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ARTICLE

Spatial Variability of Silver Carp Population Demographics in a Large Tributary River

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Abstract
Silver Carp *Hypophthalmichthys molitrix* have expanded their range to encompass most of the Mississippi River basin, including much of the Missouri River. However, there is a paucity of information concerning Silver Carp in the Missouri River basin, especially in tributaries. Little is known about how Silver Carp function in these tributaries or how connectivity with a main-stem river can influence population demographics within either system. The Kansas River is a tributary to the Missouri River and has multiple physical anthropogenic barriers creating varying levels of connectivity within the system, as well as with the Missouri River. These varying levels of connectivity, or lack thereof, provide a unique opportunity to examine population demographics in river segments separated by barriers. We collected Silver Carp from upstream and downstream of the first two barriers on the Kansas River in the summers of 2018 and 2019. No Silver Carp were captured upstream of a hydropower dam at river kilometer 84 but were found upstream of a water diversion weir at river kilometer 24. Catch rates of adult Silver Carp were lower in the reach above the weir, but Silver Carp caught in this reach exhibited greater growth rates than Silver Carp captured below the weir. Catch rates of juveniles were also lower in the reach above the weir. Limited connectivity within the Kansas River via the water diversion weir could influence size structure and catch rates of Silver Carp captured above and below the weir. Lack of juveniles above the weir indicates that reproduction may be limited in this reach, and river conditions below the weir may be more suitable for rearing juvenile Silver Carp. This information is important for understanding Silver Carp population demographics across a range of river environments, providing critical information for the development and implementation of broadscale control plans.

Introductions of nonnative species to U.S. waterways have changed biological communities (Gozlan et al. 2010; Kolar et al. 2010), often in an irreversible way (Kolar and Lodge 2002). Silver Carp *Hypophthalmichthys molitrix* were introduced into Mississippi waterways in the 1970s (Freeze and Henderson 1982; Conover et al. 2007). They have since expanded their distribution to include much of the Missouri River drainage and now range as far north as North Dakota (Hayer et al. 2014). These invasive Silver Carp can impact native filter feeders such as Gizzard Shad

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Dorosoma cepedianum and Bigmouth Buffalo *Ictiobus cyprinellus* through direct competition (Barthelmes 1984; Irons et al. 2007; Sampson et al. 2009). Additionally, Silver Carp can facilitate shifts in zooplankton community structure and composition (Sass et al. 2014; DeBoer et al. 2018). This shift in zooplankton community structure can impact other fish species by limiting food availability for larval fish that forage on plankton before their ontogenetic dietary shift (Sass et al. 2014; Solomon et al. 2016; Chick et al. 2020). Various life history aspects of Silver Carp have been investigated throughout the Mississippi River drainage to inform management decisions (DeGrandchamp et al. 2008; Sampson et al. 2009; Jerde et al. 2013; Norman and Whitledge 2015; Stuck et al. 2015); however, there is a paucity of information in other river basins, such as the highly modified Missouri River and connected tributaries.

Tributaries are crucial in the life cycle of many riverine fishes (Neely et al. 2009; Bottcher et al. 2013; Brönmark et al. 2014; Hamel et al. 2014) and may be important for certain life history attributes of Silver Carp. For example, Silver Carp populations within the Mississippi River drainage can be comprised of individuals with natal origins from multiple systems, including tributaries (Norman and Whitledge 2015). Tributaries of the Missouri River may be important because the main stem has undergone extensive alterations that have limited lateral connectivity with the river floodplain and increased mean velocity and mean channel depth (Galat et al. 1998; Pegg et al. 2003; Steffensen and Mestl 2016). Due to these alterations, optimal habitat is not readily available for Silver Carp in the Missouri River as they tend to prefer waters with lower velocities (Kolar et al. 2007; Calkins et al. 2012). Nonetheless, abundant populations exist throughout the vast tributary network of the Missouri River and little is known about how varying habitat characteristics affect population demographics. Understanding how Silver Carp demographics vary throughout their current distribution is an essential step in developing regional and basinwide control plans. One such tributary, the Kansas River, has an established population of Silver Carp that may provide insight into how Silver Carp population demographics may vary regionally and in response to anthropogenic fragmentation.

