availability of low-velocity habitat associated with carp presence. I quantified slope using spatial analysis in ArcGIS Pro by dividing the change in elevation from the upstream to downstream end of the segment by the segment length (rkm). Lastly, discharge (m^3/s) affects fish density and occurrence, habitat associations, recruitment success, and can be altered for mitigation purposes (Valdez et al. 2001; Gillete et al. 2006; Work et al. 2017; Love et al. 2017; Bašić et al. 2018). Silver Carp in the Illinois River were positively associated with discharge but avoided main channel habitats during high discharge (Coulter et al. 2017). I obtained discharge data from the USGS stream gage of the segment or from Stream Stats (https://streamstats.usgs.gov/ss/)

in instances where USGS stream gauges were not available I calculated the median discharge during the season (i.e., occupancy) and divided by the drainage area of the segment to standardize discharge across rivers for comparability (i.e., Red River, Kiamichi, Blue River, ect.).

At the reach scale, I hypothesized that distance to the nearest upstream dam, percent backwater, width-to-depth ratio, salinity, and chlorophyll-*a* were related to carp presence. Dam construction changes both biotic and abiotic riverine attributes (Catalano et al. 2007). For example, flow alteration in the Yangtze River, caused by dam construction, has led to reduced recruitment for both Bighead Carp and Silver Carp (Duan et al. 2009). Bighead Carp and Silver Carp are thought to require an estimated 100 km of free-flowing river to successfully spawn (Kolar et al. 2007). I used NHDplus flowlines and ArcPro GIS spatial analyst to quantify the distance from the downstream end of each site to the nearest upstream dam. Backwaters are off channel, relatively shallow, low-velocity areas, relative to the main flow thread within the channel (Vietz et al. 2013). These locations are often used as a refuge by juvenile fishes due to forage availability and growth potential (Humphries et al. 2006). Backwater habitats are also used by adult carp as refuge areas during higher discharge conditions (Coulter et al. 2017; MacNamara et al. 2018) and may offer higher forage potential (Williamson and Garvey 2005). I calculated the percent backwater for the reach by measuring the channel width and length within each backwater using a handheld rangefinder (Simmons VLRF 600, Overland Park, KS, +/- 1 m), and then expressed backwater area as a percent of the total reach area. Width-to-depth ratios describe the general structure of a stream channel where increasing ratios describe wider and shallower channels (Gordan et al. 1992; Dunham et al. 2002). I collected 3 channel width measurements with a handheld rangefinder and three corresponding channel depths with a boat equipped depth finder (Humminbird Helix 10, Rane, WI) at locations that incorporated the variation (i.e., predominately wide or narrow) in the reach to determine a mean reach ratio. Fishes have defined salinity tolerances and will use habitat within their salinity tolerances over appropriate dissolved oxygen and temperature conditions (e.g., Shortnose Sturgeon *Acipenser brevirostrum*; Farrae et al. 2014). Inappropriate salinity environments can hinder reproduction and in extreme instances lead to poor osmoregulation and eventual death (Oto et al. 2017; Neves et al. 2019). I collected three salinity measurements (ppt) at the upper, middle, and bottom portions of each reach using a Yellow Springs Instrument (YSI pro dds, Yellow Springs, Ohio). Chlorophyll-*a* (chl-a) concentration is widely used as a surrogate for productivity and algal biomass (Pinder et. al 1997). Carp are omnivores, consuming both zooplankton and phytoplankton (Calkins et a. 2012), and may be associated with varying chl-a densities in the catchment. A water sample was collected using an integrating tube sampler to sample the top 2-m of the water column at the most downstream end of the reach (Raikow et. al 2004). The water was stored in containers and transferred to the laboratory. Within 24 h of water collection, three 250-mL subsamples were placed into a 47-mm diameter filter tower (PALL, Port Washington, New York) and filtered through a 1-µm glass fiber filter (PALL, Port Washington, New York). The filter was then placed into a light-proof container and frozen for later laboratory analysis. In the laboratory, chl-a was extracted from the filters using 90% ethanol, filtered a second time, then estimated using a Trilogy Laboratory Fluorometer (Turner Designs, San Jose, California) (Sartory and Grobbelaar 1984).

At the reach scale, I quantified water temperature, turbidity, discharge, and sampling effort related to carp detection (Table 1). For example, Sullivan et al. (2017) found that increased catchability of Silver Carp occurred at higher water temperatures during the summer months (e.g., July and August) in the Des Moines River. I measured water temperature (°C) at a well-mixed location of the upper, middle, and bottom portions of the reach using a YSI and calculated the mean during the survey to relate water temperature to carp detection. Turbidity can affect the visual and chemical acuity of fishes thereby reducing growth and recruitment because of reduced foraging or successful spawning (Järvenpää et al. 2019; Korman et al. 2021). Turbidity also affects detection (Figueroa-Pico et al. 2020; Bunnell et al. 2021). I collected three visibility measurements (i.e., secchi depth, +/- 1 cm) as a surrogate for turbidity at the upper, middle, and bottom portions of the reach. Discharge can affect the detection of fishes. For example, Zentner et al. (2021) found that detection of sucker spp. with passive integrated transponders (PIT) in streams was negatively associated with increasing discharge. I obtained discharge data from the nearest USGS stream gage and calculated the mean discharge for the day of each survey and standardized by the drainage area of the segment to compare discharge across rivers (i.e., Red River, Kiamichi, Blue River, etc.). In instances where USGS stream gages were not available, I used the median discharge value of the segment for the month in which the survey occurred using Stream Stats. Sampling effort can affect the detection of fishes (Reid and Haxton 2017), so I calculated the electrofishing effort (i.e., seconds) for the survey.

Data Analyses

An occupancy model accounts for both detection and occupancy probabilities (MacKenzie et al. 2002). Determining detection probability is essential because it affects our ability to infer occupancy (Benoit et al. 2021). Estimates of detection account for potential species presence at a site even if they were not sampled (i.e., false absence, Royle and Kery 2007; Kery et al. 2010). I quantified the probability of detection using temporally replicated surveys during my season (MacKenzie et al. 2002). The detection history (i.e., 1 if present, and 0 if absent) was modeled with covariates using a logit function to explain heterogeneity of detection because detection covariates varied across surveys (Mackenzie et al. 2002).

$$\theta = \frac{\exp(XB)}{1 + \exp(XB)}$$

thus

$$logit(p_{ij}) = X_{ij}^{t}\beta$$

Where θ is the logit function, *X* is the covariate vector, β is the coefficient of covariate *X*, and p is the probability of detection at site i for survey j. Probability of detection was then used to estimate the probability of occupancy. The relationship between detection probability and occupancy are modeled as two Bernoulli distributions.

$$Z_i \sim Bernoulli\ (\Psi_i)$$

$$y_{ij}|z_i \sim Bernoulli\ (z_i \text{ x } p_{ij})$$

where y_{ij} represents the observed presence at site i during survey j, z_i is the true presence at site i, p_{ij} is the probability of detection at site i during survey j, and Ψ is the occupancy probability (Kery et al, 2010). Occupancy was modeled using covariates hypothesized to be related to species presence to explain the heterogeneity in occupancy. (Mackenzie et al. 2002).

$$logit(\Psi_i) = X_i^t \beta$$

where Ψ is the occupancy probability at site I, X is the covariate vector at site I, and β is the coefficient of covariate X, (Mackenzie et al. 2002). To ensure that occupancy of one site did not affect that of another, sites were separated by at least 1-rkm to maintain independence. However, after model construction I also tested this assumption by including a trap effect (i.e., an increase or decrease in detection after first capture) in my model by assigning a 1 to every survey subsequent initial capture at a site (Mollenhauer et al. 2018). Including a trap effect did not change my results and was therefore removed from all models.

Prior to model construction, I transformed my data if skewed or had natural breaks in the data, checked for multicollinearity, and standardized my remaining covariates. I log transformed percent sandstone, slope, discharge, width-to-depth, and chlorophyll-*a* because these data were skewed. I made drainage area categorical (where 0 was low, 1 was high, and 1 was the reference) and a natural break occurred in my data at 80,000 km^2 (34% of observations less than this value). I also made percent backwater categorical (0 = absence, 1 = present, where 1 was the reference) and a natural break occurred in my data at 1% backwater (57% of observations less than this value). Next, I conducted a Pearson's pairwise correlation analysis on my continuous covariates to check for correlations. If my continuous covariates were multicollinear ($|r| > 0.6$, Tables 2-3), then I selected the covariate that had the greatest number of correlations or chose continuous covariates over categorical covariates. I removed drainage area from the analysis because it was highly correlated to width-to-depth and slope. I also removed slope and percent sandstone from the analysis because they were highly correlated with width-to-depth ratio ($r = -0.63$) and discharge ($r = 0.78$), respectively. Finally, I standardized all continuous covariates to a mean of zero and a standard deviation of one.

I examined the range of my covariates and removed one due to limited variation among sites. Disturbance was relatively constant throughout all catchments ranging from 1.40 to 2.53. The LDI for tributaries ranged from 1.40 to 2.53 and was more limited in the mainstem Red River (1.91 – 2.00). Therefore, I removed this variable from consideration prior to model building.

I evaluated several multi-species single-season occupancy models in R (version 4.2.2) within a Bayesian framework using JAGS (Just Another Gibbs Sampler, Plummer 2003). I hypothesized different combinations of covariates would be important for occupancy by both species but held detection covariates constant for each hypothesis. I tested different combinations of occupancy variables to support overarching hypotheses related to factors supporting either carp growth or spawning (Tables 4-5). The most complex growth model contained sinuosity, width-to-depth ratio, chlorophyll-*a*, discharge, and the presence of backwater (Tables 4-5). The most complex spawning model contained discharge, salinity, distance to dam, and presence of backwater (Tables 4-5). I included the presence of backwater and discharge in both model frameworks as previous research indicate that carp are highly associated with the presence of backwater and discharge which may be associated with both higher forage potential, warmer water temperatures for bioenergetics, decreased energy expenditure, staging locations for spawning and carp require adequate flow for spawning (Williamson and Garvey 2005; Coulter et al. 2017, Song et al. 2018) (*see* Chapter 3). All models had grouping factors for year and river (i.e., Red River, Kiamichi, etc.) where multiple sites were nested within river (i.e., to account for pseudo replication, Wagner 2006). Broad normal priors were used for the coefficients, with gamma priors for standard deviations and uniform priors for occupancy and detection probabilities. All models were run with 3 chains in parallel beginning with a 1,000 iteration adapt phase, a 30,000 iteration burn-in, and a total of 150,000 iterations thinning every 3 iterations using the jagsUI package (Kellner 2015).

I ranked my models using the Watanabe-Akaike information criterion (WAIC) with the NIMBLE package (de Velpine et al. 2022) and selected the models with a delta WAIC score less than 2 as models with equal support (i.e., top-ranked models) (Watanabe 2010; Vranckx et al. 2021). WAIC is considered a Bayesian model selection criterion because it samples from the entirety of the posterior distribution compared to other model selection methods such as the deviance information criterion (DIC) and has been demonstrated to perform better than other model selection methods for complex Bayesian hierarchical models (Lou 2021; Vranckx et al. 2021).

For my top ranked model, I calculated the mode estimates, 90% highest density intervals (HDI), and estimated detection and occupancy probabilities for the retained covariates. I then predicted the occupancy probability and detection probability for each covariate in my final models within their observed range in the catchment (while holding the other model covariates at mean levels).

I evaluated model convergence and model fit of my top ranked models. I used the Brooks-Gelman-Rubin statistic ($\check{R}$) to assess model convergence, where an $\check{R}$ value < 1.1 indicates adequate convergence (Gelman and Rubin 1992; Gelman et al. 2000). Finally, I assessed model fit with the Bayesian p-value where a value between 0.05 and 0.95 indicates adequate model fit (Kery and Royle 2016).

Results

My sites and surveys varied spatially across the basin and carp were detected at 72% (42 of 58) of my sites during the two sampling seasons. I sampled 58 sites and conducted 127 surveys where 34 of my sites were surveyed 3 times, 11 sites were surveyed 2 times, and 13 sites were surveyed once. Of the 58 sites, 38 sites were on the mainstem Red River and 20 were on tributaries (Figure 3, Table A1). Silver Carp were detected at 23 of the mainstem Red River sites and 17 of the tributary sites with an overall naïve occupancy of 0.69 (Figure 3). Bighead Carp were detected at 10 of the mainstem Red River sites and 13 of the tributary sites with an overall naïve occupancy of 0.40 (Figure 3).

Carp were observed or captured across the catchment using a variety of gears. I captured 245 Silver Carp and 76 Bighead Carp throughout the lower Red River catchment during my 2021 and 2022 sampling seasons (Table A2). Most carp captured in the mainstem Red River were sampled from backwater locations. Carp were visually confirmed (i.e., observed jumping during sampling but not netted) during 34 surveys (Table 6). For Bighead Carp, 83% (63 of 76) were captured in gillnets and 17% (13 of 76) were captured using electrofishing. For Silver Carp, 55% (135 of 245) were captured in gillnets, 43% (105 of 245) were captured from electrofishing, and 2% (5 of 245) were fish that jumped into the boat while sampling. An average of 5 carp were captured per survey, comprising 4 Silver Carp and 1 Bighead Carp.

Physicochemical covariates

The environmental conditions of the lower Red River catchment varied between 2021 and 2022. The 2021 season was characterized by relatively high water, whereas the 2022 season was characterized by relatively low water (Table 7, Figure 4). Water temperature also varied between sample years with a mean survey temperature of 26.94 °C during 2021 and a mean survey temperature of 28.10 °C during 2022 (Table 7, Figure 5). Secchi depth was similar between the two years (mean: 37.00 cm during 2021 and 36.68 cm during 2022) (Table 7). Chlorophyll-*a* was similar temporally but varied spatially (tributaries: 12.62 – 116.60 µg/L, and mainstem Red River 10.87 – 74.35 µg/L) (Table 8). Salinity was relatively high in the upper reaches of the catchment (1.47 ppt) and decreased moving downriver to the Arkansas-Louisiana state line (0.29 ppt) (Table 8). Salinity in the tributaries had similar variation as the mainstem Red River (0.068 – 1.41 ppt), where free flowing tributaries further upstream in the network had higher salinity concentrations compared to downriver locations. The mainstem Red River channel spread out in response to changes in discharge conditions (2021: 108.35 width-to-depth ratio, 2022: 125.76 width-to-depth ratio), whereas the channel dimensions of the tributaries were relatively constant (2021: 26.11 width-to-depth ratio, 2022: 29.59 width-to-depth ratio) (Table 9). Overall, tributary channels were characterized by relatively narrow and deep channels (28.20 width-to-depth ratio), whereas the mainstem Red River was characterized by relatively wide and shallow channels (119.34 width-to-depth ratio) (Table 8).

Geospatial covariates were relatively similar throughout the catchment, with the greatest differences occurring between the tributaries and mainstem sites. As expected, drainage area increased with distance downriver of Dennison Dam (Table 8). Drainage area for the tributaries ranged from 27.08 km^2 for Buzzard Creek to 6273.98 km^2 for the Muddy Boggy River (Table 8). The majority of catchments had low percent sandstone lithology (mean = 19%), however tributary catchments had a greater range (0 – 42%) compared to the mainstem Red River (18 – 19%, Table 8). Stream sinuosity tended to be higher for the mainstem Red River (1.22 – 2.52) than the tributaries (1.34 – 2.07) (Table 8). Channel slopes were relatively low across the study area (0.0030 – 0.00066) (Table 8). Tributary sites were, on average, closer to the nearest upstream dam (mean = 82 rkm) compared to my mainstem Red River sites (mean = 123 rkm) (Table 8).

Modeling

The occupancy models that had the most support for both species (i.e., WAIC difference <2, Vranckx et al. 2021) included the covariates of backwater, sinuosity, width-to-depth ratio, and Chlorophyll-*a* (µg/L) (Tables 10 - 11). All top ranked models included the detection covariates of temperature (°C), secchi depth (cm), discharge, and electrofishing effort (s) (Table 12).

Detection probability, with my occupancy covariates held at mean levels, ranged from 0.39 to 0.40 for Bighead Carp and 0.60 to 0.63 for Silver Carp (Table 13). Bighead and Silver Carp detection was positively associated with water temperature, and electrofishing effort and negatively associated with discharge and secchi depth (cm) (Table 12, Figures 6-9).

Occupancy probability, with my detection covariates held at mean levels, ranged from 0.53 to 0.78 for Bighead Carp and 0.78 to 0.85 for Silver Carp (Table 13). Carp occupancy was positively related to reaches with the presence of backwater habitat and negatively associated with sinuosity. Both species of carp were also negatively associated with width-to-depth ratio indicating carp used reaches with narrower and deeper channels. Silver Carp occupancy was positively associated with Chlorophyll-*a,* whereas Bighead Carp occupancy had no relationship with Chlorophyll-*a* (Table 11, Figures 10-12).

My top-ranked models converged and had adequate model fit. My final models achieved convergence as evidenced by all parameters having R-hat values < 1.1 and visual assessment of the Markov chains (Tables 11-12) (Kéry and Royle 2016). The Bayesian p-values for models with equal support ranged from 0.275 to 0.292 and the c-hat values ranged from 1.094 to 1.114 indicating adequate model fit (Kéry and Royle 2016).

Discussion

Occupancy by both Bighead Carp and Silver Carp is indicative of a catchment that has been invaded for quite some time. Typically, Bighead Carp is the first to invade followed by Silver Carp which then outcompete the former. Silver Carp occupancy was relatively higher (0.78 – 0.85) across the catchment when compared to Bighead Carp (0.53 – 0.78). These occupancy rates indicate that carp, although only sampled from a subset of our sites, likely inhabit reaches across the majority of the lower Red River catchment. Estimating species distributions is an important aspect of fisheries management as it can be used to identify important locations for conservation or rehabilitation of imperiled species, or locations for targeted mitigation for invasive species (Anderson et al. 2012). Unfortunately, some of the same features leading to homogenization of the fish assemblage in the lower Red River (Mollenhauer et al. 2022) are also features that appear to benefit invasive carp.

Although catchment-level, land-use disturbance was relatively constant across my study area, both species of carp were associated with several instream habitat features that may reflect local disturbances. Across a broader geographic area, more cosmopolitan fish species in the basin were associated with land-use disturbances and altered flow regimes (Mollenhauer et al. 2022). I did not examine longer-term flow patterns due to the temporal scale of my study, and I did not relate carp occupancy to land-use disturbances because the variability was minimal across my study area. However, several of the attributes I found related to carp occupancy are related to local disturbances. Lower sinuosity reaches, for example, can reflect channelization or other degradations that result in a less complex channel (Lennox and Rasmussen 2016) and channel incision (i.e., deeper and narrow channels) (Rowe et al. 2009). Habitat complexity typically declines in areas where sinuosity is low and with-to-depth ratios reflect narrower and deeper stream channels. Degradation of natural riparian vegetation, bridge construction, and scouring associated with dams can cause erosion or armoring of stream banks, thereby increasing channel depth and these conditions tend to be associated with invasive species (Bechta and Platts 1986; Chen et al. 2010; Stein et al. 2013; Bueno et al. 2023). Altered flow regimes, common in the catchment (Mollenhauer et al. 2022), also lead to degradation of instream habitat over time where complex, braided channels tend to become greatly miniaturized over time and disconnected from the floodplain (Brewer et al. 2016). The lower Red River has also been regulated to some degree using wing dikes and other structures to direct flow and increase channel depth (Benke 2005). Calkins et al. (2012) found that Silver Carp used river reaches with wing dikes and avoided those lacking wing dikes likely due to the creation of deeper water, but also the velocity refuges formed behind the dikes (Braun et al. 2016). Ironically, these human alterations are found lower in the catchment, but I did show some correlation between width-to-depth ratio and drainage area. Higher in the stream network, most of the major tributaries are dammed or have deep incised channels associated with erodible lands (Powers 201 1). Except for periods when flood flows are released, there are no environmental flows and thus, several of the tributaries provide slow-moving, warm water that may provide important carp refuge and feeding areas.

The disconnection between the floodplain and main channel in many reaches of the Red River catchment likely exacerbates the importance of tributary habitat and reaches containing backwaters to both invasive Bighead Carp and Silver Carp. I found Silver Carp to be positively correlated with chlorophyll-a concentrations, which may relate to their feeding strategy. Silver Carp are considered obligate phytoplanktivores, incidentally consuming zooplankton (Li et al. 2013; Ochs et al. 2019). Although variability in my measured chlorophyll-a concentrations was high, some of highest densities of chlorophyll-a concentrations in the lower Red River catchment were observed in tributaries (e.g., Choctaw Creek, Bois d'arc Creek) (though not highly correlated with backwater reaches). Williamson and Garvey (2005) found that Silver Carp predominately consumed phytoplankton in the Mississippi River and proposed that Silver Carp used low-velocity habitats to maximize foraging opportunities. Both the lower tributaries in my study area and backwater habitat provide low-velocity habitats that would facilitate foraging opportunities during the warm-water period. Association with low-velocity and off-channel habitats during the warm-water periods is common to many study areas within the United States (e.g., Illinois River, DeGramdchamp et al. 2008; Wabash River, Coulter et al. 2016a). However, DeGramdchamp (2006) found Bighead Carp and Silver Carp avoided backwater habitats of the Illinois River and instead used main-channel margins during summer and autumn. Effectively monitoring these habitats over time will be beneficial to understanding future population changes.