Young-of-year Silver Carp were first documented in the Kansas River in 2010 (Mosher 2014), and adults have been found upstream as far as Lawrence, Kansas (river kilometer [rkm] 83, measured from its confluence with the Missouri River). Previous assessments in the Kansas River from 2005 to 2007 failed to detect Silver Carp (Eitzmann and Paukert 2010; White et al. 2010); however, Silver Carp were known to be in the Missouri River upstream of the Kansas–Missouri confluence at that time (Wanner and Klumb 2009), so it is likely they were present in the Kansas River at low densities.

Understanding population demographics in the Kansas River will help inform development and implementation of a control plan in this system. These data may help managers to maximize effectiveness of control efforts and provide baseline information for detecting population changes (Allen and Hightower 2010). Our objective was to assess population demographics (i.e., catch rates, condition, size structure, and age and growth) of Silver Carp throughout the lower portion of the Kansas River. These data will help managers understand how Silver Carp population demographics are influenced by tributaries of the Missouri River that provide habitat that is limited in the main-stem river.

METHODS

Study area.— The Kansas River begins at the confluence of the Smoky Hill and Republican rivers (Quist and Guy 1999) and flows easterly for 274 km to its confluence with the Missouri River in Kansas City, Kansas (Figure 1). Discharge within the basin is controlled by 18 federal reservoirs and over 13,000 small impoundments (Quist et al. 1999; Makinster and Paukert 2008). The Kansas River has three major barriers: the Topeka Weir in Topeka, Kansas, at rkm 141; Bowersock Dam in Lawrence, Kansas, at rkm 84; and the Johnson County Weir in Edwardsville, Kansas, at rkm 24. Bowersock Dam is a low-head dam and is operated to produce hydropower (Quist and Guy 1999) and is the largest barrier on the Kansas River, standing approximately 5.2 m above the tailwater. The dam top is equipped with an inflatable bladder that can increase the height to approximately 7 m when flows are less than 566 m^3/s (S. Hill-Nelsen, Bowersock Mill and Power Company, personal communication). The Johnson County Weir is a water diversion weir for local municipalities. This structure is inundated when the gauge on the Kansas River near Lake Quivira (gauge 06892518) is at approximately 4.27 m (J. Koch, Kansas Department of Wildlife, Parks and Tourism, personal communication), corresponding to flows of approximately 985 m^3/s, which occurred 16 times between 2017 and 2020 (USGS 2020).

Our study area was the lower half of the Kansas River, from its confluence with the Missouri River to the Topeka Weir. We separated the study area into three segments associated with the three main barriers on the main-stem Kansas River. Segment 1 is from the confluence with the Missouri River to the Johnson County Weir (24 km), segment 2 is from the Johnson County Weir to Bowersock Dam (60 km), and segment 3 is from Bowersock Dam to the Topeka Weir (57 km). Each segment was further stratified into sampling sites to ensure sampling effort was