Future monitoring strategies would benefit from consideration of gear detection and the use of multiple sampling gears. Not accounting for incomplete gear detection can lead to the underestimation of a species' distribution and management strategies that do not have the desired outcomes due to consideration of incorrect underlying ecological relationships (Mackenzie et al. 2002; Anderson et al. 2012). For example, ecological relationships could be inferred with discharge that are a function of detection probability where fish are simply more likely to be captured at lower discharge locations. I found detection probability for Bighead Carp was relatively low (average was 0.39 – 0.40), whereas detection for Silver Carp was higher (average was 0.60 – 0.63). However, I incorporated visual confirmations of Silver Carp into my estimates; otherwise, detection of Silver Carp would have been similar to that of Bighead Carp (0.36). My results indicate that sampling both Bighead Carp and Silver Carp during warmer water temperatures during relatively low discharge would maximize detection, particularly if the river is turbid. Detection probability of fishes in large rivers is commonly affected by water temperature, discharge, and clarity (Gwinn et al. 2016; Mollenhauer et al. 2018;

Zentner et al. 2021). Carp display schooling behavior during warm-water periods which may increase sampling detection (Sullivan et al. 2017). Silver Carp are commonly observed avoiding sampling gears (Williamson and Garvey 2005; Irons et al. 2007). With low detection probabilities, agencies would benefit from either accounting for detection or completing multiple surveys during the season if monitoring for species presence. In my study area, Bighead Carp could be present at 10 sites but only detected at less than half if I relied on a single survey. This underestimation would be exacerbated if sampling were conducted with a single gear. Moreover, use of multiple gears is necessary if agencies are concerned about monitoring both species across their various life stages (Wanner and Klumb 2009). If carp become more abundant in the Red River catchment, then sampling efficiencies may increase over time (Sullivan et al. 2017), but likely at the expense of ecological consequences.

As Bighead Carp and Silver Carp occupy the Red River catchment for longer periods of time, management strategies aimed at preventing their spread and exploiting their vulnerabilities will be key to population control. It would be beneficial for agencies to consider restrictions on locations for anglers to obtain bait. Collecting live bait from one waterway and transferring it to another can aid the spread of carp to nearby reservoirs or river locations above large dams. Although there is currently no documentation of reproduction in the Red River (Ramsey et al. Unpublished Data), regular recruitment is occurring in the catchment either from other basins, reaches further downriver, and/or intermittently in the study area (see also Chapter 3). Future efforts aimed at determining the mobility and timing associated with mobility would be beneficial to assessing the proportion of the population that can be targeted for removal at certain locations.

Moreover, if fish recruit from downriver areas, determining actions that prevent movements upstream from locks and dams may be beneficial (e.g., water movement strategies or barriers at the locks, Moy et al. 2011; Hasler et al. 2019; Cupp et al. 2021). Zielenski et al. (2018) found that alterations to lock-and-dam flows via gate operation could reduce carp passage while maintaining native fish passage. Interestingly, Bighead Carp have low salinity tolerances during their early life stages (Garcia et al. 1999) and may be useful information for determining possible spawning locations; however, it is unlikely that salinity will limit reproduction by Silver Carp (larvae tolerance of 6000–12,000 mg/L CaCO3, Abdusamadov 1987) which appear more common in the catchment (i.e., based on counts and similar detection probabilities). Targeted removal efforts at locations associated with both species (e.g., reaches with backwaters, near wing dikes, at tributary confluences) may be beneficial in reducing carp numbers, though changes in resulting population abundances have not been demonstrated to my knowledge. Moreover, caution should be taken with removal efforts as I commonly sampled native big river fishes of concern in the same habitats associated with carp (e.g., Paddlefish *Polyodon spathula,* Alligator Gar *Atractosteus spatula*). To minimize the persistence of Bighead Carp and Silver Carp, while promoting conservation of native fishes, managers would benefit from consideration of a structured approach that considers the responses of multiple species. This approach may be limited by lack of basic information related to the life-history of native fishes. However, unintended consequences can be associated with active management efforts. For example, flow management could be used to increase habitat complexity within some portions of the catchment, but it is unclear how changes in flow may affect non-native fishes (Marks et al. 2010). Agencies would benefit from considering a variety of alternatives that can be tested on a limited basis as both positive and negative feedbacks have been associated with efforts to limit invasive populations.

CHAPTER III

POPULATION DEMOGRAPHICS OF ADULT BIGHEAD CARP AND SILVER CARP IN THE LOWER RED RIVER CATCHMENT

Introduction

Population demographics are fundamental components to fisheries science and their importance relates to population monitoring, assessing population recovery or decline, and the validity of fisheries management actions (Quist and Isermann 2017). Population demographics comprise recruitment (Maceina 1997; Isermann et al. 2002; Honsey et al. 2017), mortality (Robson and Chapman 1961; Smith et al. 2012), age-structure (Maceina et al. 2007), and fish growth (Roff 1983; Campana 2001; Weisberg et al. 2010). For example, age-and-growth estimates were used to monitor the population status of Westslope Cutthroat Trout *Onchorhynchus clarki lewisi* in British Columbia tributaries (Janowicz et al. 2018). Additionally, Watkins et al. (2017) assessed population recovery of Largescale Sucker *Catostomus macrocheilus* and Mountain Whitefish *Prosopium williamsoni* and found that somatic growth and year-class strength were positively associated with nutrient mitigation in the Kootenai River, respectively. Estimates of demographic rates can be used to quantify management actions or determine if policies were successful. For example, Tsehaye et al. (2013) used estimates of natural mortality, age-structure, recruitment, and growth to predict the exploitation rate required to collapse populations of invasive Bighead Carp and Silver Carp in the middle Mississippi rivers. Demographic rates are important to understand in fish populations, especially recruitment, mortality, and growth.

Recruitment, mortality, and growth can all be estimated indirectly for fish populations. In the absence of robust recruitment analyses, the age structure of the population can be used to gauge recruitment variability and year-class strength for a population. Residuals (Maceina 1997; Maceina 2004), the coefficient of determination (RCD, Isermann 2002) and the recruitment variability index (RVI, Guy and Willis 1995) are all useful for determining both year-class strength and recruitment variability. Mortality is directly correlated with age structure and can be quantified under certain assumptions using models derived from age data (Catalano et al. 2009; Tetzlaff et al. 2011; Smith et al. 2012). For example, the slope of a catch-curve represents the instantaneous mortality (z) for a population (Catalano et al. 2009). Using simulated data, Smith et al. (2012) showed that a Chapman-Robson estimator corrected for overdispersion could be used to estimate mortality. Catch-curves can be used to determine rudimentary estimates of mortality for populations where little information is available (Catalano et al. 2009). Ageing fish can also be used to estimate fish growth which can be summarized for a population. Growth can affect certain life-history characteristics of populations such as recruitment (Francis et al. 2016; Klein et al. 2019) and can reflect the population's adaptability to environmental change (Neuheimer and Taggart 2007; Shoup and Wahl 2011; Yokouchi et al. 2018) thereby affecting recruitment. For example, Quist et al. (2004) found that poor somatic growth in Walleye *Stizostedion vitreum* resulted in decreased recruitment the following year. Additionally, Bull Trout *Salvelinus confluentus* growth was positively associated with the number of smolts in the upper Salmon River (Roth et al. 2020). Changes in growth can allow scientists to assess past, present, and future ecological conditions on fish populations and to determine whether management practices are influencing populations as desired (Schultz et al. 2013).

Ageing fish and quantifying their growth are possible by using hard, calcified, structures (Figure 13) that may or may not result in fish mortality. Annuli, or growth bands, are hypothesized to be formed by seasonal changes in water temperature and fish growth (Rugg et al. 2014; Johnson and Belk 2004) though other environmental factors may also be responsible (Quist and Isermann 2017). This periodic growth and formation of annuli permits length-at-age analyses using a subset of fish that can be extrapolated to the population (Isermann and Knight 2005). Many hard structures have been analyzed for ageing fish and quantifying growth. These structures can be grouped into two general categories: those which can be removed without causing extensive mortality, and structures that require fish to be euthanized. Scales, spines, and fin-rays allow fish to be aged without causing extensive mortality and have been shown to be quickly and easily aged (e.g., Striped Bass *Morone saxatilus,* Welch et al. 1993; Walleye *Stizostedion vitreum*, Kocovsky and Carline 2000; Isermann et al. 2003). Structures that require fish to be euthanized (i.e., bones and otoliths) are sometimes the only reliable ageing structure (e.g., Smalltooth Sawfish *Pristis pectinata*, Scharer et al. 2012).

Otoliths are often the preferred ageing structure (i.e., accuracy, Campana and Thorrold 2001) for fish if mortality is not a concern. There are three pairs of otoliths: the saggitae, asteriscus, and lapilli. The saggitae otolith is the largest of the three in many species and is the most used in adult ageing studies (Long and Stewart 2010; Quist and Isermann 2017). The asteriscus is used for ageing certain species (e.g., ostariophysans, Adams 1940) including Common Carp *Cyprinus carpio* (Phelps et al. 2007). The asteriscus are typically comprised of vaterite which makes them difficult to read (Quist and Isermann 2017). Lapilli otoliths are commonly used to estimate growth of larval fishes (Fey et al. 2005), but also age and growth of some fishes including Channel Catfish *Ictalurus punctatus* and many Cyprinid species (e.g., *Engraulicypris sardella, Hybognathus amarus, Gnathopogon caerulescens*, Morioka and Kaunda 2003; Long and Stewart 2010; Horwitz et al. 2018; Kikko et al. 2019).

Bighead Carp and Silver Carp were introduced into many catchments of the central and southeast United States (*see* Chapter I), but our general understanding of their population demographics is derived from only a few catchments. Carp recruitment can be highly variable (e.g., Silver Carp, Sullivan et al. 2018), with missing year classes followed by strong cohorts (Hayer et al. 2014, Ridgeway and Betolli 2017). The population age structure of both species varies depending on the river catchment. Hayer et al. (2014) found that Bighead Carp age ranged from 0 to 3 years and Silver Carp age ranged from 0 to 5 years in the James and Vermillion rivers; whereas, Bighead Carp and Silver Carp were 8 to 22 years old and 3 to 13 years old in the Tennessee and Cumberland rivers, respectively (Ridgway and Bettoli 2017). A meta-analysis of carp populations in the middle Mississippi River found the instantaneous natural mortality (M) was 0.685, the theoretical maximum length ($L\infty$) was 802.826 mm, and the growth-rate (K) was 0.445 for Silver Carp, whereas M was 0.654, $L\infty$ was 982.938, and k was 0.433 for Bighead Carp (Tsehaye et al. 2013). However, Sullivan et. al (2021) found that populations of Silver Carp in the Illinois River had lower $L\infty$ and k values that ranged from 691 to 740-mm and 0.28 to 0.23, respectively. Because carp population demographics vary across their invaded distribution, understanding the differences in population parameters aids our understanding of their invasions and provides insight into possible management actions.

Correspondingly, my second thesis objective was to assess the population demographics of Bighead Carp and Silver Carp in the lower Red River catchment. I determined age and population demographic rates for both species and related growth to environmental factors. Establishing baseline values for mortality, recruitment, and growth parameters (e.g., L_∞ and k) will allow managers to compare these metrics after the implementation of future mitigation efforts, or population changes over time.

Methods

Ageing carp has been accomplished using fin-rays, scales, the post-cleithrum, the urohyal bone, and otoliths and use of each to estimate age has tradeoffs. Although fin rays are easily collected, they underage Silver Carp due to the erosion of the central lumen (Figure 13) (Seibert and Phelps 2013). Scales result in under-ageing of carp, caused by crowding of the annuli and non-distinct annuli (Sikstrom 1983; Johal et al. 2000b; Seibert and Phelps 2013). The post-cleithrum is a bone contained within the pectoral girdle that provides consistent age estimates when sectioned transversely at the middle of the structure (Figure 13) (Johal et al. 2000a). Likewise, the urohyal bone can be sectioned to age Silver Carp (Figure 13) (Johal et al. 2000b). However, when compared to other structures, using these two bones results in lower between-reader agreement than lapilli otoliths (Seibert and Phelps 2013). Using the lapilli otolith to age carp and other minnows is considered the most consistent structure. For example, Horwitz et al. (2018) found that Rio Grande Silvery Minnow *Hybognathus amarus* lapilli otoliths had a higher between-reader agreement compared to scales. Additionally, Seibert and Phelps (2013) used a sample of 120 Silver Carp and found that lapilli otoliths had the highest between-reader agreement and precision compared to fin-rays, post-cleithrum, and vertebrae (Figure 13). There is no comparable study for Bighead Carp, but many managers use lapilli otoliths assuming they will provide similar results as found with Silver Carp. I conducted a comparison of ageing structures (i.e., lapilli otoliths, postcleithra, fin-rays, and pterigiophores) following Seibert and Phelps (2013) and found that lapilli otoliths had the highest precision for both Silver Carp and Bighead Carp in the lower Red River catchment. I also found that using otoliths better represented older fish in the population when compared to the other structures (see Appendix B). Therefore, I used lapilli otoliths for age and growth analyses of Silver Carp and Bighead Carp (Seibert and Phelps 2013).

Otolith Removal and Processing

Fish were collected while sampling following the methods described in Chapter I. Briefly, I sampled fishes from river reaches across the study area. Fish were sampled using a combination of gill nets and electrofishing. However, for this objective, I also used some carp that were provided through angler donations to the U.S. Fish and Wildlife Service.

I removed lapilli otoliths for age and growth analyses following Seibert and Phelps (2013). Briefly, the lapilli otoliths, located at the posterior of the skull, were accessed using a hacksaw. A cut was made through the top of skull at the juncture of the preopercle and opercula. Otoliths were then removed using forceps and placed into coin envelopes marked with an individual fish number for later laboratory analyses.

In the laboratory, otoliths were sectioned and prepared for age estimation. First, I marked the nucleus on the exterior of the otolith with a ballpoint pen. I then placed the otolith in epoxy resin (West System 105-A) and allowed it to harden for 24-h. After hardening, the otolith was sectioned using an isomet saw (Buehler IsoMet Low Speed Precision Cutter, Lake Bluff, Illinois) and a single 0.5 to 0.6-mm cross-section was removed from the center of the otolith ensuring the inclusion of the nucleus. I then polished the sectioned otolith for 1.5 min on each side with 3-μm diamond lapping paper (Diamond Lapping Film, 8" diameter, plain backing, Electron Microscopy Sciences, Hatfield, PA). Subsequently, I mounted the sectioned otolith onto a slide using thermoplastic cement. The slide was then placed under a dissecting microscope equipped with a light source and imaged with a digital camera (Luminera Infinity 2, Tyledyne Luminera, Ontario). The images were saved for later growth analyses.

Age and Growth

Two readers separately enumerated the annuli of the sectioned otolith to age each fish using transmitted light under a dissection microscope. An annulus was defined as a pair of translucent and opaque bands that continued uninterrupted around the nucleus (Dzul et al. 2012). The edge was counted as an annulus for fish captured prior to April 1st because an annulus was presumed to be created during the spawning season (Minard and Dye 1998; Ericksen 1999). There was no prior knowledge of the fish's length, weight, or age to avoid reader bias. If there was no consensus on the age of a fish, then the readers discussed how they derived the age and a consensus was obtained.

I quantified the proportional growth of carp to determine how growth related to discharge and temperature patterns and fish length (*see* Data Analyses). The annuli and edge were analyzed for proportional growth using Infinity Analyze 7 software (Tyledyne Luminera, Ontario) (Quist and Isermann 2017). Otoliths were measured for incremental growth along the midventral axis. The focus was identified, and then individual radii distances were recorded from the focus longitudinally to the outside edge of each opaque band to determine individual year growth (Weisberg et al. 2010). The distance from the focus to the edge was used to relate incremental growth to fish length.

Data Analyses

I calculated the mean back-calculated length-at-age for all ages to be used in a growth model. Back calculation for length-at-age was conducted using the Dahl-Lea method because of the lack of a known biological intercept (Quist and Isermann 2017).

$$Li = \left(\frac{Si}{Sc}\right) * Lc$$

where Li is the fish length at age i. Si is the otolith radius as age i. Sc is the otolith radius at the edge. Lc is the fish total length at capture (Francis 1990).

I fit a von Bertalanffy growth model (vBGM) to carp using the previously collected back-calculated length-at-age data. I used a vBGM for carp because it is widely used for comparing growth between fish populations (Quist and Isermann 2017) and can elucidate important population growth parameters, such as the theoretical maximum length (L_∞) and the population growth coefficient (*k*). These parameters can then be compared post mitigation if management practices aim to reduce fish growth.

$$L_t = L_\infty[1 - e^{-k(t-t_0)}],$$

Lt is the length of fish at a specific age. L_∞ is the theoretical maximum length for the population. *K* is the growth rate coefficient, and t_0 is the hypothetical age when fish length equals zero (Watkins et al. 2017).

I used a mixed-effects model, described by Weisberg et al. (2010), to relate Silver Carp and Bighead Carp growth to environmental conditions of the lower Red River catchment. It can be difficult to relate growth to the environment because growth is correlated with fish age, fish length, and fish from the same cohort because cohorts can display higher growth rates than others (Watkins et al. 2017). Advances in mixed-effects growth models have permitted us to account for the age, length, and interactions between individual fish during a given year to assess the effects of environmental factors on growth (Weisberg et al. 2010).

$$Y_{tnj} = X_j + V_{t+j-1} + F_{tn} + e_{tnj},$$

where Y_{tnj} is the annular increment *j* for fish *n* for the year-class *t*. X_j is the annular increment for the fish in the growth year *j*; V_{t+j-1} is the environmental effect for year $X=t+j-1$, which is the year that a fish in year class *t* was age *j*; F_{tn} is the effect of fish *n* in the year class *t*. e_{tnj} is the model error (Weisberg et al. 2010; Watkins et al. 2017). I modeled age, discharge, and water temperature as fixed effects while year and fish were random effects. This catchment experiences relatively high annual weather fluctuations including longer periods of flood and drought (see Mollenhauer et al. 2022).

I hypothesized that both Bighead Carp and Silver Carp growth were related to discharge and water temperature conditions. I created species-specific models relating the 75th percentile of discharge (m^3/s) (i.e., relatively high flows), the coefficient of variation (CV) of discharge (i.e., flow variability), the 75th percentile of air temperature (°C), and the CV of air temperature to fish growth from April through September across the catchment. I used air temperature as a surrogate for water temperature due to the lack of consistent water temperature data for all the years considered, and water temperature is highly related to air temperature throughout the catchment (Morrill et al. 2005; Adlam et al. 2022). The oldest fish in my sample (e.g., 17) would have recruited in 2004, however because no fish younger than age 3 were observed in the lower Red River catchment I truncated my data to model growth from age 3 through the maximum age. Thus, I collected discharge and temperature data from 2007 through 2019 and calculated the 75th percentile and CV for the season (April 1st = September 30th).

I used Akaike's information criterion corrected for small sample size (AICc) to rank several models (Segiura 1978). I constructed the following models: random effects (i.e., year, fish) and fish length with no environmental factors, all combinations with random effects, and a global model (Table 14). I conducted model averaging for models that had an Akaikes difference (ΔAIC) less than two (Burnham and Anderson 2004). I then calculated the marginal R^2 and the conditional R^2 for both fixed and random effects, respectively, for the averaged models (Nakagawa and Shielzeth 2013). I used the "lme4" (Bates et al. 2015), "AICcmodavg" (Mazerolle 2020), and "MuMIn" (Barton 2018) packages for my analyses.

I used two catch curves to analyze mortality and recruitment of Silver Carp. I used a Chapman-Robson peak-plus catch-curve corrected for overdispersion to estimate mortality and recruitment variability via the recruitment variability index (RVI) (Isermann et al. 2002) for Silver Carp only due to the small sample size for Bighead Carp (Smith et al. 2012).

$$CR(Z) = log_e\left(\frac{1+T-Tc-\frac{1}{N}}{T-Tc}\right) - \frac{(N-1)(N-2)}{(N[N(T-Tc)+1][N+N(T-Tc-1])}$$

Where Tc is age of recruitment, T is the mean age of fish equal to or greater than Tc, N is the sample size (Smith et al. 2012). Peak plus denotes that the first age class used in the analysis is the age following the age with the largest quantity (Smith et al. 2012). Catch-curves for estimating mortality and recruitment are susceptible to bias when age classes are missing from these data (Catalano 2009), however all age classes were present for Silver Carp.

Results

A total of 258 Silver Carp and 86 Bighead Carp were sampled in 2021 and 2022 and Silver Carp tended to be smaller and younger, on average, compared to Bighead Carp though Silver Carp tended to grow faster early in life (Table 15). On average, the Silver Carp I collected were 887-mm TL (range; 616-130-mm), whereas Bighead Carp were 1102-mm TL (range; 868-1360-mm). The mean age of Bighead Carp estimated using otoliths was 9 years, whereas Silver Carp mean age was lower (6 years). The oldest sampled Silver Carp and Bighead Carp were age 14 and 17, respectively (Figure 14). Silver Carp were larger (i.e., TL) than Bighead Carp, on average, until age 5 (Table 15). Silver Carp and Bighead Carp mean back-calculated lengths at age 5 were 740 and 746-mm, respectively.

Silver Carp mortality was relatively low and recruitment into the population appeared steady. My catch-curves for Silver Carp were fit using ages 6 through 14 because age 5 fish had the highest count in my sample. The instantaneous mortality estimate (*Z*) was 0.32. The proportion of fish dying from total mortality (e.g., fishing and natural mortality, *M*) was 0.27. Recruitment variability was relatively stable for Silver Carp (0.86) (Figure 15). Theoretical maximum length for both species was relatively high

(SVC = 920-mm, BHC = 1349-mm), whereas growth rate (k) was higher for Silver Carp (k = 0.31) compared to Bighead Carp (k =0.12) (Figure 16).