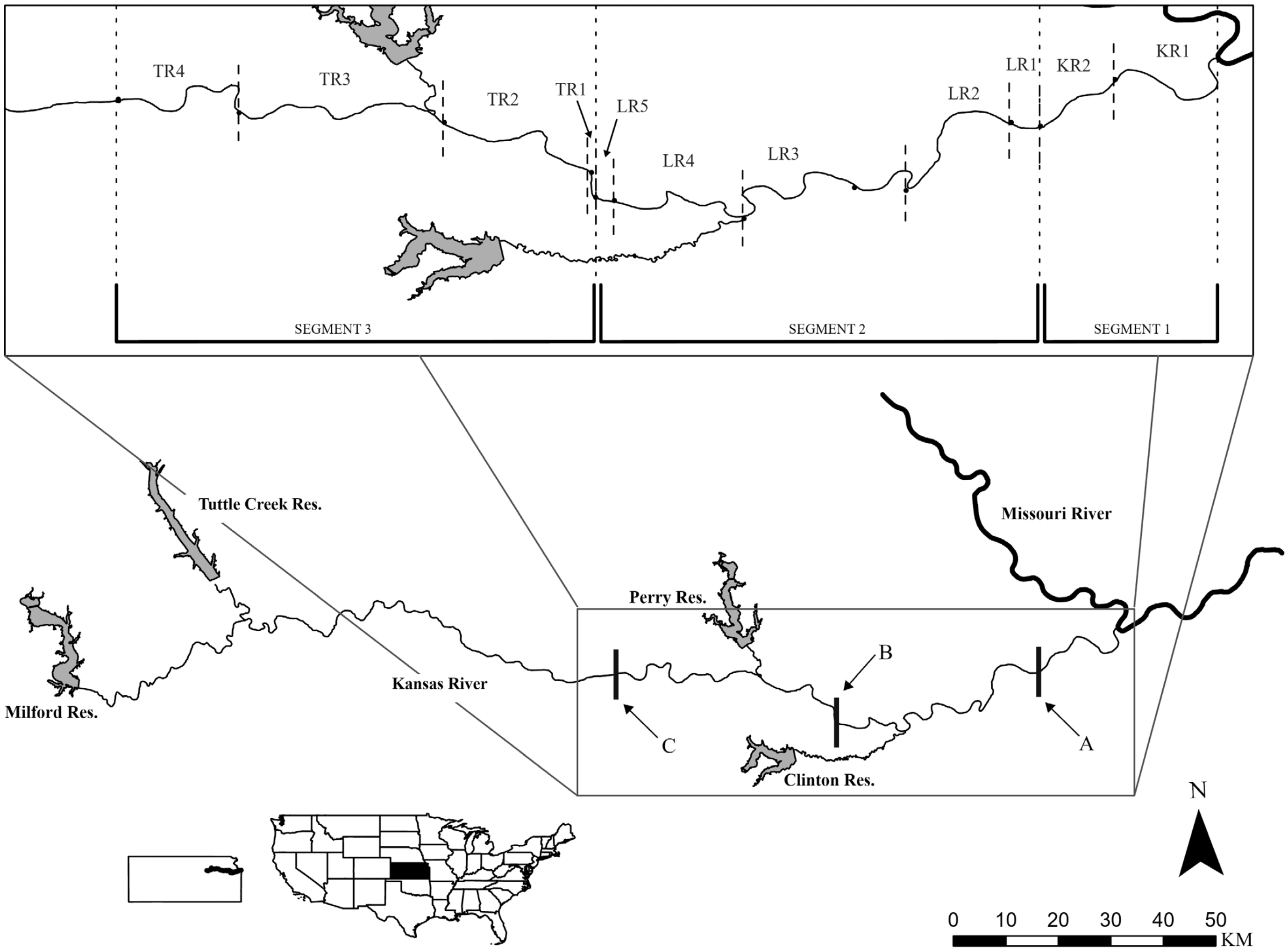

FIGURE 1. Kansas River study area, where segment 1 (24 km) is between the confluence with the Missouri River and the Johnson County Weir (labeled as A), segment 2 (60 km) is between the Johnson County Weir and Bowersock Dam (at B), and segment 3 (57 km) is between Bowersock Dam and the Topeka Weir (at C). Segments were further divided into sampling sites (e.g., KR1, KR2, etc.).

distributed throughout each segment. Sampling sites were determined as sections of the river between access locations or between access locations and the three main barriers on the river (Figure 1).