Discharge and air temperature patterns varied over the 13 years (i.e., oldest fish at age 3) that Silver Carp and Bighead Carp have likely been in the lower Red River catchment. The 75th percentile of discharge during April – September from 2007 - 2019 ranged from 400.68 to 1659.17 m^3/s with a mean of 584.78 cm^3/s (Table 16). The CV of discharge was also highly variable and ranged from 57.06 to 164.74. The average 75th percentile of air temperature was 25.05 °C with little variability (24.89 to 25.58 °C). The CV of air temperature was more variable (17.00 – 23.17).

Air temperature, discharge variability, and high discharge conditions were related to growth of Silver Carp and Bighead Carp. I model averaged a total of 13 Weisberg models associated with Silver Carp growth and 2 models associated with Bighead Carp that had a delta AIC score less than 2 to reduce model bias and address uncertainty (Tables 17-18) (Kruse et al. 2022). Bighead Carp growth was positively associated with warmer air temperature as a surrogate of water temperature (75th percentile of air temperature) and negatively associated discharge variability (CV of discharge). Similarly, Silver Carp growth was positively associated with the warm air temperature (75th percentile of air temperature) and negatively associated with discharge variability (i.e., CV of discharge). However, Silver Carp growth was also positively related to high discharge conditions (75th percentile of discharge) and the variability of air temperature as a surrogate for water temperature (i.e., CV of air temperature) (Table 19).

My fixed and random effects explained a large portion of the variability in my growth models. The marginal R^2s for my Silver Carp models having equal support ranged from 0.51 to 0.56. Including random effects explained 22% to 27% more variability in my data (R^2- 0.73 to 0.78). The fixed effects in my top-ranked Bighead Carp models with equal support explained 57% of the variation in my data (marginal R^2- 0.57). Including the random effects of year and fish explained an additional 10% of the variation in growth (conditional R^2- 0.67).

Discussion

Both Silver Carp and Bighead Carp in the Red River catchment have body sizes (i.e., length-at-age) that are commonly associated with relatively recent or continued population invasions. No individuals of either species younger than 3 years of age were collected; however, the younger fish were relatively large with a mean back-calculated total length of 603-mm for Silver Carp and 569-mm for Bighead Carp at age 3. Coulter et. al (2018) found that individuals with greater body condition are more likely to be located on the fringe of the species distribution and are primarily responsible for expanding the species range. River fishes with higher body condition are generally more mobile (Kanno et al. 2023). Furthermore, rivers with robust populations of Silver Carp have relatively smaller fish. For example, Sullivan et al. (2021) found that the mean total-length for Silver Carp ranged from 532 – 737-mm in the Missouri, Mississippi, Wabash, and Illinois rivers, whereas the mean total-length was 887-mm for the lower Red River catchment. Additionally, total length for newly established populations of Silver Carp in the Mississippi River and Bighead Carp in the Missouri River ranged from 600 to 800-mm and 450 to 1099-mm, respectively (Shrank and Guy 2002; Williamson and Garvey 2005).

It is unknown where carp recruit in the Red River catchment. Silver Carp recruitment variability was relatively stable (RVI of 0.86), which is comparable to what is observed in other catchments such as the Missouri, Mississippi, De Moines, and Wabash rivers (RVI 0.66 – 0.95, Sullivan et al. 2021). This may be due to fish consistently recruiting to the catchment from other river systems (i.e., Atchafalaya River) or steady recruitment in the Red River. However, reproduction was not documented in my study area in 2021-2022 (Ramsey et al. Unpublished data) suggesting these fish were originally from a different basin (i.e., Mississippi River) expanding the invasion front or recruiting from Louisiana. Lack of recruitment in this study area could be due to improper environmental conditions or skewed sex ratios. Fertilization rates by carp can be quite low (e.g., 37%, Gonzal et al. 1987; Lenaerts et al. 2023). If sex ratios are skewed, fertilization rates may be even lower. Moreover, carp exhibit schooling behaviors (Murchy et al. 2017), and chemical cues associated with schools may be necessary for attracting females. If the populations are relatively low density compared to other populations, then they may currently lack emergent properties that facilitate successful reproduction.

Bighead Carp and Silver Carp in the Red River catchment appear to live longer and grow larger than other populations. Silver Carp theoretical maximum length in the Missouri and Mississippi rivers ranged from 691 to 802-mm TL and Bighead Carp theoretical length was 983-mm in the Mississippi River (Tsehaye et al. 2013; Ridgeway and Bettoli 2017), whereas Silver Carp and Bighead Carp in the lower Red River had a theoretical maximum length of 920 and 1348-mm TL, respectively. This may be because older age classes were present in the lower Red River population, as Silver Carp maximum age was much higher in the lower Red River (i.e., 14 years old) than that typically seen in the Mississippi River basin (i.e., 7 years old) (Schrank and Guy 2002; Williamson and Garvey 2005). This is further highlighted by Silver Carp growth coefficient (*k*). The growth coefficient represents the speed at which fish length approaches the theoretical maximum length, with a higher *k* indicating faster growth (Quist and Isermann 2017). Although Silver Carp theoretical maximum length was higher than other populations, the rate of growth (k = 0.31) was similar to populations in the Mississippi and Illinois rivers (0.23 – 0.445, Tsehaye et al. 2013, Sullivan et. al 2021), whereas Bighead Carp growth rate (k = 0.12) was slower relative to Mississippi River populations (0.433, Tsehaye et al. 2013). However, several of the previous studies conducted on carp in the Mississippi and Illinois rivers used different ageing structures (i.e., fin rays) which may underage carp compared to lapilli otoliths. This may bias growth estimates, because growth models estimate parameters such as L_∞ and k from length-at-age estimates.

I recommend agencies use lapilli otoliths for ageing and monitoring populations of both Bighead Carp and Silver Carp even though between-reader-agreement (BRA) was lower than found in other fishes. Proper age estimates are critical for assessing any of these rates (Koenigs et al. 2013; Anderson et al. 2023). Determining the accuracy of an ageing structure can be difficult for invasive species using known-age fish or marginal increment analysis (Rugg et al. 2014; Anderson et al. 2023). Precision estimates are used as a surrogate to determine the best structure to age fish when no structure has been validated (Campana et al. 2001). Common precision metrics include between-reader-agreement and the mean coefficient of variation (CV), where the highest BRA and lowest mean CV indicate the highest precision (Seibert and Phelps 2013). Between-reader-agreement was relatively low for lapilli otoliths (SVC = 0.79, BHC = 0.69) compared other species such as Walleye *Stizostedion vitreum* (BRA = 0.98), Largemouth Bass *Micropterus salmoides* (BRA = 0.91), Smallmouth Bass *Micropterus dolomieu* (BRA = 0.94), Yellow Perch *Perca flavescens* (BRA = 0.98), and Brown Bullhead *Ameiurus nebulosus* (BRA = 0.92) (Isermann et al. 2003; Maceina and Sammons 2006). Longer lived fishes are inherently more difficult to age compared to fishes with shorter life spans due to crowding of annuli, especially in warm-water systems when growth is more consistent (Quist and Isermann 2017). For example, Dunton et al. (2016) found that BRA for Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus* was 63% for fin spines and Labay et al. (2011) found that BRA for Blue Sucker *Cycleptus elongatus* was 50% for fin-rays.

Like Seibert and Phelps (2013), I found that using lapilli otoliths for ageing Silver Carp resulted in the highest precision. I am the first to find the same pattern when ageing Bighead Carp. It is dangerous to speculate that patterns observed in one species would be the same for another. For example, both the asteriscus and lapilli otoliths have been validated for ageing Bigmouth Buffalo (Lackmann et al. 2021), yet only lapilli otoliths have been used to age Smallmouth Buffalo and Black Buffalo (Paukert and Long 1999; Love et al. 2019). Although it may be easier to use other structures (Shrank and Guy 2002) to age Bighead Carp, the resulting age would likely be underestimated compared to using otoliths. Age-bias plots comparing age-estimates between lapilli otoliths and all other structures indicated that all other structures in the analysis underestimated fish-age compared to lapilli otoliths (Figures B1 – B2). Similar results have been found with other species including Saugeye *Sander canadensis x vitreus*, Catastomid *Catostomidae spp.*, and Cyprinids *Cyprinidae spp.* species. (Quist et al. 2007; Koch et al. 2018). In addition, the lapilli otolith was useful for determining patterns in growth.

Factors that increase water temperatures and stabilize flows may positively affect growth and recruitment for both species of carp; however, taxing of water resources and declines in precipitation reducing flows may negatively affect Silver Carp growth. Climate models predict that air temperatures will increase over the next several decades (Dixon et al. 2020; Portner and Roberts 2022). These increasing water temperatures throughout the catchment may lead to an environment that fosters increased growth and an extended spawning period for both carp species (once successful) as optimal feeding and spawning temperature for carp ranges from 18 to 31 °C and a minimum of 18 °C, respectively (Cooke et al. 2012; Cooke 2016; Nico et al. 2022a). Pease and Paukert (2014) found that Smallmouth Bass *Micropterus salvinius* growth would increase with warming water temperature due to climate change. Furthermore, McCann et al. (2018) found that Sea Lamprey *Petromyzon marinus* spawning occurred earlier in the year due to increased stream water temperature resulting in possible increased growth and survival of juveniles in the Great Lakes basin. The combination of warming water temperatures increasing carp growth (assuming available food) and their observed tendency to supplant native species may exacerbate the invasive capabilities of these species. Additionally, growth for both species of carp was negatively associated with discharge variability. Major impoundments exist on the mainstem Red River (i.e., Dennison Dam) and many of the tributaries (i.e., Kiamichi, Muddy Boggy, Sulpher River) which lead to stabilized flows (Gison et al. 2005; Wang et al. 2016; Zhang et al. 2017). Additional impoundments have recently been constructed or are planned in the catchment (e.g., Bois'd Arc Creek)

(Payne et al. 2021), which may further decrease flow variability and lead to increased growth for both carp species. Flow variability is also positively associated with occupancy of several native species (Mollenhauer et al. 2022). However, the taxing of water resources in the Southern Great Plains and a slight reduction in precipitation is projected to decrease the overall duration and magnitude of flows (Brikowski 2008: Dixon et al. 2020; Portner and Roberts 2022). For example, the city of Dallas, TX requires additional water resources which are being allocated from the Red River catchment and Oklahoma City will be diverting additional water from the Kiamichi River (Burch et al. 2020; Payne et al. 2021). This may result in a decrease in the consistency of year-to-year growth for Silver Carp punctuated by increased growth during flood years in the lower Red River catchment.

Carp growth and low mortality may be related to low fish density, high food availability, and decreased fishing mortality in the lower Red River. For example, Lorenzen and Endberg (2002) found that asymptotic length for 9 teleost populations had an inverse relationship with species specific biomass density. Additionally, the lower Red River catchment may offer abundant forage which facilitates increased growth. My chlorophyll-*a* concentrations were on average 32.97 µg/L in the Red River, whereas chlorophyll-*a* levels in the Mississippi River from 1998 to 2018 were over 20 µg/L only 12% of the time (Turner et al. 2022). Silver Carp exhibited lower mortality (0.32) than populations in the Mississippi River basin (0.65, Tsehaye et al. 2013). This may be related to density dependent mortality or lower fishing mortality compared to other river catchments. For example, Matte et al. (2020) found that mortality of Brook Trout *Salvelinus fontinalis* was positively associated with density. Densities of carp are currently perceived lower than many other rivers (though not as low as perceived based on sampling at some locations) that may improve overall survival. A commercial fishery for Buffalofishes persists in the Arkansas portion of the lower Red River, with incidental carp bycatch. However, commercial harvest is not permitted in the Oklahoma or Texas portions of the catchment which may alleviate harvest pressure for these carp populations (but also on native fishes as bycatch). High fishing mortality from commercial harvest and mitigation efforts persists in the Missouri, Mississippi, and Illinois rivers. However, in many cases, it is unknown if removal efforts have resulted in any change in overall population abundance (but see USFWS 2021) or if they alter the reproductive potential in those populations (i.e., compensatory response). Elevated fishing mortality in these rivers could cause the observed difference in Silver Carp mortality.

As Silver Carp and Bighead Carp continue to expand their invasion front, proper assessment and management of these populations will be beneficial if the goal is to reduce their numbers or overall body size. Experimental flows are a mitigation tool that may be used to reduce carp growth and overall body size via increased discharge variation. For example, Oliveira et al. (2020) found that experimental flows increased body condition of a barbell *Luciobarbus bocagei* in the Vouga River basin. Additionally, Kelly et al. (2017) found that Longnose Dace *Rhinichthys cataractae* and Slimy Sculpin *Cottus cognatus* mortality increased with flow alterations. Altering hydrographs to increase flow variability could negatively affect carp growth and survival. However, Silver Carp recruitment has been positively related to flow variability in their native ranges (Coulter et al. 2016b). Therefore, caution is warranted when devising experimental flows with goals related to invasive species as they are sometimes met with unintended consequences. If carp are not currently successfully recruiting in the lower Red River catchment, then focusing control efforts in this catchment on where fish are immigrating from is warranted (i.e., telemetry). Moreover, examination of possible reproduction over multiple years will be needed to determine when and if reproduction can occur, particularly if the population continues to grow. Current climate predictions indicate increases in growth and survival are likely for carp. Consequently, the populations in this catchment are likely to increase without mitigation efforts. Implementing commercial harvest or other removal efforts could potentially increase annual mortality of these populations; however, this could harm species of concern (i.e., Alligator Gar *Atractosteus spatula* and Paddlefish *Polyodon spathula*) which shared habitat with these invasive fishes. Novel strategies for attracting carp, even to artificial habitat, during specific times of the year when native fish mortality would be lower (i.e., cooler water) or timing mitigation efforts when native species densities are lower in these habitats (i.e., backwaters) would seem prudent to reduce the associated risk to native species.

TABLES

Table 1. Covariates used to estimate occupancy probability (Ψ) and detection (*p*) hypothesized to be related to carp distributions in the lower Red River catchment with the corresponding state (occupancy [Ψ], and detection [*p*]), scale, data source, unit, URL, and citation.

Habitat factor	State	Scale	Data source	Unit	URL
Drainage area[1]	Ψ	Catchment	NHD+/Stream Stats	km^2	https://apps.nationalmap.gov/downloader/#/
Disturbance[2]	Ψ	Catchment	NLCD	LDI	https://apps.nationalmap.gov/downloader/#/
Lithology[3]	Ψ	Catchment	U.S. Geological Survey	% limestone	https://mrdata.usgs.gov/geology/state/
Sinuosity[1]	Ψ	Segment	ArcPro GIS		https://apps.nationalmap.gov/downloader/#/
Slope[1]	Ψ	Segment	ArcPro GIS	%	https://apps.nationalmap.gov/downloader/#/
Discharge[4]	Ψ	Segment	U.S. Geological Survey	m^3/s	https://waterdata.usgs.gov/nwis/rt
Distance to Dam[1]	Ψ	Reach	ArcPro GIS	rkm	https://apps.nationalmap.gov/downloader/#/
Percent backwater	Ψ	Reach	Field collection	%	
Width to depth	Ψ	Reach	Field collection		
Salinity	Ψ	Reach	YSI pro dds	ppt	
Chlorophyll-a	Ψ	Reach	Water sample	mg/L	
Temperature	*P*	Reach	Field collection	°C	
Discharge[4]	*P*	Reach	U.S. Geological Survey	m^3/s	https://waterdata.usgs.gov/nwis/rt
Secchi depth	*P*	Reach	Field collection	cm	
Electrofishing effort	*p*	Reach	Field collection	S	

[1]U.S. Geological Survey 2017, [2]Dewitz 2019, [3]Horton 2017, [4]U.S. Geological Survey 2016

Table 2. Pearson's correlation coefficients for occupancy covariates (percent sandstone [Pcnd], disturbance [Dist], sinuosity [Sin], slope [Slp], discharge [Q], width-to-depth [W.D], salinity [Sal], distance to dam [Dtd], chlorophyll-a [Chla], and drainage area [DA]) for the lower Red River catchment.

	Pcnd	Dist	Sin	Slp	Q	W.D	Sal	Dtd	Chla	DA
Dist	-0.39									
Sin	0.25	-0.45								
Slp	-0.56	0.12	-0.38							
Q	-0.78	0.18	-0.11	0.53						
W.D	0.27	0.06	0.01	-0.63	-0.33					
Sal	-0.28	0.55	-0.30	0.02	0.13	0.41				
Dtd	0.29	0.12	0.32	-0.26	-0.21	0.07	0.09			
Chla	-0.53	0.31	-0.08	0.04	0.42	0.01	0.29	0.33		
DA	0.39	0.18	0.04	-0.74	-0.41	0.82	0.32	0.29	0.04	
Pcbck	0.20	0.04	0.07	-0.41	-0.15	0.19	-0.17	0.16	0.04	0.37

Table 3. Pearson's correlation coefficients for detection covariates (temperature [Temp], secchi depth [Secchi], electrofishing effort [Sec], and discharge) for the lower Red River catchment.

	Temp	Secchi	Sec
Secchi	0.53		
Sec	0.03	-0.07	
Discharge	-0.35	-0.34	0.30

Table 4. Covariate combinations (backwater [Bck], discharge [Q], chlorophyll-*a* [Chla], width-to-depth ratio [W:D], sinuosity [Sin], distance to dam [Dtd], and salinity [Sal]) for the two overarching hypothesized models (growth and spawn) related to carp occupancy.

Model framework	Model combinations
Growth	Bck
	Q
	Bck + Q
	Chla
	W:D
	Bck + Chla
	Bck + Sin
	Bck + W:D
	Q + Chla
	Q + Sin
	Q + W:D
	Sin + Chla
	Sin + Chla
	W:D + Chla
	W:D + Sin
	Bck + Q + Chla
	Bck + Q + Sin
	Bck + Q + W:D
	Bck + Sin + Chla
	Bck + W:D + Chla
	Bck + W:D + Sin
	Bck + Q + W:D + Chla
	Bck + Q + W:D + Sin
	Bck + W:D + Sin + Chla
	Q + W:D + Sin + Chla
	Bck + Q + W:D + Sin + Chla
Spawn	Bck
	Q
	Bck + Q
	Dtd
	Sal
	Bck + Dtd
	Bck + Sal
	Q + Dtd

Q + Sal
Sal + Dtd
Bck + Q + Dtd
Bck + Q + Sal
Bck + Sal + Dtd
Sal + Dtd + Q
Bck + Q + Sal + Dtd

Table 5. Overarching hypothesized model (growth and spawn) with associated covariates (backwater [Bck], discharge [Q], width-to-depth ratio [W:D], sinuosity [Sin], chlorophyll-*a* [Chla], salinity [Sal], and distance to dam [Dtd]) and the corresponding hypothesis of their relationship to occupancy.

Model	Covariate	Hypothesis
Growth	Bck	Backwaters can offer higher forage potential, growth potential because of warmer water temperature for bioenergetics, and decreased energy expenditure. [1,2,3]
	Q	Negatively associated because of increased energy expenditure and lower forage availability. [4, 5, 6, 7]
	W:D	Carp growth positively associated due to low-velocity habitats, increased forage, and decreased competitor species due to lower habitat complexity [8, 9, 10, 11]
	Sin	Increased growth because of decreased competitor species and decreased habitat complexity. [10, 11]
	Chla	Increased forage available for growth. [12, 13, 14]
Spawn	Bck	Possibly used as staging locations for spawning. [15, 16, 17]
	Q	Positively associated with discharge because of increased flow requirements for pelagic spawners and successful spawning associated with high discharge. [18, 19, 20]
	Sal	Improper salinity can hinder spawning. [21, 22, 23]
	Dtd	Positively associated with presence because of minimum flow distance requirements for successful spawning and flow alteration can affect recruitment. [24, 25, 26]

[1]Williamson and Garvey 2005, [2]Humphries et al. 2006, [3]Coulter et al. 2017, [4]Newbold et al. 2016, [5]Hoover et al. 2017, [6]MacNamara et al. 2018, [7]Pretchel et al. (2018), [8]Williamson and Garvey 2005, [9]Scheler et al. 2012, [10]Hasegawa and Maekawa (2008), [11]Alexander et al. (2015), [12]Calkins et al. 2012, [13]Li et al. 2013, [14]Ochs et al. 2019, [15]Junk et al. 1989, [16]Coulter et al. 2017, [17]Whitten et al. 2021, [18]Kolar et al. 2007, [19]Gibson-Reinemer et al. 2017, [20]Lenaerts et al. 2021, [21]Hicks et al. 2012, [22]Akimova et al. 2016, [23]Neves et al. 2019, [24]Duan et al. 2009, [25]Song et al. (2018), [26]Parkos III et al. 2021

Table 6. Carp visually confirmed (i.e., observed jumping or jumped in boat) from May 2021 through December 2022 within a site but not collected during fish sampling on the Red River and its tributaries. The observations indicate the state, date, location, habitat, and species observed (SC =Silver Carp, BC=Bighead Carp).

River	State	Date	Latitude	Longitude	Species
Muddy Boggy	OK	7/2/2021	33.94339	-95.60174	SC
Muddy Boggy	OK	7/27/2021	33.93557	-95.63493	SC
Muddy Boggy	OK	7/28/2021	33.92844	-95.65096	SC
Red River	OK	7/29/2021	33.65393	-94.56868	SC/ BC
Pine Creek	TX	8/3/2021	33.86477	-95.30788	BC
Red River	AR	8/31/2021	33.39703	-93.71171	SC
Red River	AR	10/8/2021	33.39703	-93.71171	SC
Red River	AR	4/1/2022	33.39703	-93.71171	SC
Red River	AR	4/5/2022	33.5515	-94.39453	SC
Red River	OK	4/19/2022	33.88111	-95.50545	SC
Red River	OK	4/21/2022	33.95053	-95.24028	SC
Red River	AR	4/26/2022	33.57537	-94.08128	SC
Red River	AR	5/6/2022	33.5515	-94.39453	SC
Buzzard Creek	OK	5/9/2022	33.90033	-95.05406	SC
Red River	AR	5/12/2022	33.13784	-93.82909	SC
Garland Creek	OK	5/16/2022	33.92473	-95.08337	SC
Muddy Boggy	OK	5/31/2022	33.92844	-95.65096	SC
Red River	AR	6/7/2022	33.57537	-94.08128	SC
Red River	AR	6/8/2022	33.60915	-93.8242	SC
Red River	AR	6/13/2022	33.13784	-93.82909	BC
Pine Creek	TX	6/14/2022	33.86477	-95.30788	SC
Red River	AR	6/15/2022	33.5998	-94.44686	SC
Red River	AR	6/17/2022	33.34793	-93.71021	SC/ BC
Choctaw	TX	6/22/2022	33.72223	-96.41024	SC
Red River	AR	7/15/2022	33.55708	-94.04868	SC
Red River	AR	7/20/2022	33.34793	-93.71021	SC
Muddy Boggy	OK	7/21/2022	33.93833	-95.60911	SC
Red River	AR	7/25/2022	33.60915	-93.8242	SC
Choctaw	TX	8/3/2022	33.71952	-96.3907	SC
Red River	OK	8/4/2022	33.96302	-95.22118	BC
Red River	AR	8/23/2022	33.59898	-93.81232	SC
Red River	OK	8/26/2022	33.96302	-95.22118	BC

Kiamichi	OK	9/9/2022	33.95095	-95.29142	SC
Red River	AR	9/21/2022	33.55718	-94.0195	SC

Table 7. The mean, minimum (Min), maximum (Max), and standard deviation (SD) of detection covariates (water temperature (°C), secchi depth (cm), and electrofishing effort [seconds]) for the entire catchment, mainstem Red River, and tributaries for both 2021 and 2022.

	Year	Covariate	Mean	Min	Max	Sd
Catchment	2021	temperature	26.94	15.40	32.23	4.20
		secchi	37.00	10.00	183.67	25.38
		seconds	1714.66	0.00	3390.00	754.38
	2022	temperature	28.10	16.67	33.17	3.58
		secchi	36.68	8.67	77.00	14.79
		seconds	1949.80	0.00	3304.00	670.13
Red River	2021	temperature	28.67	25.33	32.23	1.80
		secchi	51.96	25.00	183.67	42.14
		seconds	1290.23	0.00	3390.00	1143.97
	2022	temperature	26.40	15.40	31.77	4.58
		secchi	32.29	10.00	75.00	14.35
		seconds	1848.06	0.00	2833.00	519.08
Tributaries	2021	temperature	28.21	21.07	31.97	2.92
		secchi	39.09	19.87	55.67	10.47
		seconds	2132.90	0.00	3250.00	885.46
	2022	temperature	28.07	16.67	33.17	3.77
		secchi	36.00	8.67	77.00	15.80
		seconds	1897.49	714.00	3304.00	592.33

Table 8. The mean, minimum (Min), maximum (Max), and standard deviation (SD) of occupancy covariates (percent sandstone [Pc.Snd], drainage area (km^2) [DA], disturbance (LDI) [Dist], sinuosity [Sin], slope [Slp], discharge (m^3/s) [Q], percent backwater [Pc.Bck] width-to-depth ratio [W:D], salinity (µS) [Sal], distance to dam (km) [Dtd], and chlorophyll-a (µg/L) [Chla],) for the mainstem Red River, and tributaries.

	Covariate	Mean	Min	Max	SD
Red River	Pc.Snd	18.87	17.60	19.35	0.43
	DA	120972.26	100012.78	133739.85	7983.32
	Dist	1.95	1.91	2.00	0.02
	Sin	1.79	1.22	2.52	0.36
	Slp	0.00030	0.00020	0.00056	0.00007
	Q	287.08	69.94	764.55	207.82
	Pc.Bck	22.04	0.00	100.00	40.57
	W:D	119.34	40.05	278.78	59.86
	Sal	914.09	289.00	1470.56	309.20
	Dtd	123.29	1.16	277.81	69.38
	Chla	32.97	10.87	74.35	11.34
Tributaries	Pc.Snd	17.95	0.00	41.52	15.76
	DA	2818.05	27.08	6273.98	2526.46
	Dist	1.87	1.40	2.53	0.37
	Sin	1.76	1.34	2.07	0.28
	Slp	0.00066	0.00026	0.00108	0.00026
	Q	2.35	0.03	13.42	3.73
	Pc.Bck	0.88	0.00	13.07	3.00
	W:D	28.20	9.76	61.37	13.85
	Sal	674.99	68.40	1410.00	402.83
	Dtd	82.15	1.58	177.91	59.77
	Chla	35.85	12.62	116.60	25.61

Table 9. The mean, minimum (Min), maximum (Max), and standard deviation (SD) of occupancy covariates (percent sandstone [Pc.Snd], drainage area (km^2) [DA], disturbance (LDI) [Dist], sinuosity [Sin], slope [Slp], discharge (m^3/s) [Q], percent backwater [Pc.Bck] width-to-depth [W:D], salinity (µS) [Sal], distance to dam (km) [Dtd], and chlorophyll-a (µg/L) [Chla],) for the mainstem Red River, and tributaries for both 2021 and 2022.

	Year	Covariate	Mean	Min	Max	SD
Red River	2021	Q	415.36	181.51	764.55	200.67
		Pc.Bck	29.44	0.00	100.00	45.49
		W:D	108.35	40.05	223.83	51.89
		Sal	1054.82	719.00	1360.67	229.59
		Dtd	117.50	1.16	277.81	76.52
		Chla	31.32	10.87	46.43	10.91
	2022	Q	133.15	69.94	220.87	57.77
		Pc.Bck	17.72	0.00	100.00	37.23
		W:D	125.76	49.46	278.78	63.70
		Sal	831.99	289.00	1470.56	321.87
		Dtd	126.66	28.75	243.98	65.47
		Chla	33.94	20.42	74.35	11.59
Tributaries	2021	Q	2.52	0.03	13.42	4.50
		Pc.Bck	1.63	0.00	13.07	4.46
		W:D	26.11	12.60	61.37	14.51
		Sal	684.57	70.25	1253.33	390.72
		Dtd	95.52	1.58	177.91	63.57
		Chla	42.02	12.62	116.60	34.11
	2022	Q	2.18	0.03	8.30	3.08
		Pc.Bck	0.37	0.00	4.49	1.27
		W:D	29.59	9.76	53.83	13.52
		Sal	668.61	68.40	1410.00	418.91
		Dtd	73.23	1.58	177.91	56.70
		Chla	31.74	12.62	79.06	17.58

Table 10. Occupancy model covariate combinations (width-to-depth ratio [W:D], sinuosity [Sin], backwater [Bck], chlorophyll-*a* [Chla], salinity [Sal], discharge [Q], and distance to dam [Dtd]) hypothesized to be related to carp presence with the corresponding WAIC and ΔWAIC scores.

Model	WAIC	ΔWAIC
W:D + Sin	249.53	0
Bck	249.73	0.2
Bck + W:D + Sin	250.02	0.49
Bck + W:D	251.04	1.51
Bck + W:D + Chla	251.29	1.76
Bck + Sin	252.91	3.38
Bck + W:D + Sin + Chla	253.68	4.15
W:D	253.81	4.28
Sal	253.92	4.39
Q	254.26	4.73
W:D + Chla	255.03	5.5
Bck + Sin + Chla	255.16	5.63
Chla	255.27	5.74
Sin + Chla	255.71	6.18
Bck + Q	257.14	7.61
Bck + Sal	257.22	7.69
Bck + Chla	257.38	7.85
Q + Sin	258.2	8.67
Sin + Chla	258.39	8.86
Bck + Dtd	258.61	9.08
Bck + Q + W:D	260.02	10.49
Dtd	260.57	11.04
Bck + Q + Sin	260.99	11.46
Q + W:D	261.94	12.41
Bck + Q + Dtd	263.24	13.71
Q + Dtd	263.53	14
Sal + Dtd	265.59	16.06
Bck + Q + W:D + Chla	266.03	16.5
Bck + Sal + Dtd	266.71	17.18
Sal + Dtd + Q	267.02	17.49
Q + Sal	267.27	17.74
Q + Chla	269.1	19.57

Bck + Q + W:D + Sin	270.06	20.53
Bck + Q + Sal + Dtd	272.67	23.14
Bck + Q + Chla	273.31	23.78
Bck + Q + Sal	276.74	27.21
Q + W:D + Sin + Chla	277.31	27.78
Bck + Q + W:D + Sin + Chla	295.63	46.1

Table 11. The mode, 90% highest density interval (HDI), standard error (SE), and Rhat values for occupancy covariates (backwater [Bck], width-to-depth [W:D], chlorophyll-*a* [Chla], and sinuosity [Sin]) for the top ranked occupancy models for Bighead Carp and Silver Carp in the lower Red River catchment.

Species	Model	Covariate	Mode	SE	90% HDI	Rhat
Bighead Carp	Bck	Bck	2.348	0.08	(0.04, 7.43)	1.004
	Bck + W:D	Bck	1.193	0.07	(-0.73, 3.21)	1
	Bck + W:D + Chla	Bck	1.203	0.07	(-0.90, 3.42)	1.001
	Bck + W:D + Sin	Bck	2.619	0.08	(-0.15, 6.72)	0.999
	Bck + W:D + Chla	Chla	0.004	0.09	(-1.37, 1.16)	1
	Bck + W:D + Sin	Sin	-1.748	0.06	(-3.28, -0.50)	0.999
	W.D + Sin	Sin	-1.218	0.06	(-2.15, -0.32)	1
	Bck + W:D	W:D	-1.638	0.08	(-3.06, -0.42)	1.001
	Bck + W:D + Chla	W:D	-1.784	0.08	(-3.39, -0.46)	1.001
	Bck + W:D + Sin	W:D	-2.217	0.10	(-4.12, -0.69)	0.999
	W.D + Sin	W:D	-2.051	0.10	(-3.77, -0.68)	1
Silver Carp	Bck	Bck	2.311	0.08	(-0.33, 7.67)	1.003
	Bck + W:D	Bck	1.159	0.07	(-1.01, 3.70)	1
	Bck + W:D + Chla	Bck	1.177	0.07	(-1.24, 3.90)	1.001
	Bck + W:D + Sin	Bck	2.42	0.08	(-0.37, 6.95)	0.999
	Bck + W:D + Chla	Chla	0.621	0.09	(-0.66, 2.00)	1
	Bck + W:D + Sin	Sin	-1.575	0.06	(-3.16, -0.30)	0.999
	W.D + Sin	Sin	-1.176	0.06	(-2.24, -0.25)	1
	Bck + W:D	W:D	-1.177	0.08	(-2.46, -0.02)	1
	Bck + W:D + Chla	W:D	-1.284	0.08	(-2.67, -0.02)	1
	Bck + W:D + Sin	W:D	-1.436	0.10	(-3.05, 0.12)	0.999
	W:D + Sin	W:D	-1.323	0.10	(-2.64, -0.02)	1

Table 12. The mode, 90% highest density interval (HDI), standard error (SE), and Rhat values for detection covariates (discharge [Q], electrofishing effort [Sec], secchi depth [Secchi], and water temperature [Temp]) for the top ranked models (backwater [Bck], width-to-depth ratio [W:D], Chlorophyll-*a* [Chla], and sinuosity [Sin]) for Bighead Carp and Silver Carp in the lower Red River catchment.

Species	Model	Covariate	Mode	SE	90% HDI	Rhat
Bighead Carp	Bck	Q	-0.418	0.03	(-0.83, -0.04)	1
	Bck + W:D	Q	-0.462	0.03	(-0.88, -0.06)	1
	Bck + W:D + Chla	Q	-0.465	0.03	(-0.89, -0.07)	1
	Bck + W:D + Sin	Q	-0.437	0.03	(-0.84, -0.05)	1
	W:D + Sin	Q	-0.48	0.03	(-0.90, -0.07)	1
	Bck	Sec	0.69	0.03	(0.24, 1.14)	1
	Bck + W:D	Sec	0.599	0.03	(0.13, 1.05)	1
	Bck + W:D + Chla	Sec	0.597	0.03	(0.14, 1.06)	1
	Bck + W:D + Sin	Sec	0.667	0.03	(0.22, 1.13)	1
	W:D + Sin	Sec	0.584	0.03	(0.10, 1.03)	1
	Bck	Secchi	-0.393	0.04	(-0.90, 0.13)	1.001
	Bck + W:D	Secchi	-0.403	0.04	(-0.90, 0.11)	1
	Bck + W:D + Chla	Secchi	-0.399	0.04	(-0.87, 0.12)	1
	Bck + W:D + Sin	Secchi	-0.457	0.04	(-0.94, 0.04)	1
	W:D + Sin	Secchi	-0.482	0.04	(-0.98, 0.01)	1
	Bck	Temp	0.818	0.04	(0.28, 1.41)	1
	Bck + W:D	Temp	0.736	0.03	(0.22, 1.31)	1
	Bck + W:D + Chla	Temp	0.725	0.03	(0.21, 1.29)	1.001
	Bck + W:D + Sin	Temp	0.836	0.04	(0.31, 1.43)	1
	W:D + Sin	Temp	0.749	0.03	(0.23, 1.33)	1
Silver Carp	Bck	Q	-0.39	0.03	(-0.74, -0.03)	1
	Bck + W:D	Q	-0.418	0.03	(-0.79, -0.04)	1
	Bck + W:D + Chla	Q	-0.41	0.03	(-0.78, -0.04)	1
	Bck + W:D + Sin	Q	-0.408	0.03	(-0.78, -0.05)	1
	W:D + Sin	Q	-0.421	0.03	(-0.81, -0.04)	1
	Bck	Sec	0.795	0.03	(0.41, 1.21)	1
	Bck + W:D	Sec	0.736	0.03	(0.33, 1.16)	1

Bck + W:D + Chla	Sec	0.744	0.03	(0.33, 1.16)	1
Bck + W:D + Sin	Sec	0.764	0.03	(0.38, 1.18)	1
W:D + Sin	Sec	0.743	0.03	(0.34, 1.16)	1
Bck	Secchi	-0.731	0.04	(-1.17, -0.31)	1
Bck + W:D	Secchi	-0.722	0.04	(-1.17, -0.31)	1
Bck + W:D + Chla	Secchi	-0.704	0.04	(-1.14, -0.28)	0.999
Bck + W:D + Sin	Secchi	-0.752	0.04	(-1.19, -0.33)	1
W:D + Sin	Secchi	-0.777	0.04	(-1.22, -0.36)	1
Bck	Temp	0.525	0.04	(0.13, 0.93)	1
Bck + W:D	Temp	0.534	0.03	(0.14, 0.94)	1
Bck + W:D + Chla	Temp	0.522	0.03	(0.12, 0.92)	1
Bck + W:D + Sin	Temp	0.535	0.04	(0.13, 0.95)	1.001
W:D + Sin	Temp	0.527	0.03	(0.12, 0.93)	1

Table 13. Occupancy and detection estimates and corresponding 90% highest density intervals (HDI) for the top ranked models (backwater [Bck], width-to-depth ratio [W:D], chlorophyll-a [Chla], and sinuosity [Sin]) for Silver Carp (SVC) and Bighead Carp (BHC).

	Model	Occupancy	90% HDI	Detection	90% HDI
Silver Carp	Bck	0.83	(0.51, 0.97)	0.6	(0.50, 0.70)
	Bck + W:D	0.78	(0.33, 0.96)	0.61	(0.51, 0.71)
	Bck + W:D + Chla	0.79	(0.32, 0.97)	0.61	(0.50, 0.71)
	Bck + W:D + Sin	0.8	(0.27, 0.98)	0.61	(0.51, 0.71)
	W:D + Sin	0.85	(0.43, 0.97)	0.63	(0.53, 0.72)
Bighead Carp	Bck	0.78	(0.39, 0.96)	0.39	(0.25, 0.54)
	Bck + W:D	0.61	(0.23, 0.91)	0.4	(0.27, 0.55)
	Bck + W:D + Chla	0.65	(0.23, 0.94)	0.4	(0.27, 0.54)
	Bck + W:D + Sin	0.53	(0.15, 0.91)	0.39	(0.27, 0.53)
	W.D + Sin	0.68	(0.29, 0.92)	0.4	(0.28, 0.55)

Table 14. Model combinations for evaluating the relationship between Silver Carp and Bighead Carp growth and environmental factors. Model combinations for Weisberg models: model intercept [B0], fish age [A], CV of discharge [CV.Q], CV of air temperature [CV.T], discharge [Q], and air temperature [T]. Random effects (i.e., fish and year) were included in all models.

Models
~ B0 + A
~ B0 + A + CV.Q
~ B0 + A + CV.T
~ B0 + A + Q
~ B0 + A + Q + CV.Q
~ B0 + A + Q + CV.T
~ B0 + A + Q + CV.T + CV.Q
~ B0 + A + Q + T
~ B0 + A + T
~ B0 + A + T + CV.Q
~ B0 + A + T + CV.T
~ B0 + A + T + CV.T + CV.Q
~ B0 + A + T + Q
~ B0 + A + T + Q + CV.Q
~ B0 + A + T + Q + CV.T
~ B0 + A + T + Q + CV.T + CV.Q

Table 15. Mean back-calculated length-at-age (mm) for Silver Carp and Bighead Carp collected from May 2021 through October 2022 in the lower Red River catchment.

Age	Silver Carp	Bighead Carp
1	275	272
2	465	438
3	603	569
4	694	674
5	740	746
6	759	808
7	797	862
8	833	922
9	868	963
10	891	995
11	899	1019
12	914	1040
13	917	1059
14	905	1108
15	-	1151
16	-	1216
17	-	1299

Table 16. Summary statistics (mean, minimum [Min], maximum [Max], and standard deviation [SD]) of the environmental conditions (75th percentile of discharge (m^3/s), 75th percentile of air temperature (°C), the coefficient of variation of discharge, and the coefficient of variation of air temperature) for the lower Red River catchment near Index, Arkansas from 2007 through 2021 during the hypothesized growing season (April through September).

	Mean	Min	Max	SD
75th Discharge	584.78	400.68	1659.37	298.23
75th Air Temp	25.05	24.89	25.58	0.18
CV Discharge	101.05	57.06	164.74	30.86
CV Air Temp	20.04	17.00	23.17	1.86

Table 17. The top ranked models with the corresponding parameter number (k), Akaike information criterion corrected for small sample size (AICc), model difference (ΔAIC), and model weight for models that were averaged for Bighead Carp in the lower Red River catchment. B0 is the model intercept, A is fish age, T is air temperature, and CV.Q is the coefficient of variation of discharge.

Model	K	AICc	ΔAIC	Weight
~ B0 + A + T	6	1324.39	0	0.34
~ B0 + A + T + CV.Q	7	1326.00	1.62	0.15

Table 18. The top ranked models with the corresponding parameter number (k), Akaike information criterion corrected for small sample size (AICc), model difference (ΔAIC), and model weight for models included in the averaged Weisberg model for Silver Carp in the lower Red River catchment. B0 is the model intercept, A is fish age, T is air temperature, Q is discharge, CV.T is the coefficient of variation of air temperature, and CV.Q is the coefficient of variation of discharge.

Model	K	AICc	ΔAIC	Weight
~ B0 + A + T + Q	7	2177.33	0	0.11
~ B0 + A + T + Q + CV.T + CV.Q	9	2177.79	0.46	0.08
~ B0 + A + T	6	2177.81	0.49	0.08
~ B0 + A + T + Q + CV.Q	8	2177.86	0.53	0.08
~ B0 + A + Q + CV.T + CV.Q	8	2177.88	0.55	0.08
~ B0 + A + T + CV.Q	7	2177.95	0.63	0.08
~ B0 + A + Q	6	2178.26	0.93	0.07
~ B0 + A + T + Q + CV.T	8	2178.42	1.09	0.06
~ B0 + A	5	2178.59	1.26	0.06
~ B0 + A+ Q + CV.T	7	2178.62	1.29	0.06
~ B0 + A + CV.Q	6	2178.88	1.55	0.05
~ B0 + A + Q + CV.Q	7	2178.92	1.59	0.05
~ B0 + A + T + CV.T + CV.Q	8	2179.12	1.79	0.04

Table 19. Averaged model estimates for evaluating the relationship between Silver Carp and Bighead Carp growth and environmental factors. The final average Weisberg model estimates with the corresponding standard error (SE), p-value (Pr(>|z|)), and 90% confidence intervals (90% C.I.) for Bighead Carp and Silver Carp in the lower Red River catchment.