Field sampling.— We collected Silver Carp in May through August of 2018 and 2019 using a suite of gears to maximize our potential for collecting fish and informing future collection efforts on the best gear types and methodologies. We used boat-mounted electrofishers (Irons et al. 2007; Bouska et al. 2017), an electrified dozer trawl (Hammen et al. 2019), and mini-fyke nets (Collins et al. 2017; Gibson-Reinemer et al. 2017) to collect data in a standardized format to facilitate comparisons among gear types and methods. We used a MBS-2D Wisconsin control box (ETS Electrofishing, Madison, Wisconsin) powered by a 3,500-W generator mounted on a 4.9-m (16-ft) jon boat and a larger boat equipped with Smith-Root 5.0 GPP box (Smith-Root, Vancouver, Washington) for electrofisher sampling. We also used two different electrofishing methods: high frequency using pulsed DC at 60 Hz with a target amperage of 20 A (jon boat) or 10 A (large boat) and low frequency using pulsed DC at 15 Hz with a target amperage of 4 A. Voltage output was adjusted on both boats to account for changes in water temperature and conductivity to reach amperage goals. Electrofishing runs for the high-frequency method were conducted going upstream in a manner similar to the method described in Bouska et al. (2017). Runs for the low-frequency method were conducted going downstream. Both methods had run lengths of approximately 30 min, focusing on channel sides, backwater habitats, and side channels (DeGrandchamp et al. 2008). Each sampling site was sampled once a month during the summer when water conditions allowed, and run locations were haphazardly selected within each sampling site.

We also used an electrified dozer trawl for 3 d in 2018 and 2019. The dozer trawl runs were conducted going upstream at 30 Hz with a target amperage of 30 A, adjusting voltage to meet amperage goals, and had run lengths of 5 min. Each run location was chosen at random every kilometer and varied between the north bank, south bank, and thalweg. Mini-fyke nets (two 121.9- × 61-cm box frames with a 4-m lead, two 64.8-cm-diameter hoops, and 7-mm mesh netting) were deployed as described in Hubert (1983) in shallow (<1 m) backwater areas and fished overnight with the intent of capturing age-0 Silver Carp.

All Silver Carp captured were measured in total length (mm) and weighed to the nearest gram. The sex of all Silver Carp was identified by inspecting reproductive organs. Lapilli otoliths were extracted from Silver Carp for aging analysis because these structures were reported to have the greatest between-reader agreement and between-reader precision (Seibert and Phelps 2013).

Discharge and turbidity data from the Kansas River were downloaded from the U.S. Geological Survey (USGS 2020) gauging station located near De Soto, Kansas, at rkm 48 (gauge 06892350) to demonstrate differences in discharge and turbidity between sampling seasons in 2018 and 2019 (Figure 2).

Laboratory methods.— We used deionized water to clean excess tissue from the otoliths, then mounted the otoliths in epoxy (Epoxicure Epoxy Resin and Hardener; Beuhler, Lake Bluffs, Illinois) and sectioned the otoliths into 0.5-mm sections across the transverse plane through the nucleus using an Isomet low-speed saw (Model 11-1280-160; Beuhler, Lake Bluffs, Illinois) and mounted the sectioned otoliths on microscope slides with double-sided tape. Sections were then sanded using 1,500- and 3,000-grit sandpaper and polished using 3-μm lapping paper to reveal annuli. Ages were estimated by examining the polished section beneath a dissecting scope and counting the annuli, where the edge of the otolith was the last radii. Ages were estimated for each fish by a concert reading by three readers, and discrepancies were reconciled by a consensus between the readers (Stuck et al. 2015). Back-calculated length-at-age measurements were obtained by measuring the distance from the focus of the otolith to the outside edge of each radii to determine individual year growth using the ImageJ tool in the Fiji software package (Schindelin et al. 2012).

Data analysis.— We compared Silver Carp population demographics between segments of the Kansas River. All data were tested for normality with Shapiro–Wilks tests