		Estimate	SE	Pr(>|z|)	90% C.I.
Bighead Carp	Age	-0.28	0.01	0.00	(-0.49, -0.26)
	Air temperature	0.19	0.07	0.00	(0.08, 0.30)
	CV of discharge	-0.01	0.03	0.74	(-0.06, 0.04)
Silver Carp	Age	-0.37	0.01	0.00	(-0.39, -0.35)
	Discharge	0.15	0.16	0.34	(-0.10, 0.40)
	Air temperature	0.13	0.14	0.36	(-0.01, 0.37)
	CV of temperature	0.05	0.08	0.59	(-0.09, 0.19)
	CV of discharge	-0.05	0.07	0.44	(-0.16, 0.06)

FIGURES

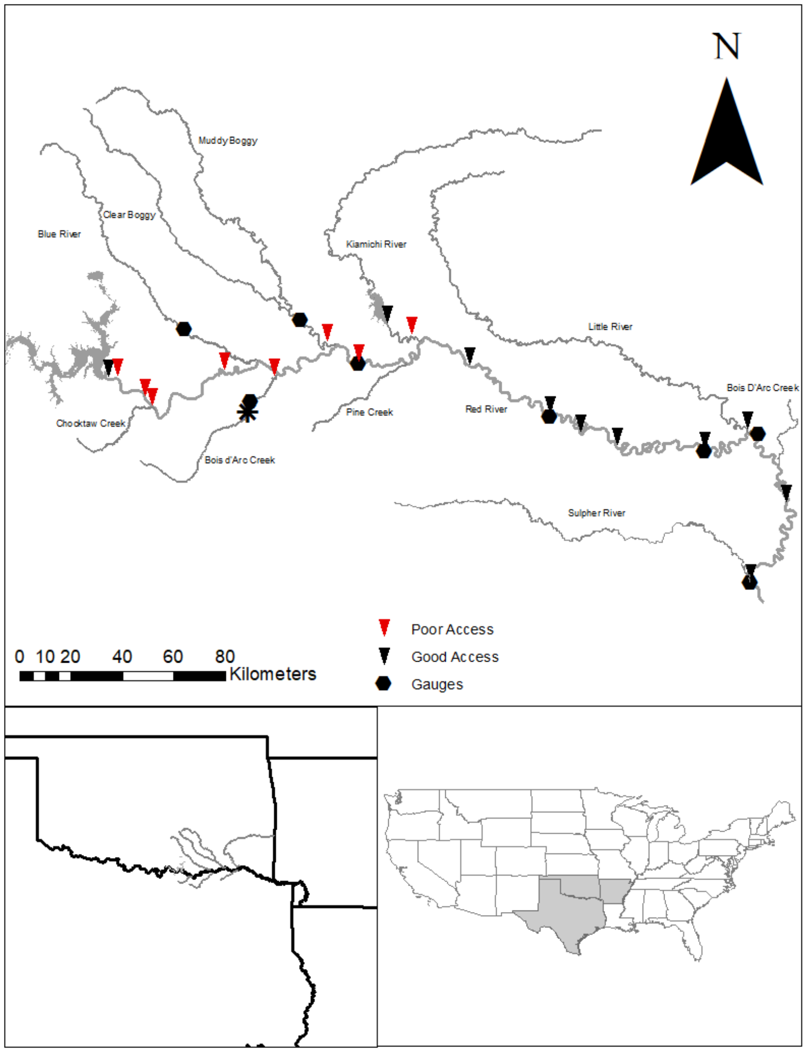

Figure 1. The lower Red River from Lake Texoma, OK to the Arkansas-Louisiana border. In the upper panel, the gray lines indicate rivers whereas the gray polygons are reservoirs. The black hexagons are U.S. Geological Survey stream gages, and the triangles reference boat access locations. The black triangles are access points that are available all year, and the red triangles are access points that are limited to higher-discharge periods.

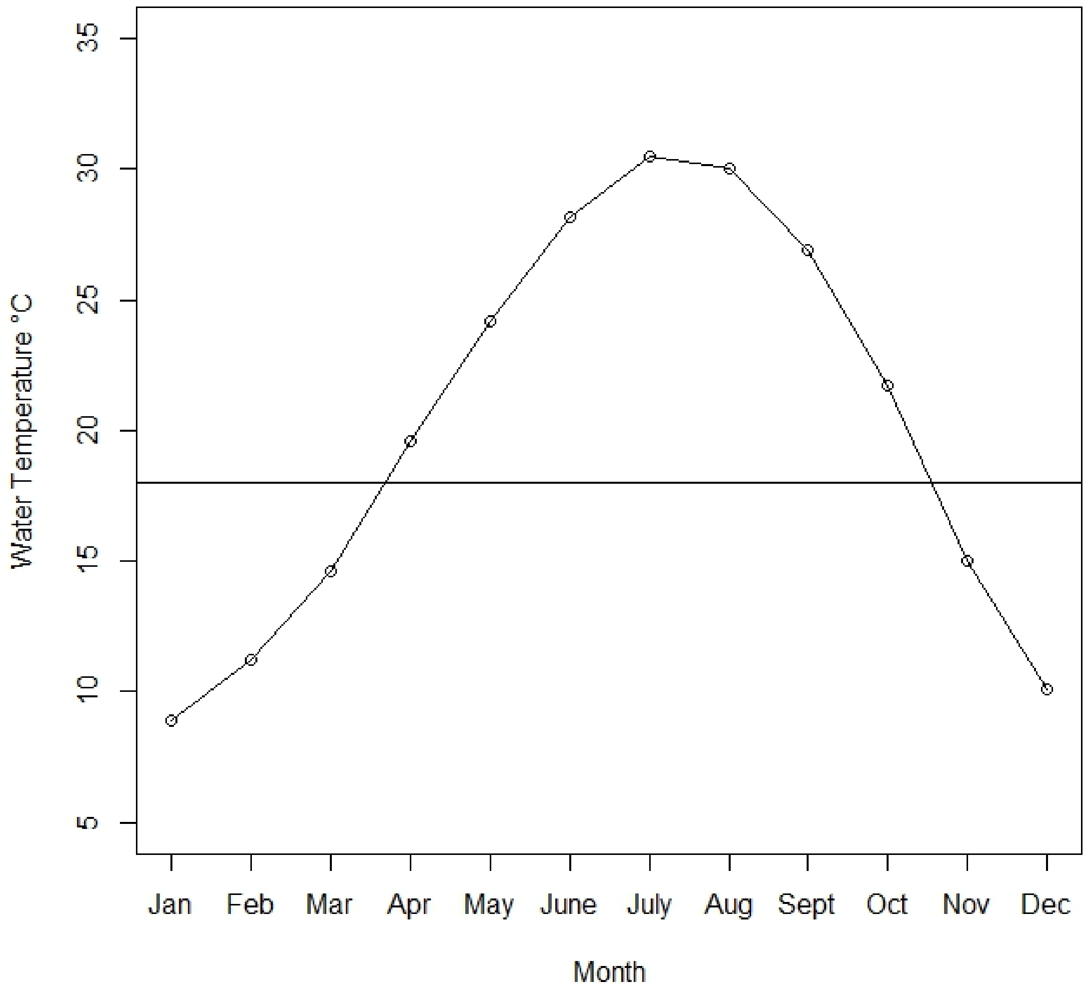

Figure 2. The mean monthly water temperature (°C) for the lower Red River (1997 to 2021) from the U.S. Geological Survey stream gage located near Index (07337000). The horizontal line indicates 18 °C, which is hypothesized to be required for carp spawning (Cooke et al. 2012; Nico et al. 2022a).

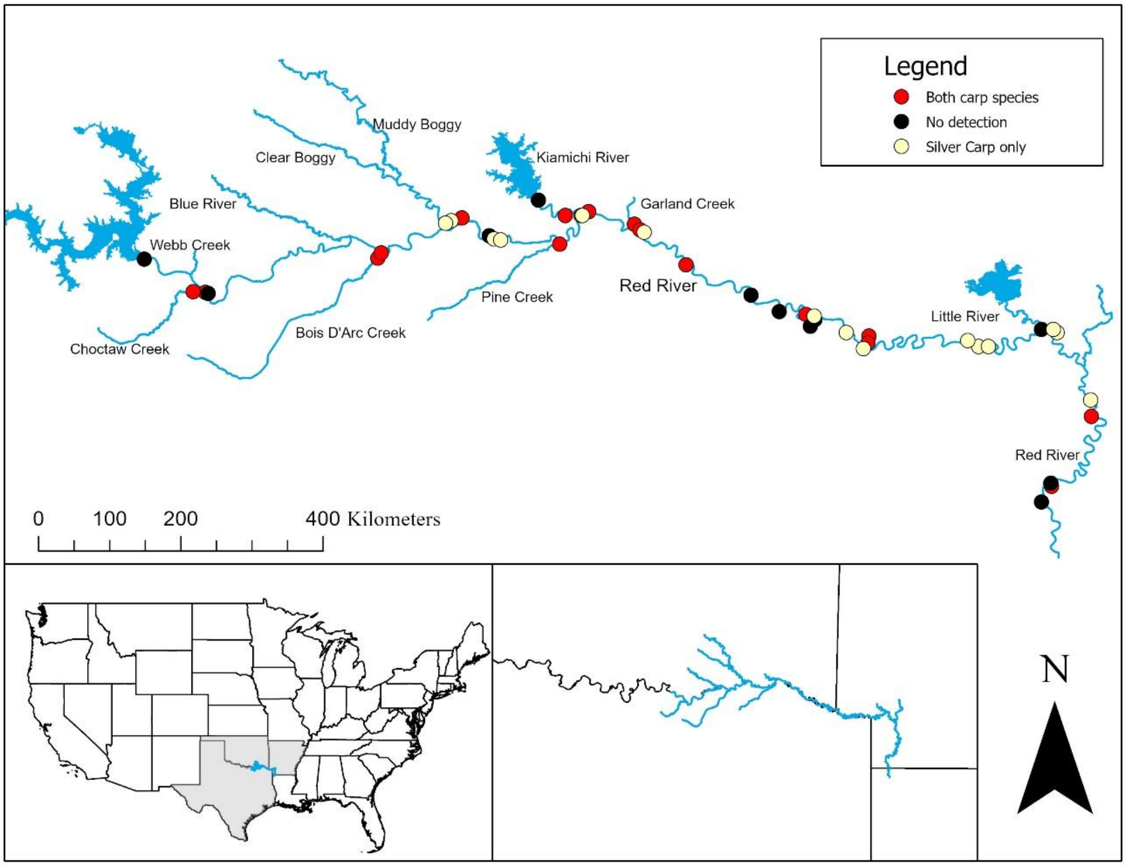

Figure 3. A map of all sites sampled in the lower Red River catchment from May 2021 through September 2022 where no carp were detected (black circle), only Silver Carp was detected (yellow circle), or both carp species were detected (red circle).

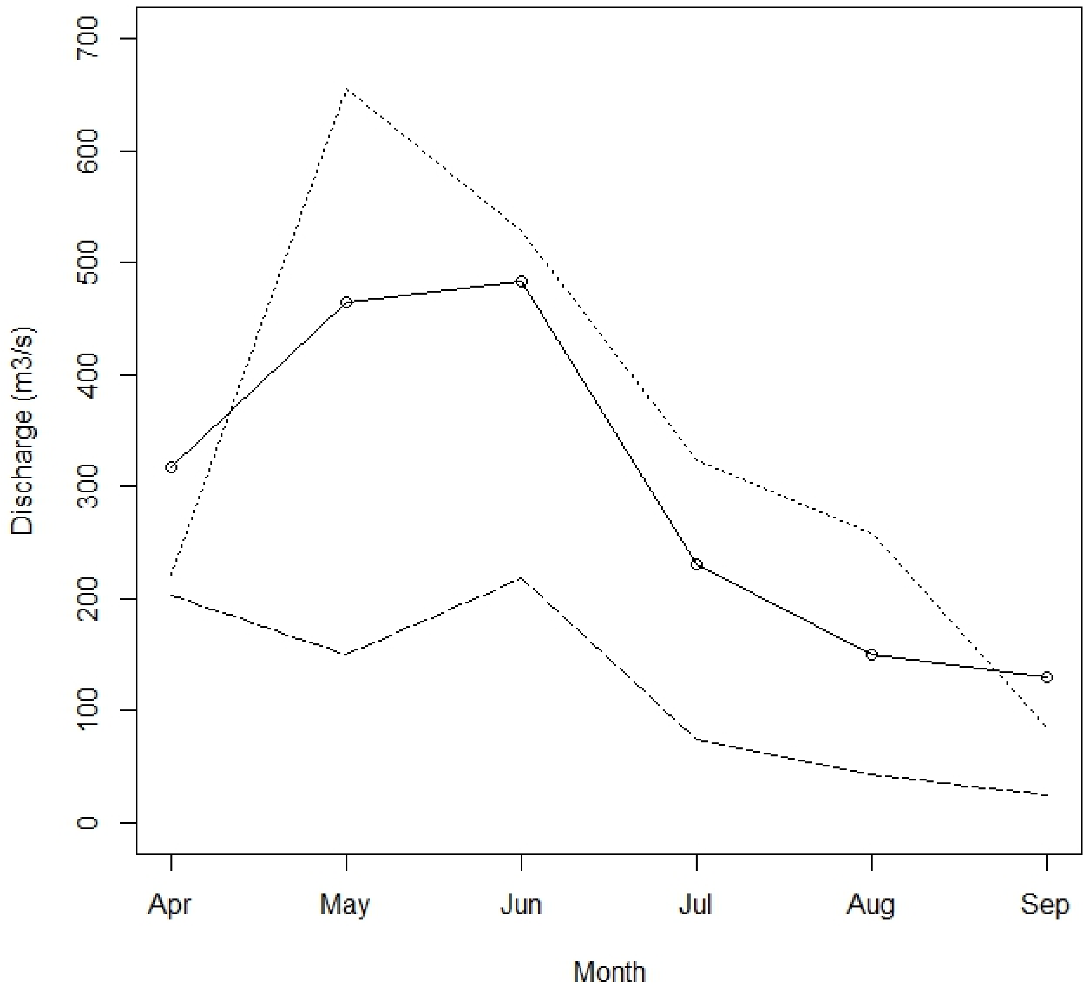

Figure 4. The average monthly discharge (m^3/s) for the 30-year average (solid line with hallow circles), 2021(dotted line), and 2022 (dashed line) for the lower Red River at the Arthur City, TX USGS stream gage.

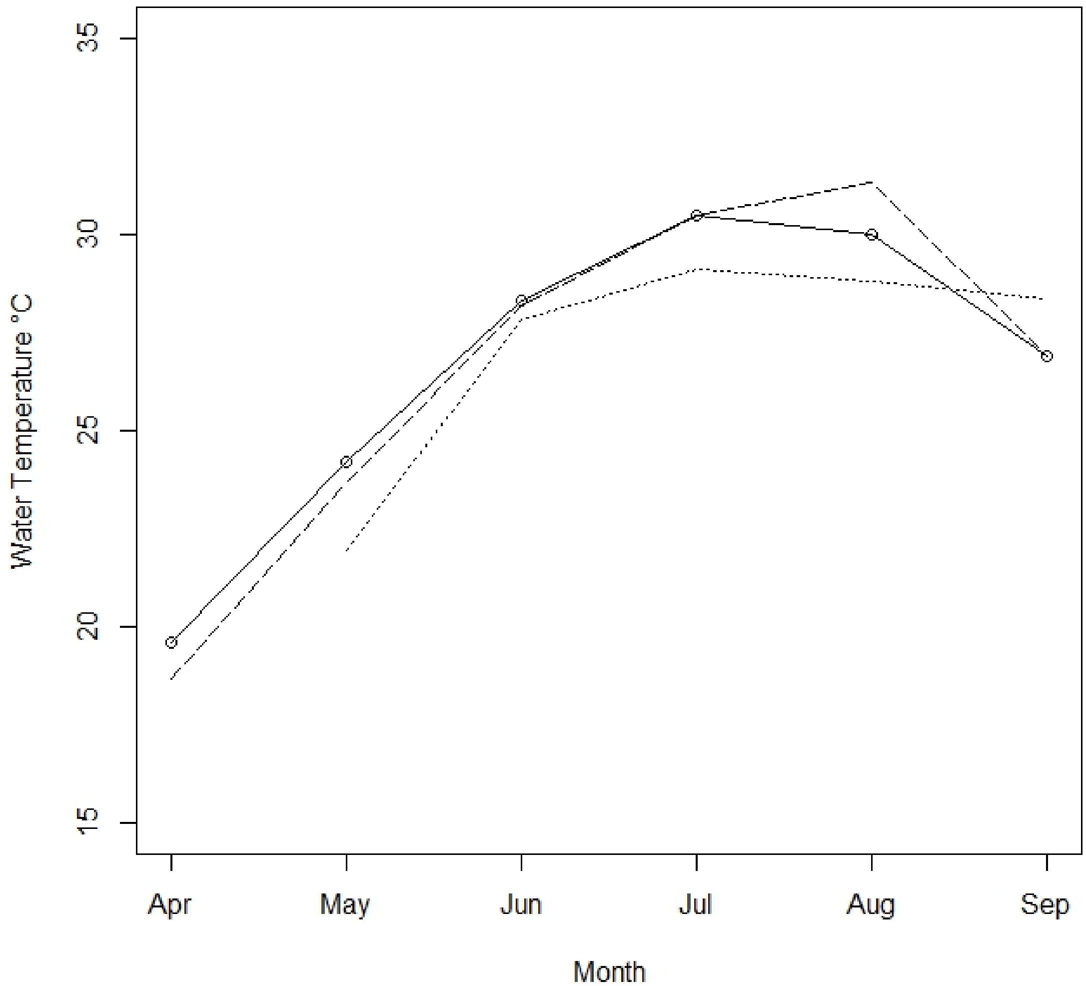

Figure 5. The average monthly water temperature (°C) for the 30-year average (solid line with hallow circles), 2021(dotted line), and 2022 (dashed line) for the lower Red River.

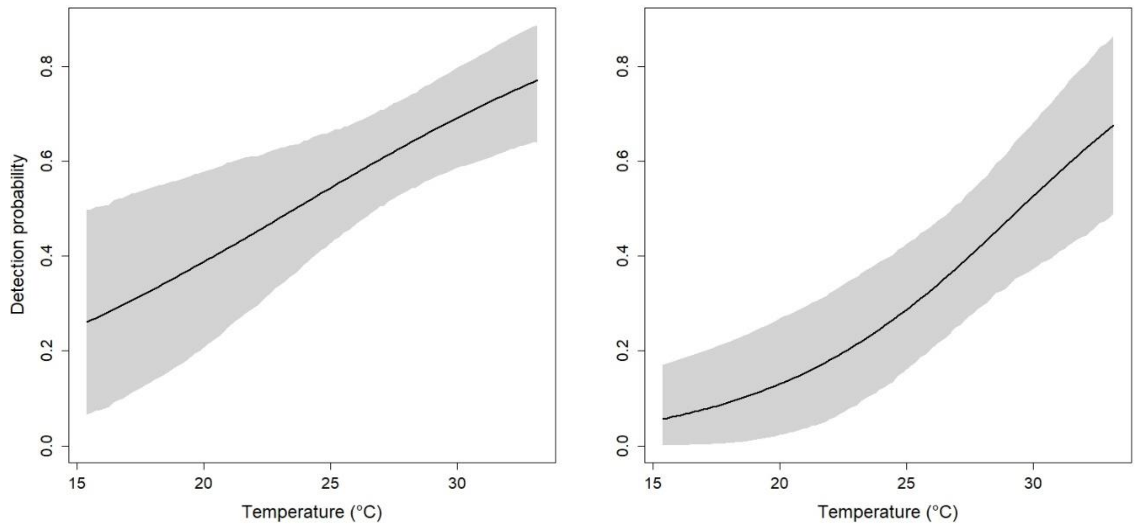

Figure 6. Silver Carp (left) and Bighead Carp (right) detection probability related to water temperature (°C) in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

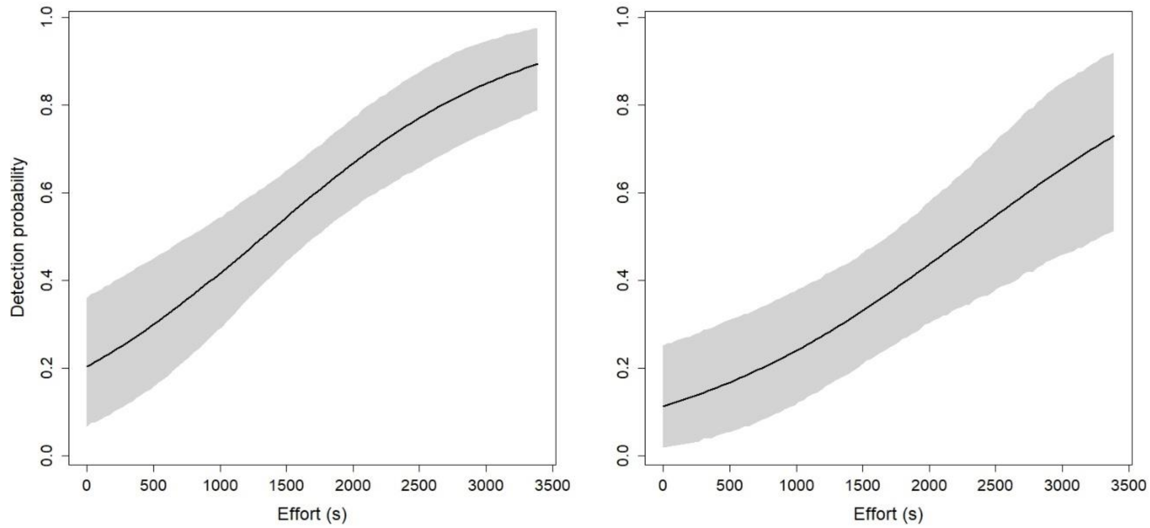

Figure 7. Silver Carp (left) and Bighead Carp (right) detection probability related to electrofishing effort (s) in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

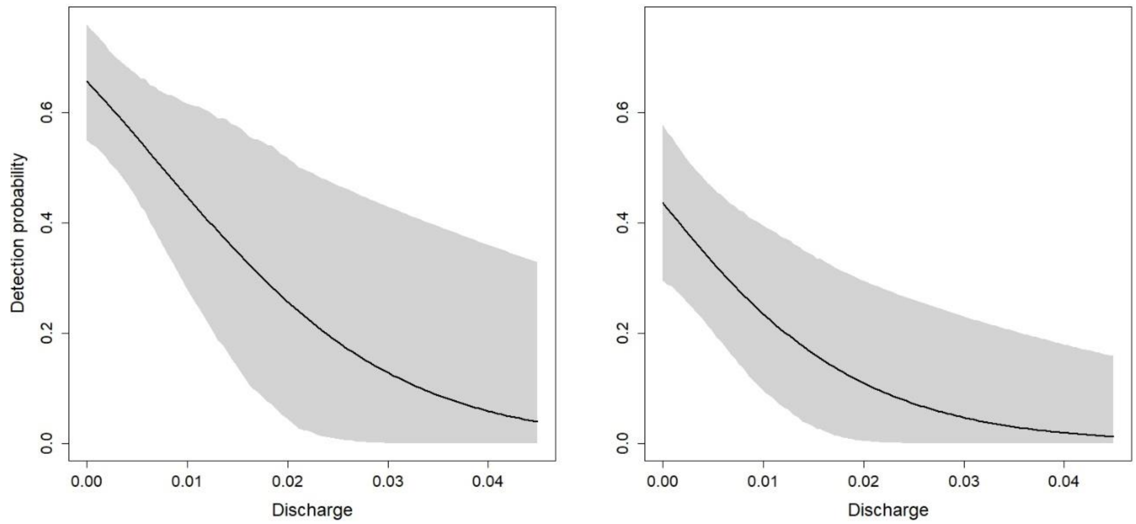

Figure 8. Silver Carp (left) and Bighead Carp (right) detection probability related to discharge in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

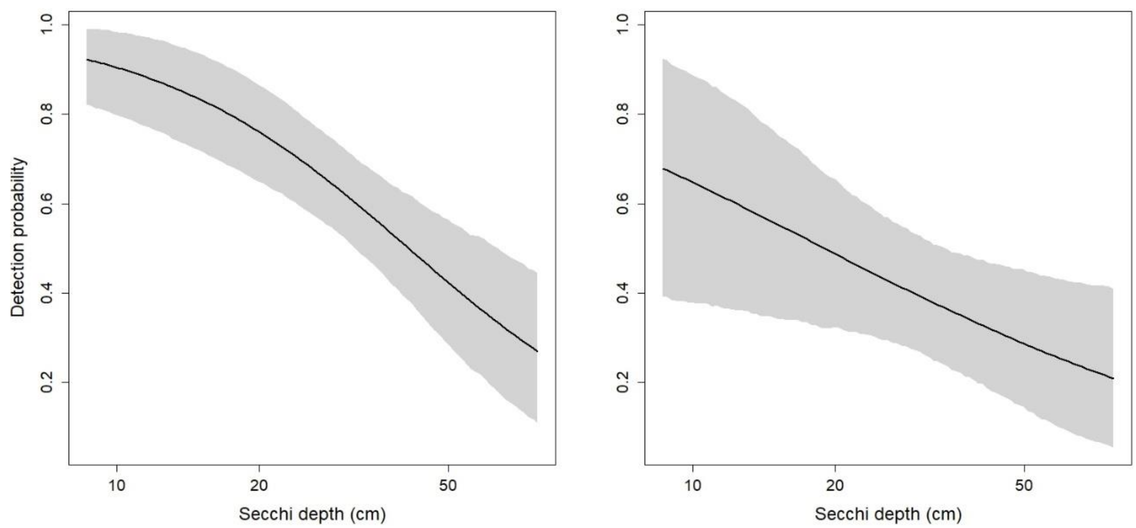

Figure 9. Silver Carp (left) and Bighead Carp (right) detection probability related to Secchi depth (cm) in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

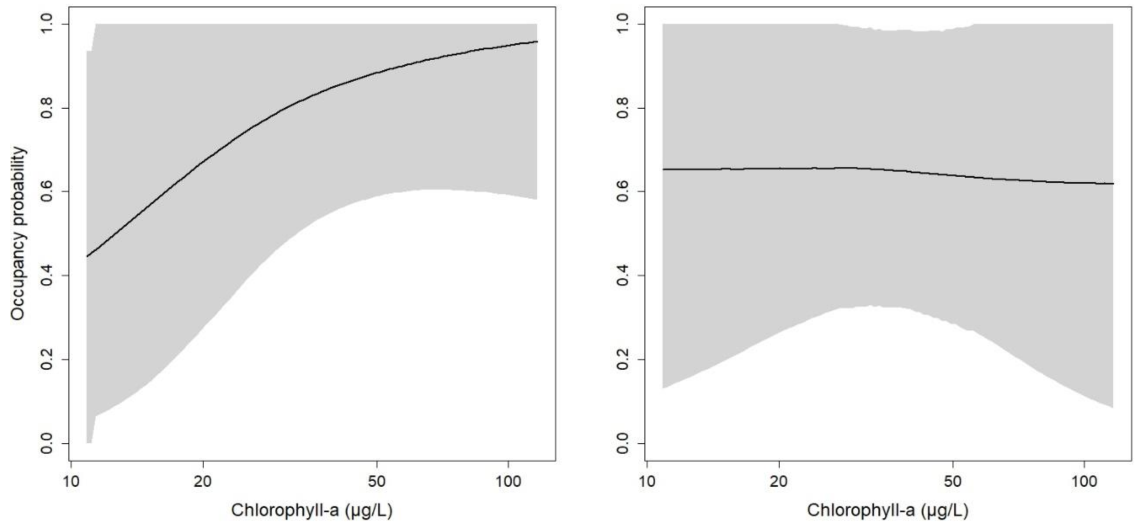

Figure 10. Silver Carp (left) and Bighead Carp (right) occupancy probability related to chlorophyll-*a* in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

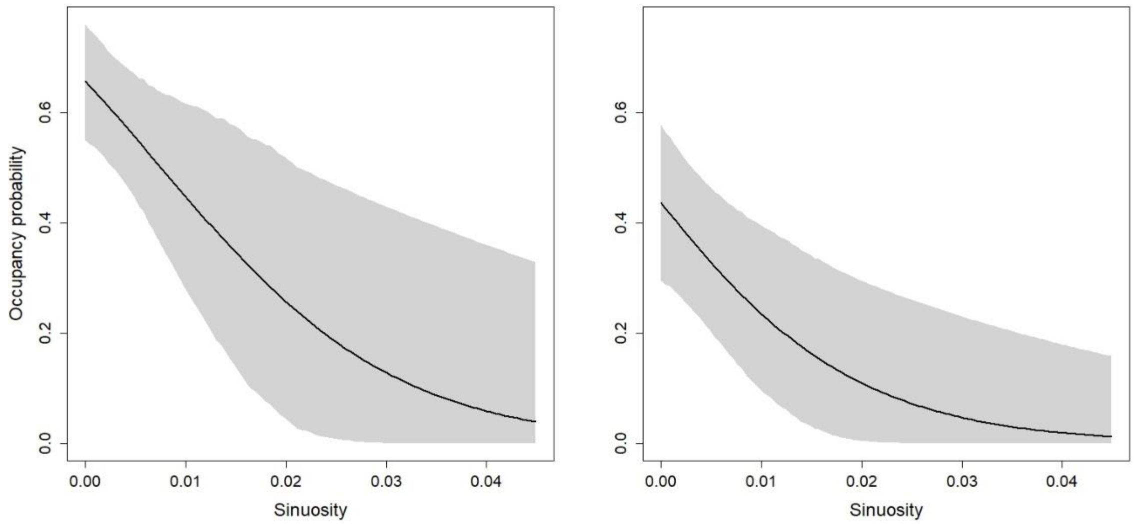

Figure 11. Silver Carp (left) and Bighead Carp (right) occupancy probability related to sinuosity in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

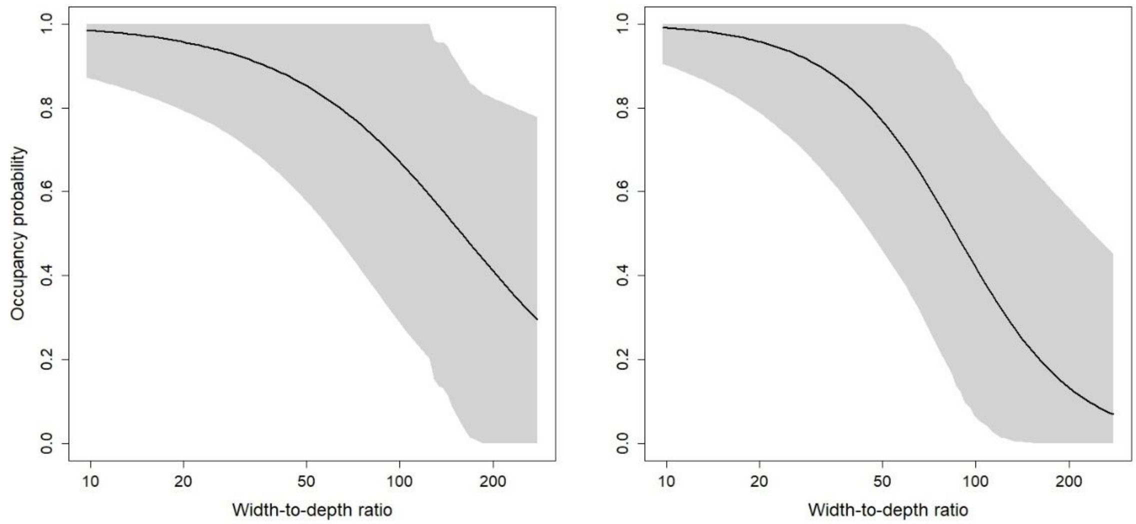

Figure 12. Silver Carp (left) and Bighead Carp (right) occupancy probability related to with-to-depth ratio in the lower Red River catchment. The solid line is the mode estimate, and the gray polygon is the 90% highest density interval (HDI). The mode was estimated with all other model covariates held at mean values.

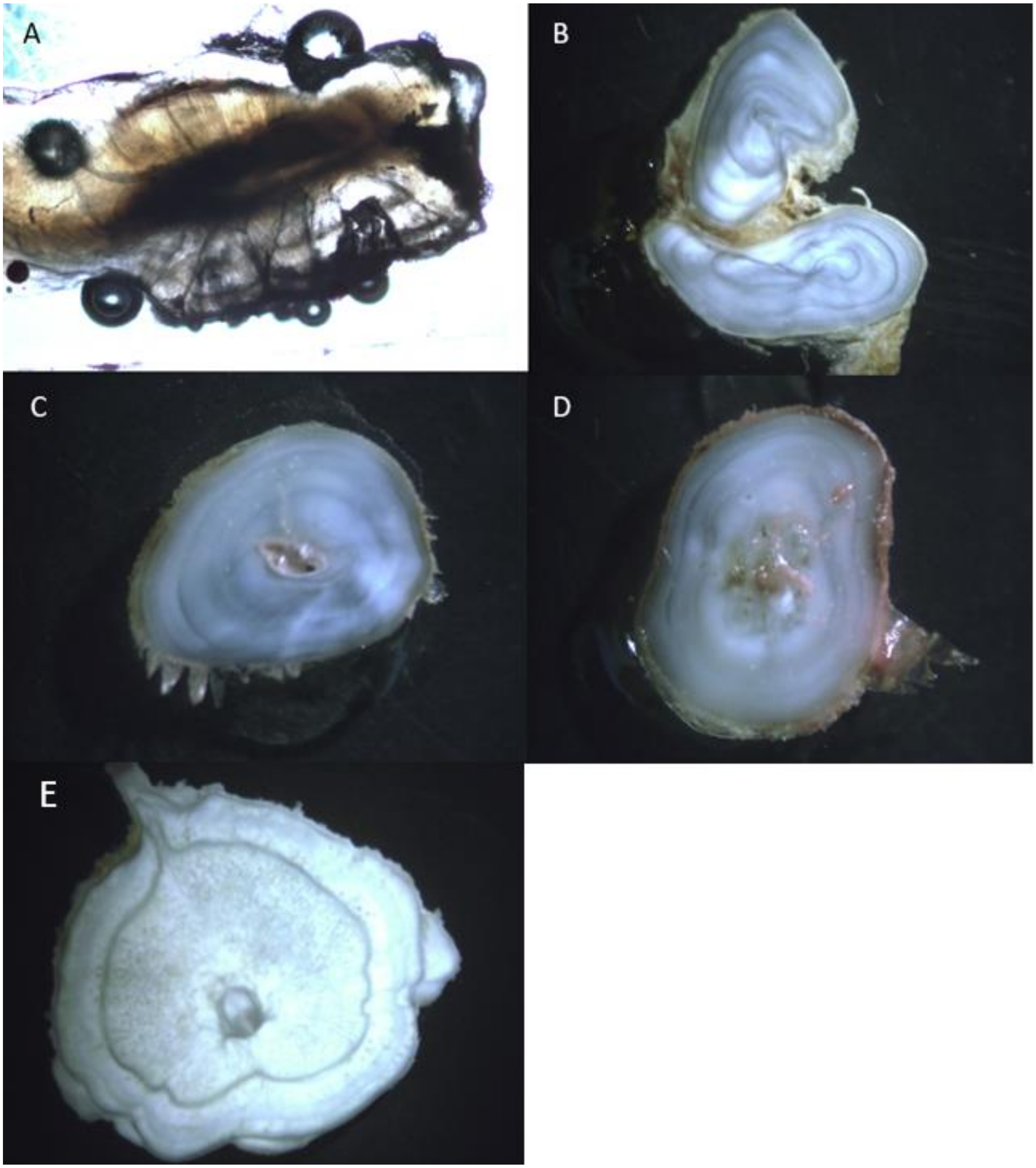

Figure 13. Sectioned ageing structures (lapilli otolith [A], fin-ray [B], post-cleithra [C], urohyal [D], and pterygiophore [E]) from a Silver Carp captured in the lower Red River catchment during the summer of 2021.

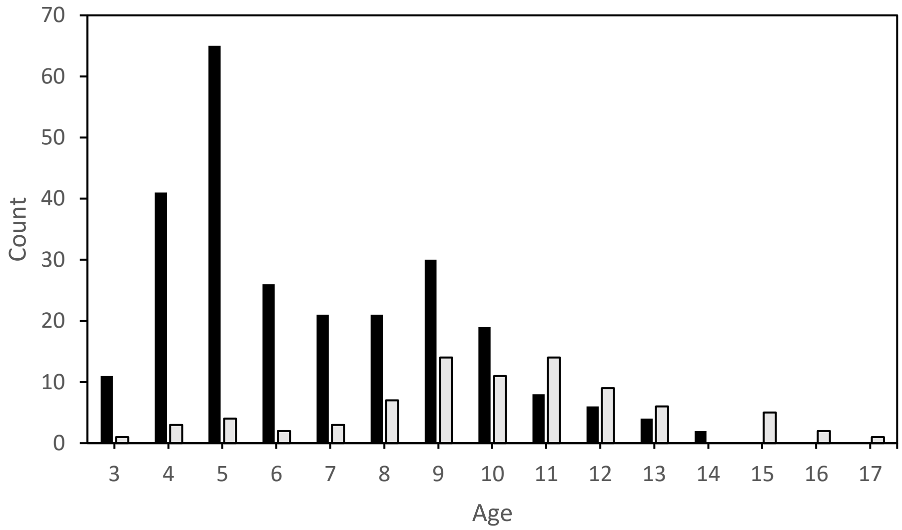

Figure 14. Age frequency histogram for Silver Carp (black bars) and Bighead Carp (grey bars) sampled from the lower Red River catchment from 2021 and 2022.

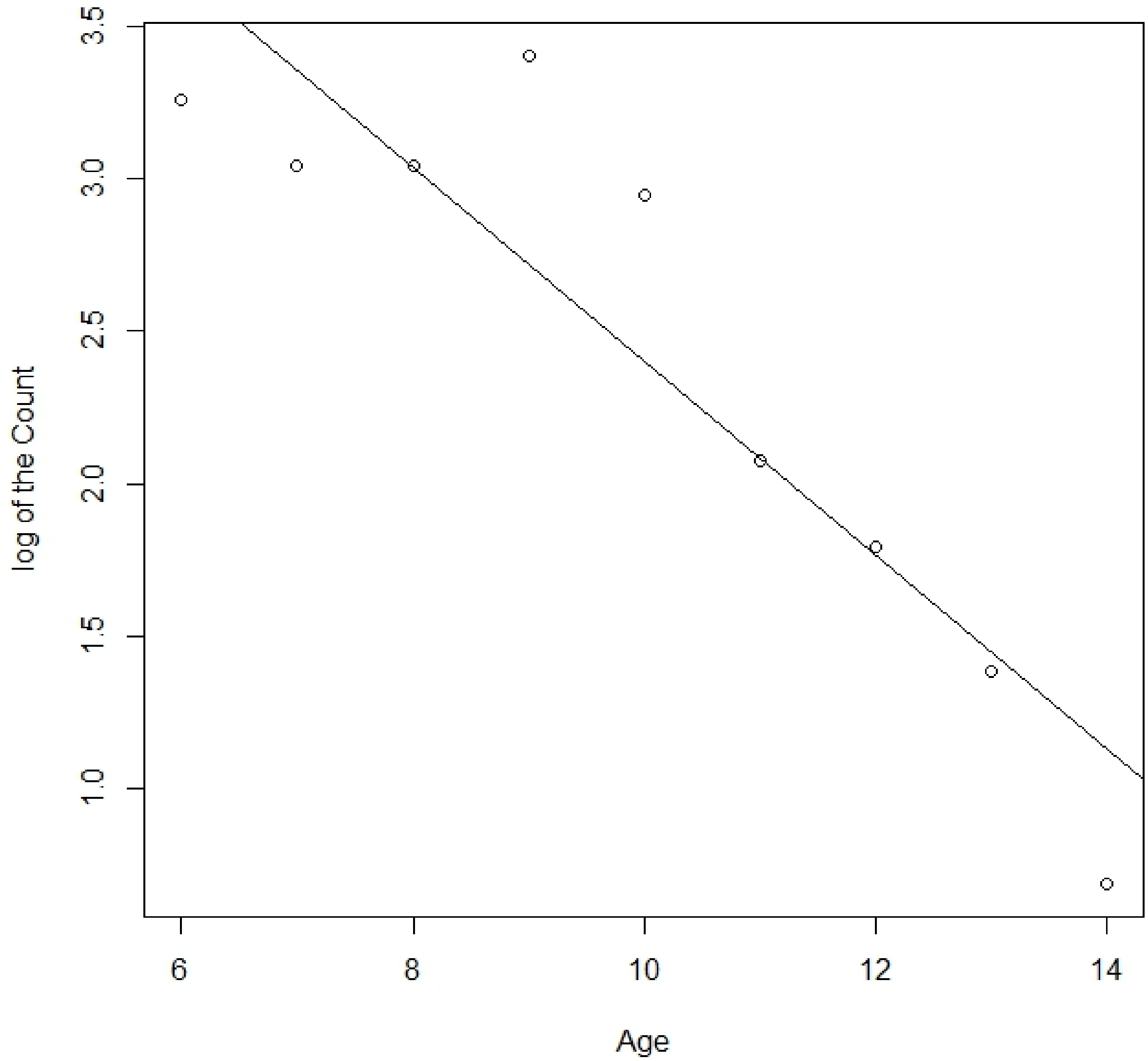

Figure 15. A catch-curve assessing mortality and recruitment variability of Silver Carp in the lower Red River catchment.

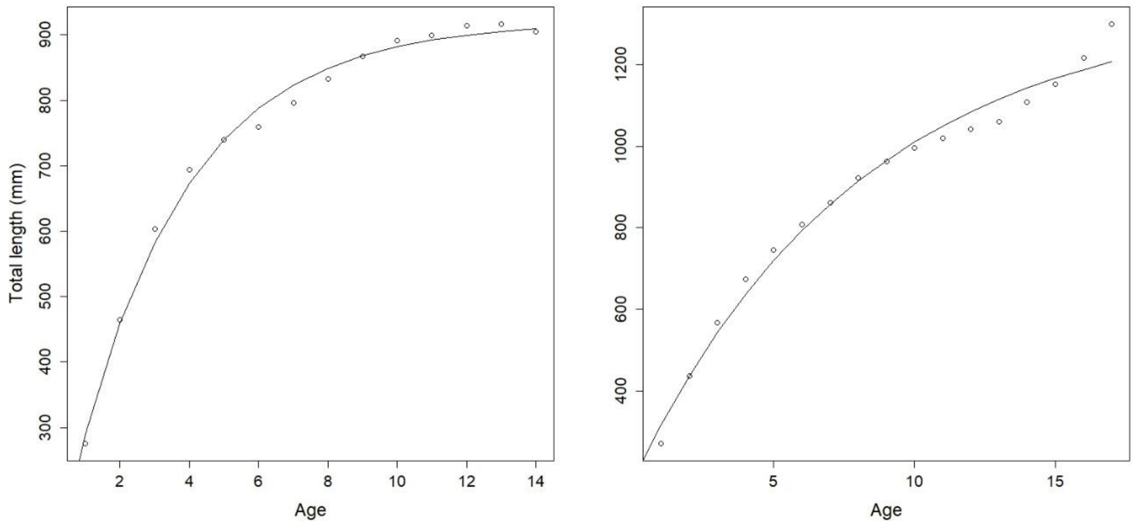

Figure 16. A von Bertalanffy growth curve fit to the mean back-calculated length-at-age for Silver Carp (left) and Bighead Carp (right) in the lower Red River catchment.