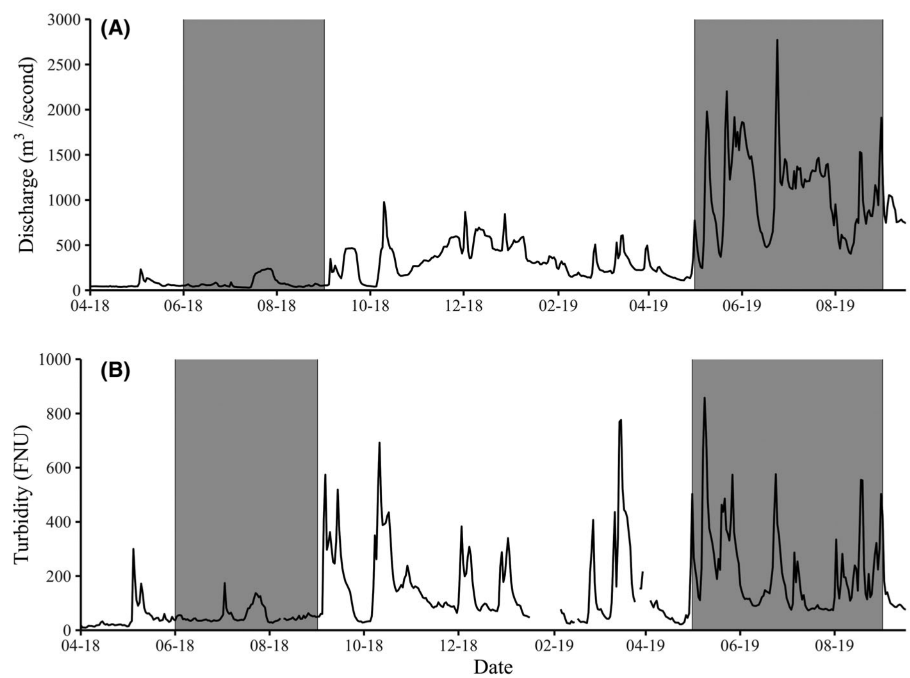

FIGURE 2. Graphs of **(A)** discharge, measured in cubic meters per second, and **(B)** turbidity, measured in formazin nephelometric units (FNU), in the Kansas River from April of 2018 to October of 2019. Shaded regions represent river conditions during the 2018 (left) and 2019 (right) sampling seasons.

and visually inspected with density plots. Data that were not normally distributed were analyzed using nonparametric tests.

Catch rates were estimated by calculating catch per unit of effort (CPUE) as the number of Silver Carp captured per hour of electrofishing. The CPUE data were assessed with Kruskal–Wallis tests and combined across years if there was no difference in catch rates in each segment between sampling years. Combined data were then tested for differences between segments for the dozer trawl, high-frequency, and low-frequency electrofishing methods. We also performed comparisons of CPUE between sampling gears as a benchmark for overall success in collecting Silver Carp. All CPUE comparisons were conducted with Kruskal–Wallis tests followed by a Dunn's test for pairwise comparisons. The *P*-value was adjusted using the Holmes method after the Dunn's test.

Silver Carp greater than 350 mm in total length were classified as adults because age of maturation was predicted to be at age 2 (Williamson and Garvey 2005), which was at approximately 350 mm in North Dakota tributaries (Hayer et al. 2014). We analyzed body condition using analysis of covariance (ANCOVA) to test differences in $\log_{10}$ transformed length–weight regressions of adult Silver Carp across sex, sampling years, and segment of capture in a hierarchical fashion. If differences were detected in any covariates, then the subsequent models were nested inside the proceeding covariate. For example, if differences in the slope of the regressions were detected across sampling years, then models assessing the slope of the regressions across segments would be nested within each year.

Differences in size structure were assessed by grouping fish by segment of capture and placing them in 25-mm length bins. Differences in the length-frequency distributions among river segments were tested using a bootstrapped Kilmogorov–Smirnov cumulative distributions test (Massey 1951). Mean lengths of sexually mature Silver Carp (>350 mm) from each segment were compared using an analysis of variance (ANOVA).

Ages were estimated for 73 Silver Carp in segment 1 and 114 Silver Carp in segment 2. We compared the median ages of adult fish between segments with a Kruskal–Wallis test. We used back-calculated lengths at age to assess age and growth using the Dahl–Lea method (Dahl 1907; Lea 1910). Back-calculated length at age was performed for 31 Silver Carp in segment 1 and 60 Silver Carp in segment 2. Back-calculations were performed for fewer individual Silver Carp from each segment because not all radii were visible in a single straight line from the focus to the edge of the otolith for all the aged individuals. We then used the back-calculated lengths-at-age data combined with the age data from Silver Carp that could not have back-calculations performed to test for differences in growth between segments with an ANCOVA (Isely and Grabowski 2007), truncating the data to ages 1 through 6. We then used the untruncated data set to model growth for each segment using von Bertalanffy growth functions. All tests were deemed significant at $\alpha = 0.05$.

RESULTS

A total of 1,612 Silver Carp were captured from segments 1 and 2 over the course of this study. No Silver Carp were captured in segment 3 (Table 1). Low water conditions in 2018 limited dozer trawl sampling largely to segment 1, but in 2019, effort was equally divided among segments 1, 2, and 3.

Catch per unit effort was similar in segments 1 and 2 for all three sampling gears between 2018 and 2019 (Table 2). Catch rates were highest in segment 1 for all sampling gears (Table 2; Figure 3), and the dozer trawl was generally the most effective for capturing the largest number of Silver Carp (Table 3; Figure 3).

Mean length of adult Silver Carp was greater in segment 2 (mean TL = 657.3, SD = 58.6) than segment 1 (mean TL = 592.7, SD = 49.3) ($F_{1,\,1{,}036} = 455.39$, $P < 0.01$) (Figure 4). Additionally, length-frequency distributions were different between segments (n boots = 5,000, $D = 0.66$, $P < 0.001$). Multiple year-classes were observed in segment 1, with the 2018 year-class dominating the catch of juvenile Silver Carp in both 2018 and 2019. Juvenile Silver Carp were observed in segment 2 only in 2019 in all gears deployed (Figure 4).

Slopes of the length–weight regressions were similar between sexes ($F_{2,\,793} = 0.906$, $P = 0.40$). There was a difference in the y-intercepts between sampling years ($F_{1,\,1{,}127} = 646.6$, $P < 0.01$), where Silver Carp captured in 2018 were heavier at a given length than Silver Carp captured in 2019 in both segment 1 ($F_{1,\,668} = 16.82$, $P < 0.01$) and segment 2 ($F_{1,\,454} = 6.75$, $P = 0.01$). There were also differences in the length–weight relationships between segments in 2018 ($F_{1,\,337} = 6.22$, $P = 0.01$), where Silver Carp captured in segment 2 had heavier weights at a given length than Silver Carp captured from segment 1.

TABLE 1. Total catch of all Silver Carp per segment in 2018 and 2019 from the Kansas River from all gears.

Gear type and total	Segment 1	Segment 2	Segment 3	Total catches
High frequency	215	280	0	495
Low frequency	563	152	0	715
Dozer trawl	348	39	0	387
Mini-fyke nets	13	2	0	15
Total	1,139	473	0	1,612

TABLE 2. Results of Dunn's test for catch rate comparison between sampling years in segments 1 and 2 (e.g., segment 1: 2018–2019) for each of the three electrified sampling gears. Segment 1–segment 2 years combined shows results of Kruskal–Wallis tests comparing catch rates for each gear between segments with catch data from 2018 and 2019 combined.

Gear	Segment 1: 2018–2019	Segment 2: 2018–2019	Segment 1–segment 2 years combined
High frequency	$Z = 0.50$	$Z = 0.24$	$\chi^2 = 4.47$
	df = 1	df = 1	df = 1
	$P = 0.48$	$P = 0.63$	$P = 0.035$
Low frequency	$Z = 1.13$	$Z = 3.29$	$\chi^2 = 42.36$
	df = 1	df = 1	df = 1
	$P = 0.29$	$P = 0.07$	$P < 0.001$
Dozer trawl	$Z = 0.05$	$Z = 0.10$	$\chi^2 = 4.6$
	df = 1	df = 1	df = 1
	$P = 0.83$	$P = 0.75$	$P = 0.032$