APPENDICES

Appendix A

Table A1. Sites surveyed in the lower Red River catchment for Silver Carp and Bighead Carp with the corresponding river, river type (i.e., tributary, oxbow, or mainstem), state (Oklahoma [OK], Texas [TX], and Arkansas [AR]), year, latitude, longitude, and number of surveys conducted.

River	River Type	State	Year	Latitude	Longitude	Surveys
Buzzard Creek	Tributary	OK	2022	33.9003	-95.0541	3
Bois d'Arc	Tributary	TX	2022	33.8386	-95.8448	3
Bois d'Arc	Tributary	TX	2022	33.8231	-95.8553	3
Chcotaw Creek	Tributary	TX	2022	33.7202	-96.3733	3
Chcotaw Creek	Tributary	TX	2022	33.7222	-96.4102	3
Garland Creek	Tributary	OK	2022	33.9247	-95.0834	3
Kiamichi	Tributary	OK	2022	33.9974	-95.3722	3
Kiamichi	Tributary	OK	2022	33.9507	-95.2438	3
Kiamichi	Tributary	OK	2022	33.951	-95.2914	3
Muddy Boggy	Tributary	OK	2022	33.9434	-95.6017	3
Muddy Boggy	Tributary	OK	2022	33.9284	-95.651	3
Pine Creek	Tributary	TX	2022	33.8648	-95.3079	2
Red River	Mainstem	AR	2022	33.5571	-94.0487	3
Red River	Mainstem	OK	2022	33.8811	-95.5055	3
Red River	Mainstem	AR	2022	33.6092	-93.8242	3
Red River	Oxbow	AR	2022	33.5888	-94.378	3
Red River	Mainstem	AR	2022	33.0908	-93.8596	3
Red River	Oxbow	OK	2022	33.6539	-94.5687	3
Red River	Mainstem	AR	2022	33.5515	-94.3945	3
Red River	Mainstem	OK	2022	33.8772	-95.4853	3
Red River	Mainstem	OK	2022	33.908	-95.0666	3
Red River	Mainstem	OK	2022	33.6625	-94.648	3
Red River	Oxbow	OK	2022	33.8026	-94.9285	2
Red River	Mainstem	OK	2022	33.6485	-94.5432	3
Red River	Mainstem	AR	2022	33.397	-93.7117	3
Red River	Mainstem	OK	2022	33.9505	-95.2403	3
Red River	Mainstem	AR	2022	33.5754	-94.0813	3
Red River	Mainstem	AR	2022	33.5998	-94.4469	3

Red River	Mainstem	AR	2022	33.5572	-94.0195	3
Red River	Mainstem	AR	2022	33.3479	-93.7102	3
Red River	Mainstem	OK	2022	33.6183	-94.5548	3
Red River	Mainstem	AR	2022	33.1474	-93.8313	3
Red River	Oxbow	AR	2022	33.1378	-93.8291	2
Red River	Mainstem	OK	2022	33.963	-95.2212	3
Red River	Mainstem	AR	2022	33.599	-93.8123	3
Red River	Mainstem	OK	2022	33.6378	-94.5414	3
Bois d'Arc	Tributary	TX	2021	33.8386	-95.8448	2
Kiamichi	Tributary	OK	2021	33.9974	-95.3722	2
Red River	Mainstem	AR	2021	33.6092	-93.8242	2
Red River	Oxbow	AR	2021	33.5684	-94.3812	3
Red River	Oxbow	OK	2021	33.6539	-94.5687	2
Red River	Mainstem	AR	2021	33.5515	-94.3945	2
Red River	Mainstem	OK	2021	33.7115	-94.7327	2
Red River	Mainstem	OK	2021	33.8772	-95.4853	2
Red River	Oxbow	AR	2021	33.5888	-94.378	2
Chcotaw Creek	Tributary	TX	2021	33.7202	-96.3733	1
Chcotaw Creek	Tributary	TX	2021	33.7222	-96.4102	1
Muddy Boggy	Tributary	OK	2021	33.9434	-95.6017	1
Muddy Boggy	Tributary	OK	2021	33.9356	-95.6349	1
Muddy Boggy	Tributary	OK	2021	33.9284	-95.651	1
Pine Creek	Tributary	TX	2021	33.8648	-95.3079	1
Red River	Mainstem	OK	2021	33.8197	-96.5565	1
Red River	Mainstem	OK	2021	33.7167	-96.3647	1
Red River	Mainstem	OK	2021	33.6625	-94.648	1
Red River	Mainstem	AR	2021	33.6093	-93.8599	1
Red River	Oxbow	OK	2021	33.8026	-94.9285	1
Red River	Mainstem	OK	2021	33.9505	-95.2403	1
Red River	Mainstem	OK	2021	33.8897	-95.5202	1

Table A2. Demographic information of most Bighead Carp (BHC) and Silver Carp (SVC) collected from May 2021 through December 2022 during sampling events. The sample date, location, and gears used are provided. Total length (TL, mm), weight (W, g), and sex (male [M] or female [F]) of each fish are provided. The age estimates using otoliths are provided. These carp were sampled using gillnets (GN), electrofishing (EF), bow-fishermen (BF) which were received from the U.S. Fish and Wildlife Service or jumped in the boat during a survey (JM).

State	River	Date	Latitude	Longitude	Species	TL	W	Gear	Sex	Age
TX	Bois d'Arc	7/7/2021	33.82851	-95.85503	BHC	1048	12840	GN	F	11
OK	Red River	7/16/2021	33.63824	-94.58038	BHC	1240	-	GN	F	4
TX	Bois d'Arc	7/23/2021	33.82851	-95.85503	BHC	1245	-	GN	M	11
TX	Bois d'Arc	7/23/2021	33.82851	-95.85503	BHC	1090	-	GN	F	13
AR	Red River	8/4/2021	33.57763	-94.36778	BHC	1108	13670	GN	M	9
TX	Choctaw	8/10/2021	33.71952	-96.3907	BHC	1097	14220	GN	F	12
TX	Choctaw	8/10/2021	33.71952	-96.3907	BHC	1100	13480	GN	M	11
TX	Choctaw	8/10/2021	33.71952	-96.3907	BHC	1140	15180	GN	M	6
TX	Choctaw	8/10/2021	33.71952	-96.3907	BHC	990	9260	GN	M	5
TX	Choctaw	8/11/2021	33.72068	-96.39828	BHC	1069	12000	GN	M	11
OK	Red River	8/23/2021	33.8032	-94.91955	BHC	1230	21500	GN	-	6
AR	Red River	8/24/2021	33.57763	-94.36778	BHC	960	17500	GN	-	9
TX	Choctaw	11/16/2021	33.71952	-96.3907	BHC	1205	18000	GN	M	13
TX	Choctaw	11/16/2021	33.71952	-96.3907	BHC	1033	10025	EF	F	13
TX	Choctaw	12/15/2021	33.71952	-96.3907	BHC	1225	23000	EF	F	16
TX	Choctaw	1/4/2022	33.71952	-96.3907	BHC	974	11000	EF	M	8
TX	Choctaw	1/5/2022	33.71952	-96.3907	BHC	1252	-	EF	F	15

OK	Kiamichi	1/19/2022	34.00923	-95.38224	BHC	1092	12400	EF	F	9
OK	Red River	2/8/2022	33.77009	-96.42174	BHC	1020	11600	EF	M	8
OK	Red River	2/8/2022	33.77009	-96.42174	BHC	1232	20450	GN	M	10
OK	Red River	2/8/2022	33.77009	-96.42174	BHC	1152	17200	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	BHC	1052	17100	GN	M	15
AR	Red River	3/23/2022	33.58165	-94.36528	BHC	968	8870	GN	F	9
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1204	17600	GN	M	11
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1200	18000	GN	M	8
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1114	15500	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1180	16500	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1164	18500	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1142	15300	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1206	18300	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1148	16400	GN	M	11
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1092	15400	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1050	13000	GN	M	4
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1062	9784	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1090	14500	GN	M	13
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1299	20000	GN	M	17
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1123	14600	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1151	14600	GN	M	11
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1210	16100	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	BHC	1120	18400	GN	M	12
TX	Choctaw	4/13/2022	33.72068	-96.39828	BHC	1258	17000	GN	F	15
TX	Choctaw	4/13/2022	33.72068	-96.39828	BHC	1152	12500	GN	F	10
OK	Red River	5/13/2022	33.91901	-95.07648	BHC	1063	10600	GN	M	9
OK	Kiamichi	5/26/2022	33.9605	-95.25517	BHC	1050	9300	GN	M	11
OK	Kiamichi	5/26/2022	33.9605	-95.25517	BHC	1068	11400	GN	M	8
AR	Red River	5/28/2022	33.58165	-94.36528	BHC	1004	11892	GN	M	9

AR	Red River	5/28/2022	33.58165	-94.36528	BHC	1198	16750	EF	F	12
AR	Red River	5/28/2022	33.58165	-94.36528	BHC	1350	27750	EF	F	12
OK	Red River	6/6/2022	33.8032	-94.91955	BHC	1298	-	EF	F	11
OK	Red River	6/6/2022	33.8032	-94.91955	BHC	1016	-	GN	M	10
OK	Red River	6/16/2022	33.63824	-94.58038	BHC	1050	16600	GN	-	-
AR	Red River	6/21/2022	33.58165	-94.36528	BHC	1172	15250	EF	M	15
OK	Kiamichi	6/23/2022	33.9605	-95.25517	BHC	1015	10300	GN	F	9
OK	Kiamichi	6/23/2022	33.9605	-95.25517	BHC	1250	25250	GN	M	16
OK	Kiamichi	6/23/2022	33.9605	-95.25517	BHC	1048	11600	GN	M	11
OK	Garland Creek	6/24/2022	33.92015	-95.07693	BHC	1122	14900	GN	F	5
OK	Garland Creek	6/24/2022	33.92015	-95.07693	BHC	1333	13700	GN	M	-
OK	Garland Creek	6/24/2022	33.92015	-95.07693	BHC	949	11100	GN	M	4
TX	Pine Creek	6/28/2022	33.87272	-95.30441	BHC	952	10200	GN	M	9
OK	Muddy Boggy	7/5/2022	33.94254	-95.59405	BHC	1033	12000	GN	M	9
OK	Muddy Boggy	7/5/2022	33.94254	-95.59405	BHC	979	11900	GN	M	12
OK	Muddy Boggy	7/5/2022	33.94254	-95.59405	BHC	1022	21000	GN	M	11
OK	Muddy Boggy	7/5/2022	33.94254	-95.59405	BHC	1046	11400	GN	M	12
OK	Muddy Boggy	7/5/2022	33.94254	-95.59405	BHC	1033	18000	GN	-	11
TX	Choctaw	7/19/2022	33.72068	-96.39828	BHC	1073	20500	GN	F	13
OK	Kiamichi	7/28/2022	33.9605	-95.25517	BHC	1051	11600	GN	M	11
OK	Kiamichi	7/28/2022	33.9605	-95.25517	BHC	1050	11100	GN	M	13
OK	Kiamichi	8/1/2022	33.96159	-95.28264	BHC	1021	9500	EF	F	10
OK	Kiamichi	8/1/2022	33.96159	-95.28264	BHC	1201	21100	GN	M	12
TX	Bois d'Arc	8/2/2022	33.82851	-95.85503	BHC	1000	12900	GN	M	10
TX	Choctaw	8/3/2022	33.71952	-96.3907	BHC	1054	19500	GN	F	15
TX	Bois d'Arc	8/5/2022	33.82851	-95.85503	BHC	1004	10000	GN	M	7
TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	BHC	1105	15500	GN	M	8
TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	BHC	1018	14500	EF	M	9
TX	Bois d'Arc	8/11/2022	33.82252	-95.86404	BHC	868	9000	GN	M	11

TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	BHC	1061	15500	GN	M	12
OK	Kiamichi	11/3/2022	33.00632	-95.37972	BHC	1020	11200	EF	F	
OK	Kiamichi	11/3/2022	33.00632	-95.37972	BHC	1012	10500	EF	F	
OK	Cutoff Oxbow	11/7/2022	33.75273	-94.75616	BHC	1360	35500	GN	F	
AR	Red River	11/16/2022	33.54689	-94.38066	BHC	1134	18600	GN	M	
AR	Red River	11/16/2022	33.54689	-94.38066	BHC	1133	14450	GN	M	
AR	Red River	7/5/2021	33.60848	-93.81358	SVC	710	3880	EF	F	4
AR	Red River	7/9/2021	33.57763	-94.36778	SVC	897	7260	GN	M	-
AR	Red River	7/12/2021	33.58165	-94.36528	SVC	912	7460	GN	M	6
OK	Kiamichi	7/15/2021	33.96051	-95.29222	SVC	708	3850	GN	M	3
AR	Red River	8/4/2021	33.57763	-94.36778	SVC	808	6460	EF	M	5
TX	Choctaw	8/10/2021	33.71952	-96.3907	SVC	850	7600	GN	M	7
TX	Choctaw	8/11/2021	33.72068	-96.39828	SVC	851	8100	EF	M	8
TX	Choctaw	8/11/2021	33.72068	-96.39828	SVC	882	8350	EF	F	3
AR	Red River	8/24/2021	33.57763	-94.36778	SVC	850	9000	EF	-	8
AR	Red River	8/24/2021	33.57763	-94.36778	SVC	752	5020	EF	F	5
AR	Red River	8/24/2021	33.57763	-94.36778	SVC	783	6300	GN	-	4
AR	Red River	9/21/2021	33.58165	-94.36528	SVC	876	8500	JM	F	4
AR	Red River	9/21/2021	33.58165	-94.36528	SVC	752	4800	GN	F	3
AR	Red River	10/24/2021	33.58165	-94.36528	SVC	952	9500	GN	-	8
AR	Red River	10/24/2021	33.58165	-94.36528	SVC	830	6000	JM	-	5
TX	Choctaw	11/16/2021	33.71952	-96.3907	SVC	932	10750	GN	F	3
TX	Choctaw	11/16/2021	33.71952	-96.3907	SVC	765	6000	EF	F	5
TX	Choctaw	11/16/2021	33.71952	-96.3907	SVC	1020	12050	EF	F	10
TX	Choctaw	12/15/2021	33.71952	-96.3907	SVC	902	8000	GN	M	7
TX	Choctaw	1/4/2022	33.71952	-96.3907	SVC	911	8500	EF	F	4
AR	Red River	1/6/2022	33.05954	-93.82767	SVC	750	4750	GN	M	5
AR	Red River	1/6/2022	33.05954	-93.82767	SVC	820	5500	GN	M	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	915	11000	EF	F	5

AR	Red River	1/12/2022	33.58165	-94.36528	SVC	865	8600	EF	M	9
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	902	8600	EF	M	9
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	904	7000	EF	M	8
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	894	7000	EF	M	8
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	848	7000	EF	M	6
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	850	7700	EF	M	10
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	899	10000	EF	F	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	868	7000	EF	M	7
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	945	12600	EF	F	6
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	815	7500	EF	M	4
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	852	8000	EF	F	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	1090	15200	EF	F	12
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	842	7500	EF	F	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	926	11500	EF	M	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	915	11400	EF	F	13
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	1036	12900	EF	F	11
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	872	9500	EF	F	6
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	945	11800	EF	F	11
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	821	6250	EF	M	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	828	6750	GN	M	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	828	8000	GN	M	11
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	822	8200	GN	F	5
AR	Red River	1/12/2022	33.58165	-94.36528	SVC	820	8750	GN	M	6
AR	Red River	1/18/2022	33.33958	-93.69724	SVC	872	6750	EF	M	4
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	928	10000	GN	M	8
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	834	7400	GN	F	5
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	878	7100	GN	M	4
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	892	8000	GN	M	9
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	920	8900	GN	M	9

OK	Red River	2/8/2022	33.77009	-96.42174	SVC	798	6000	GN	M	4
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	828	6400	GN	M	5
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	780	6250	GN	F	5
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	818	6000	GN	M	4
OK	Red River	2/8/2022	33.77009	-96.42174	SVC	854	7600	GN	M	9
TX	Choctaw	3/2/2022	33.72068	-96.39828	SVC	797	5750	GN	M	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	938	9478	EF	M	10
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	870	6732	EF	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	898	8860	EF	F	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	829	4768	EF	M	7
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	811	6406	EF	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	910	8076	EF	M	7
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	888	8718	EF	F	6
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	920	8616	EF	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	919	9728	EF	F	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	813	6668	EF	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	939	9402	EF	F	7
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	1021	12646	EF	F	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	900	9776	EF	F	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	922	7674	EF	M	11
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	902	8484	EF	M	6
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	818	6486	EF	M	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	933	8404	EF	M	14
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	920	9034	EF	M	13
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	874	8328	EF	F	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	875	7622	EF	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	999	11980	EF	F	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	954	9654	EF	M	11
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	988	11412	EF	F	7

AR	Red River	3/15/2022	33.57763	-94.36778	SVC	882	8256	EF	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	832	7998	GN	M	10
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	902	8340	GN	M	10
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	847	7836	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	900	7878	GN	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	920	8904	GN	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	790	5890	GN	M	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	792	6700	GN	M	6
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	901	7256	GN	M	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	870	7832	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	798	6592	GN	M	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	901	7518	GN	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	905	8166	GN	M	7
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	834	7080	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	844	5888	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	833	6996	GN	M	8
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	911	9292	GN	M	10
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	772	5470	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	802	9546	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	910	9098	GN	M	9
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	946	11584	GN	F	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	800	6306	GN	M	5
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	894	8016	GN	M	12
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	858	6208	GN	M	4
AR	Red River	3/15/2022	33.57763	-94.36778	SVC	856	7390	GN	M	5
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	858	5982	GN	M	7
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	862	7488	GN	M	9
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	874	9482	GN	M	12
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	912	9138	GN	M	7

AR	Red River	3/23/2022	33.58165	-94.36528	SVC	854	7824	GN	F	4
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	740	-	EF	F	7
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	820	6300	GN	F	7
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	838	7134	EF	M	5
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	850	6974	EF	M	6
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	890	8000	GN	M	11
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	784	5300	EF	M	5
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	930	-	EF	F	10
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	808	5964	GN	M	6
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	1040	12200	EF	F	8
AR	Red River	3/23/2022	33.58165	-94.36528	SVC	928	-	EF	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	788	5850	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	876	6502	GN	M	14
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	918	9408	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	908	8700	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	850	6914	GN	M	-
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	852	6302	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	824	5912	GN	M	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	1070	15600	GN	F	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	1056	13250	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	992	11288	GN	F	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	968	10756	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	873	7524	GN	M	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	918	8322	EF	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	988	10432	EF	F	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	1050	13500	EF	F	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	886	9752	EF	F	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	966	10716	EF	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	924	9352	EF	M	9

AR	Red River	3/24/2022	33.57763	-94.36778	SVC	830	6824	EF	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	838	7328	EF	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	976	12020	EF	F	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	874	9176	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	878	6896	GN	M	8
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	960	10902	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	936	11272	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	794	5698	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	998	10056	GN	F	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	1010	13400	GN	F	8
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	946	10834	GN	F	8
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	904	11096	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	888	9218	GN	F	-
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	916	8822	GN	M	7
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	912	9860	GN	F	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	920	11484	GN	F	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	856	8964	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	938	12100	GN	F	7
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	948	11300	GN	F	9
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	885	9200	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	875	9260	GN	F	12
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	820	6000	GN	M	8
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	818	5858	GN	M	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	806	6158	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	888	9212	GN	M	11
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	878	7626	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	980	10894	GN	F	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	904	10266	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	898	9604	GN	M	10

AR	Red River	3/24/2022	33.57763	-94.36778	SVC	910	8956	GN	M	12
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	852	6174	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	864	7476	GN	M	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	866	9756	GN	F	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	928	9302	GN	M	-
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	816	6510	GN	M	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	890	8332	GN	M	9
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	934	9078	GN	M	13
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	941	9136	GN	M	8
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	902	8780	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	874	10392	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	830	6382	GN	M	4
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	920	10268	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	976	10612	GN	F	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	870	8194	GN	M	6
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	928	9964	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	942	9370	GN	M	10
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	891	8850	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	822	8978	GN	F	5
AR	Red River	3/24/2022	33.57763	-94.36778	SVC	1042	13700	GN	F	11
AR	Red River	4/4/2022	33.60848	-93.81358	SVC	891	9000	EF	M	7
TX	Choctaw	4/13/2022	33.72068	-96.39828	SVC	842	7100	EF	M	5
AR	Red River	4/29/2022	33.58165	-94.36528	SVC	915	9000	EF	F	4
OK	Red River	5/4/2022	33.8032	-94.91955	SVC	888	8000	GN	F	3
OK	Garland Creek	5/13/2022	33.92015	-95.07693	SVC	937	9400	EF	F	9
OK	Kiamichi	5/26/2022	33.9605	-95.25517	SVC	752	4750	EF	M	4
OK	Kiamichi	5/26/2022	33.9605	-95.25517	SVC	887	7100	GN	M	6
OK	Kiamichi	5/26/2022	33.9605	-95.25517	SVC	859	6500	GN	M	9
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	789	4338	GN	M	8