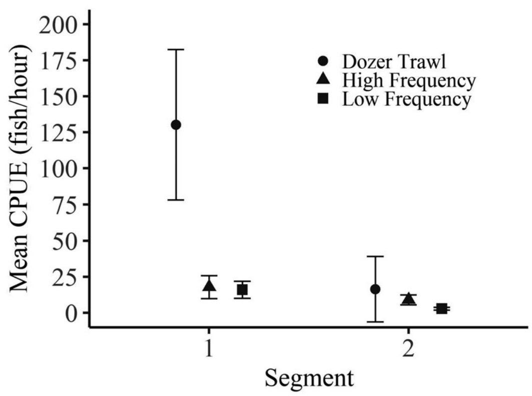

FIGURE 3. Mean and 95% confidence intervals of catch per unit effort (CPUE; number per hour) for the dozer trawl, high-frequency, and low-frequency electrofishing methods in segments 1 and 2 of the Kansas River. Error bars represent the 95% confidence intervals for the mean.

TABLE 3. Results of Dunn's tests comparing catch rates among the three electrified sampling gears in segment 1 and segment 2 of the Kansas River.

Gear comparison	Segment 1	Segment 2
Low frequency–high frequency	$Z = 0.48$	$Z = 4.74$
	df = 1	df = 1
	$P = 0.63$	$P < 0.01$
Low frequency–dozer trawl	$Z = 4.62$	$Z = 1.42$
	df = 1	df = 1
	$P < 0.01$	$P = 0.31$
High frequency–dozer trawl	$Z = 3.37$	$Z = -0.57$
	df = 1	df = 1
	$P < 0.01$	$P = 0.57$

Conversely, Silver Carp captured from segment 2 in 2019 had lower weights at a given length than Silver Carp captured in segment 1 ($F_{1,785} = 6.45$, $P = 0.01$).

The median age of adult Silver Carp was similar between segment 1 (median age = 6 years, interquartile range = 1) and segment 2 (median age = 5 years, interquartile range = 1.75) ($Z = 10.49$, df = 6, $P = 0.11$). Silver Carp in segment 2 grew faster than those in segment 1 ($F_{1,553} = 5.99$, $P = 0.015$) (Figure 5), reaching approximately 490 mm total length at age 3, 570 mm at age 4, and 620 mm at age 5. Silver Carp in segment 1 reached approximately 450 mm total length at age 3, 510 mm at age 4, and 570 mm at age 5 (Figure 5).

DISCUSSION

We examined spatial variability in population demographics of Silver Carp in the Kansas River, and differences were likely driven by both biological and anthropogenic influences. Longer-bodied Silver Carp and lower catch rates of adult Silver Carp in segment 2 were typical of patterns observed in populations on the invasion front that are likely driven by density-dependent responses (e.g., MacNamara et al. 2016). However, Silver Carp have been documented in this segment since 2010 (Mosher 2014), and other variables likely perpetuated discrepancies in population demographics between segments as well. For example, differences in habitat between segments 1 and 2 could have influenced growth rates. Segment 1 has undergone more alterations than segment 2, having a higher proportion of urban influence and rip-rap banks, fewer islands and channels, a narrower bank-full width (Paukert and Makinster 2009), and consistent depths (Eitzmann and Paukert 2010). Segment 2 is more sinuous and is characterized by more variable depths, numerous sandbars, and a further agricultural riparian influence (Paukert and Makinster 2009). Systems or reaches with fewer anthropogenic modifications, like segment 2, have more habitat and resource availability for