AR	Red River	5/28/2022	33.58165	-94.36528	SVC	912	8876	GN	M	6
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	813	6324	GN	M	5
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	886	8662	GN	F	4
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	919	11388	GN	F	4
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	850	8168	GN	M	5
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	869	8812	EF	F	4
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	616	3122	EF	M	5
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	850	10284	EF	F	10
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	921	12020	GN	F	4
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	907	9692	EF	F	4
AR	Red River	5/28/2022	33.58165	-94.36528	SVC	891	9318	EF	F	7
OK	Muddy Boggy	6/1/2022	33.94254	-95.59405	SVC	892	7600	GN	-	6
TX	Choctaw	6/3/2022	33.72068	-96.39828	SVC	831	7100	JM	-	4
TX	Choctaw	6/4/2022	33.71952	-96.3907	SVC	-	-	GN	-	8
TX	Choctaw	6/4/2022	33.71952	-96.3907	SVC	-	-	GN	-	4
AR	Red River	6/5/2022	33.56936	-94.06402	SVC	964	9500	JM	M	9
AR	Red River	6/5/2022	33.56936	-94.06402	SVC	891	8000	GN	M	4
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	940	12000	EF	F	5
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	992	12250	EF	F	7
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	999	12250	EF	F	4
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	1014	13500	EF	F	7
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	985	8750	EF	F	4
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	952	8250	EF	M	6
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	949	11000	JM	F	4
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	942	7500	EF	M	9
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	901	7400	JM	M	4
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	1062	13800	EF	F	8
AR	Red River	6/21/2022	33.58165	-94.36528	SVC	849	7100	GN	M	3
OK	Red River	6/24/2022	33.91901	-95.07648	SVC	1091	12000	EF	F	12

OK	Garland Creek	6/24/2022	33.92015	-95.07693	SVC	928	0	EF	M	8
OK	Red River	6/30/2022	33.88492	-95.46896	SVC	900	0	GN	M	6
OK	Muddy Boggy	7/5/2022	33.94254	-95.59405	SVC	792	6000	GN	M	3
OK	Red River	7/14/2022	33.91901	-95.07648	SVC	875	7250	EF	M	6
TX	Choctaw	7/19/2022	33.72068	-96.39828	SVC	808	7000	EF	-	5
OK	Red River	7/22/2022	33.6583	-94.54367	SVC	881	8500	EF	M	4
OK	Kiamichi	8/1/2022	33.96159	-95.28264	SVC	748	5100	EF	M	6
TX	Bois d'Arc	8/2/2022	33.82851	-95.85503	SVC	805	7000	JM	M	3
TX	Bois d'Arc	8/2/2022	33.82851	-95.85503	SVC	853	7900	GN	M	8
TX	Bois d'Arc	8/5/2022	33.82851	-95.85503	SVC	814	2500	EF	F	5
TX	Bois d'Arc	8/5/2022	33.82851	-95.85503	SVC	855	8000	GN	M	10
OK	Kiamichi	8/9/2022	33.96159	-95.28264	SVC	861	6800	EF	F	7
AR	Red River	8/10/2022	33.56399	-94.00924	SVC	945	9000	EF	M	9
TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	SVC	964	13500	EF	F	5
TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	SVC	906	10000	EF	F	9
TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	SVC	902	10000	EF	F	9
TX	Bois d'Arc	8/11/2022	33.82851	-95.85503	SVC	902	10000	EF	F	6
OK	Red River	8/26/2022	33.96024	-95.20688	SVC	894	8500	EF	M	7
AR	Red River	8/29/2022	33.56399	-94.00924	SVC	855	7900	EF	M	5
AR	Red River	10/18/2022	33.54988	-94.36266	SVC	740	4100	EF	M	3
AR	Red River	10/18/2022	33.54988	-94.36266	SVC	841	7000	EF	M	5
AR	Red River	10/18/2022	33.54988	-94.36266	SVC	825	7500	EF	M	9
AR	Red River	11/8/2022	33.56936	-94.06402	SVC	796	5600	EF	M	
AR	Red River	11/8/2022	33.56936	-94.06402	SVC	835	6750	GN	M	
AR	Red River	11/15/2022	33.56399	-94.00924	SVC	861	7500	GN	M	
AR	Red River	11/16/2022	33.54689	-94.38066	SVC	844	7100	EF	M	
AR	Red River	11/16/2022	33.54689	-94.38066	SVC	801	5200	GN	M	
AR	Red River	11/16/2022	33.54689	-94.38066	SVC	753	5200	GN	M	
TX	Choctaw	6/23/2021	33.77368	-96.41828	SVC	745	4900	BF	M	3

TX	Choctaw	7/19/2021	33.72074	-96.3769	SVC	910	9500	BF	M	9
TX	Choctaw	7/21/2021	33.72004	-96.39876	SVC	850	8160	JM	M	7
OK	Webb Creek	7/25/2021	33.77368	-96.41828	SVC	720	4620	BF	M	3
OK	Red River	8/10/2021	33.77693	-96.47263	BHC	925	6350	BF	M	7
OK	Red River	9/5/2021	33.79629	-96.51525	BHC	1130	15600	BF	F	10
OK	Red River	9/6/2021	33.79629	-96.51525	BHC	1130	19700	BF	F	-
OK	Red River	9/6/2021	33.79629	-96.51525	BHC	1090	14600	BF	F	12
OK	Webb Creek	12/1/2021	33.7729	-96.41801	SVC	883	7940	BF	M	-
OK	Webb Creek	12/1/2021	33.7729	-96.41801	SVC	864	8300	BF	F	8
OK	Red River	2/27/2022	33.82107	-96.56023	BHC	990	13050	BF	F	8
OK	Webb Creek	6/21/2022	33.77355	-96.41837	SVC	820	6500	BF	F	6
OK	Red River	5/18/2022	33.82131	-96.55203	BHC	1095	19100	BF	F	8
OK	Red River	4/21/2022	33.82131	-96.55203	BHC	1010	17000	BF	F	10
OK	Red River	9/3/2022	33.82042	-96.56031	SVC	920	9150	BF	F	8
OK	Red River	9/7/2022	33.82042	-96.56031	SVC	850	7160	BF	M	10
OK	Red River	10/8/2022	33.82147	-96.54313	SVC	916	8390	BF	M	3
OK	Kiamichi	4/1/2022	34.00912	-95.38141	SVC	1040	13640	BF	F	13
OK	Red River	8/15/2022	33.82042	-96.56031	SVC	860	9300	BF	F	8
OK	Red River	6/30/2022	33.82042	-96.56031	BHC	1040	14850	BF	M	7

APPENDIX B

Methods

Lapilli otoliths are located at the posterior of the skull and were accessed using a hacksaw. A cut was made through the dorsal of the skull in line with the juncture of the pre-opercle and the opercle. Both lapilli otoliths were removed, cleaned of all tissue, and placed into coin envelopes marked with an individual fish identification number. In the laboratory one otolith from each fish was immersed in epoxy resin and allowed to harden for 24-h. I sectioned each otolith with an IsoMet saw (Buehler IsoMet Low Speed Precision Cutter, Lake Bluff, Illinois) and two 0.35 to 0.5-mm cross-sections were removed from the center of the otolith, ensuring the inclusion of the nucleus. I then polished each cross-section with 3-μm diamond lapping paper (Diamond Lapping Film, 8" diameter, plain backing, Electron Microscopy Sciences, Hatfield, PA) and mounted it onto a slide with thermoplastic cement.

The left poscleithrum was removed from the pectoral girdle by making an incision posterior of the pectoral fin-ray and placed into a gallon bag labeled with an individual fish ID number and frozen. In the laboratory the postcleithrum were immersed in 60-70 °C water for approximately 3 – 5m and then cleaned of any flesh and allowed to air dry for 24-h (Johal et al. 2000b). I took two 0.5-0.6mm cross-sections from each postcleithrum using an IsoMet saw. The cross-sections were polished with 3-μm diamond lapping paper and mounted on a slide with thermoplastic cement.

The urohyal bone is located in the lower jaw and was removed by making an incision at the anterior juncture with the ventral hypohyals and the dorsal juncture with the first basibranchial (Johal et al. 2000a). The urohyal was placed in a gallon bag labeled with an individual fish ID number and frozen. In the laboratory the urohyal were immersed in 60-70 °C water for approximately 3 – 5m and then cleaned of any flesh and allowed to air dry for 24-h. I took two 0.5-0.6mm cross-sections from each postcleithrum using an IsoMet saw. The cross-sections were polished with 3-μm diamond lapping paper and mounted on a slide with thermoplastic cement.

The left primary fin-ray was removed in most instances, however if the left fin-ray was damaged or missing then I removed the right fin-ray. Fin-rays were placed in a gallon bag labeled with an individual fish ID number and frozen. In the laboratory the fin-rays were allowed to dry for 24 to 48-h and any residual flesh was removed. I removed one 0.5-0.6mm cross-section at the juncture of the knuckle and the ray. The cross-sections were then polished with 3-μm diamond lapping paper and mounted on a slide with thermoplastic cement.

The pterygiophore is located in the dorsal of the fish between the dorsal fin-ray and vertebrae. I used a hacksaw and made two vertical cuts: one behind the first dorsal fin-ray and one approximately 8 to 10-cm anterior. An incision was then made down the dorsal of the fish to the vertebrae between the two vertical cuts. The flesh was peeled away and the anterior pterygiophore was removed and placed in a gallon bag labeled with an individual fish ID number and frozen. In the laboratory the pterygiophores were immersed in 60-70 °C water for approximately 3 – 5m, cleaned of any flesh, and allowed to air dry for 24-h. I removed one 0.5-0.6mm cross-section from the center of each pterigiophore. The cross-sections were then polished with 3-μm diamond lapping paper and mounted on a slide with thermoplastic cement.

Two readers separately enumerated the annuli of the sectioned structures using a compound microscope with transmitted light. An annulus was defined as a pair of translucent and opaque bands that continued uninterrupted around the nucleus (Dzul et al. 2012). The edge was counted as an annulus for fish captured prior to April 1st because an annulus may be created during the spawning season (Minard and Dye 1998; Ericksen 1999). There was no prior knowledge of the fish length, weight, or age to avoid reader bias. If there was no consensus on the age of a fish, then the readers discussed how they derived the age a consensus was obtained.

Data analyses

I calculated the between-reader-agreement (BRA) and mean coefficient of variation (CV) for each structure to assess agreement and precision of each ageing structure. The assumption is that a higher BRA value indicates that annuli are easily discernable and results in more consistent age estimates between readers (Seibert and Phelps 2013). Although similar to BRA, a low mean CV indicates that the difference in age estimates between readers when they do not agree is relatively less than that of a high mean CV. Finally, I constructed age-bias plots to compare each structure to lapilli otoliths (Campana et al. 1995).

Results

I removed the lapilli otoliths, postcleithrum, urohyal bone, primary left fin-ray, and the anterior pterygiophore from 258 Silver Carp and 86 Bighead Carp to compare ageing structures. Silver carp ages ranged from 3–13 using lapilli otoliths, 3–10 using postcleithra, 3–11 using the urohyal bone, 3–12 using the fin-ray, and 2–7 using the pterygiophore (Table B1). Bighead Carp ages ranged from 3–17 using lapilli otoliths but were estimated as younger when using all other structures (max age 9-11) (Table B1). The lapilli otolith resulted in the highest between reader agreement (77%) for ageing Silver Carp. Between reader agreement ranged from 76% to 63% (Table B2). The average CV associated with Silver Carp ageing was the highest for the urohyal bone and lowest for the postcleithrum (Table B2). For Bighead Carp, lapilli otoliths had the highest between reader agreement (70%) while other structures ranged from 68% to 52% (Table B2). The mean CV associated with Bighead Carp was the lowest for lapilli otoliths and highest for the pterygiophore (Table B2). Age-bias plots indicated that all structures under-estimated age compared to lapilli otoliths for most age-classes of both species (Figures B1-B2). Ageing individuals of both species > age 4 using lapilli otoliths consistently estimated the fish 2-5 years older than then compared to estimated ages when using other structures.

Table B1. Age estimates for Silver Carp and Bighead Carp for multiple ageing structures (i.e., lapilli otoliths, postcleithra, fin-rays, urohyals, and pterigiophores) with the corresponding mean, minimum (min), maximum (max), and standard deviation (SD).

	Structure	Mean	Min	Max	SD
Bighead Carp	Otolith	10.05	3	17	2.96
	Post-cleithrum	5.89	3	11	1.62
	Fin-ray	6.24	3	10	1.79
	Urohyal	5.62	3	11	1.79
	Pterygiophore	5.03	2	9	1.57
Silver Carp	Otolith	6.67	3	14	2.54
	Post-cleithrum	4.60	3	10	1.35
	Fin-ray	4.54	3	12	1.79
	Urohyal	4.55	3	11	1.73
	Pterygiophore	3.38	2	7	0.99

Table B2. The between-reader-agreement (BRA) (with sample size) and mean coefficient of variation (mean CV) for ageing structures for Silver Carp and Bighead Carp collected from May 2021 through October 2022 in the lower Red River catchment.

	Structure	BRA	Mean CV
Bighead Carp	Otolith	70% (56 of 82)	4.7
	Post-cleithrum	60% (49 of 81)	5.95
	Fin-ray	68% (56 of 82)	6.43
	Urohyal	62% (53 of 85)	6.27
	Pterygiophore	52% (31 of 60)	7.31
Silver Carp	Otolith	77% (194 of 252)	3.6
	Post-cleithrum	76% (190 of 251)	3.31
	Fin-ray	73% (187 of 256)	3.88
	Urohyal	68% (171 of 252)	5.98
	Pterygiophore	63% (122 of 194)	5.89

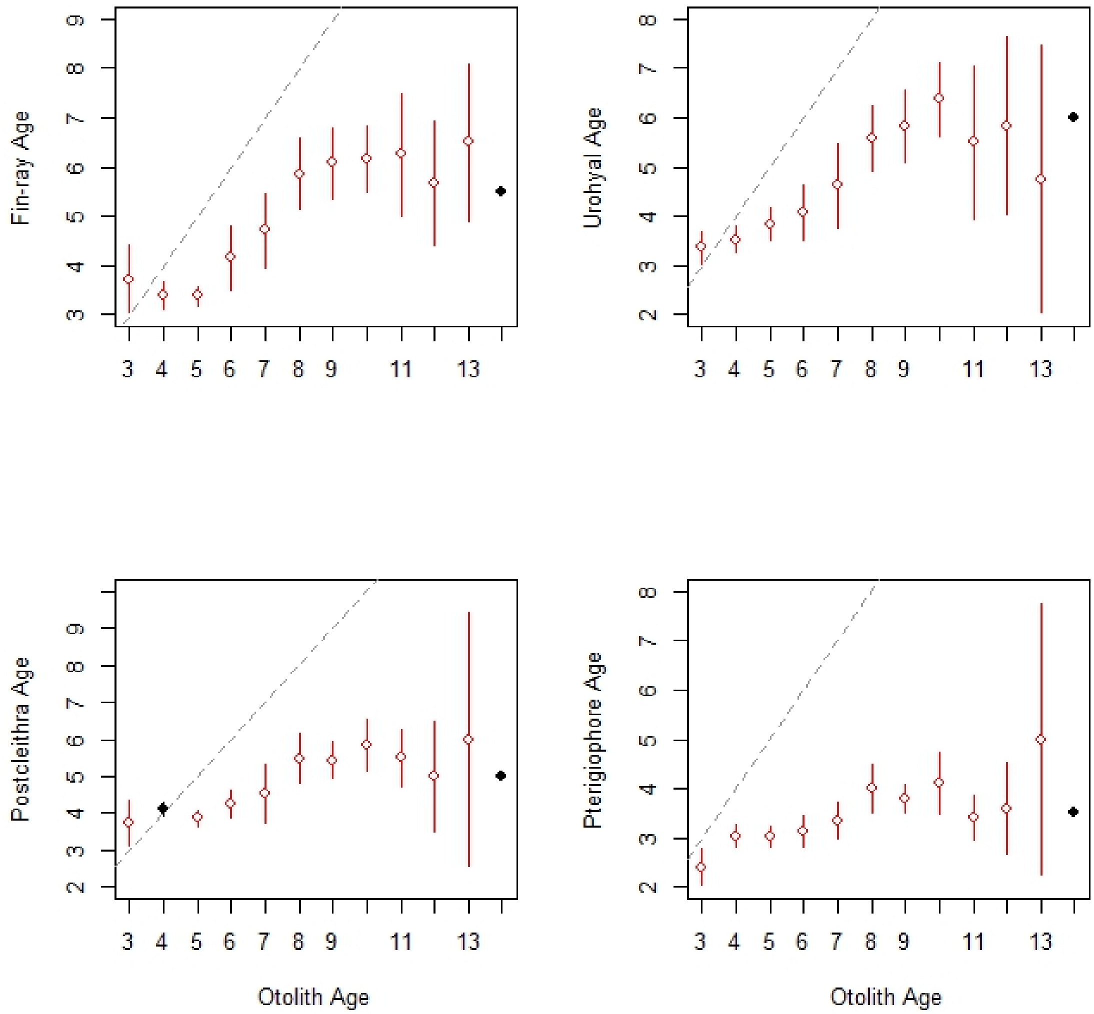

Figure B1. Age-bias plots for Bighead Carp comparing Fin-rays, urohyal bones, postcleithrum, and pterigiophores to lapilli otoliths. The x-axis is the age estimate from otoliths and the y-axis is the age estimate from each structure. The dashed line is exact agreement between structures. Mean estimates of age are indicated by the polygons. Polygons above the dashed line indicate the structure over-estimates age and polygons below the dashed line indicate the structure under-estimates the age compared to lapilli otoliths.

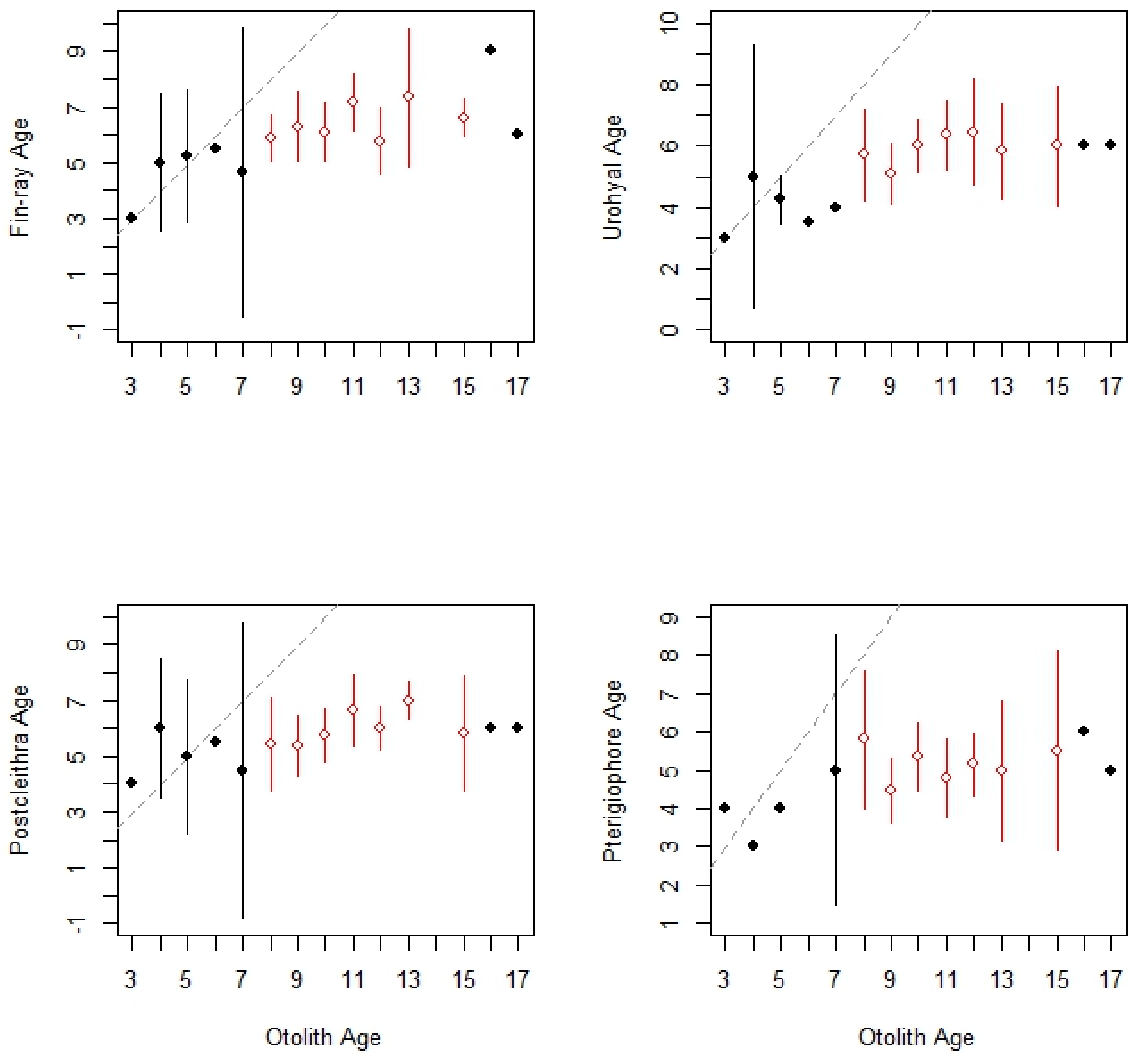

Figure B2. Age-bias plots for Bighead Carp comparing Fin-rays, urohyal bones, postcleithrum, and pterigiophores to lapilli otoliths. The x-axis is the age estimate from otoliths and the y-axis is the age estimate from each structure. The dashed line is exact agreement between structures. Mean estimates of age are indicated by the polygons. Polygons above the dashed line indicate the structure over-estimates age and polygons below the dashed line indicate the structure under-estimates the age compared to lapilli otoliths.

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