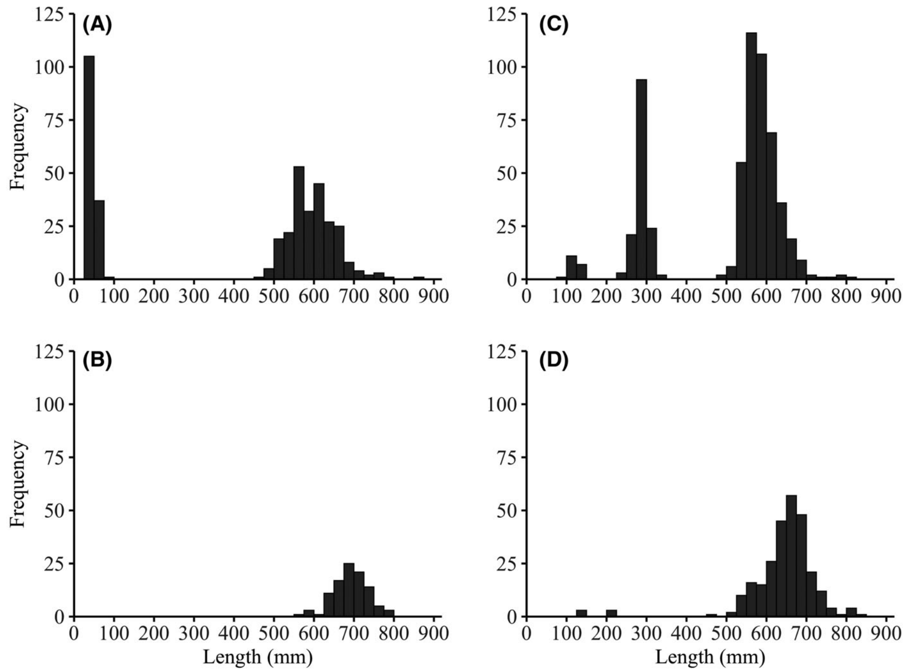

FIGURE 4. Length-frequency histograms of Silver Carp captured in segment 1 in **(A)** 2018 and **(C)** 2019 and segment 2 in **(B)** 2018 and **(D)** 2019. Silver Carp were separated into 25-mm length bins and enumerated.

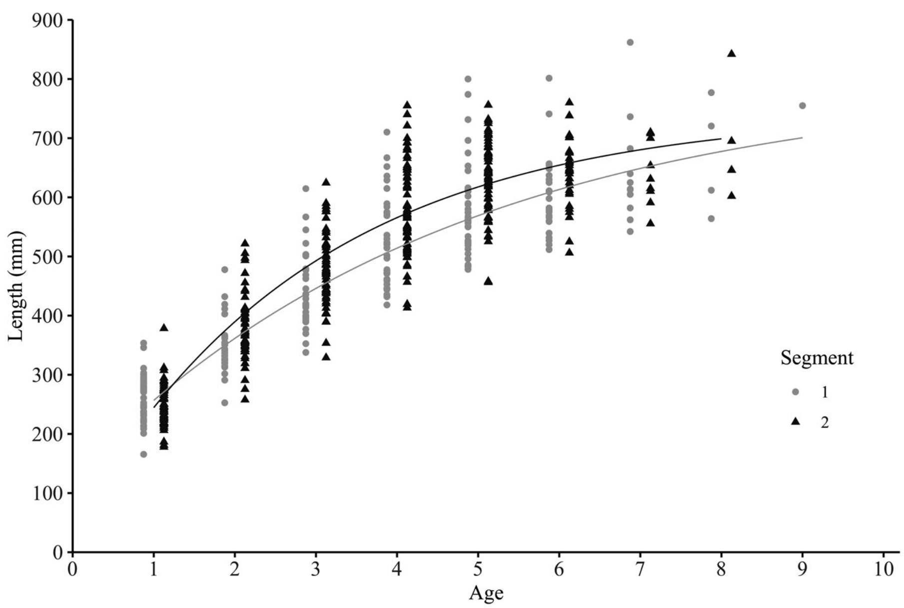

FIGURE 5. Length at age of Silver Carp in segment 1 (light gray circles) and segment 2 (dark gray triangles); data points at each age are offset for clarity. Von Bertalanffy growth curves were modeled for Silver Carp from segment 1 (light gray line) and segment 2 (dark gray line). Growth curves were not offset.

native species (Rolls et al. 2012), maintaining functional redundancy (Rosenfeld 2002) and limiting resources available to invading fishes, as hypothesized by Stuck et al. (2015).

Silver Carp are notoriously difficult to sample, prompting investigation into experimental gear configurations, such as the electrified dozer trawl (Hammen et al. 2019). Although our study design did not examine gear efficiencies, our results were similar to findings of Hammen et al. (2019), indicating that the higher catch rates of the electrified dozer trawl are likely due to this gear being more effective than conventional electrofishers when it can be implemented in ideal conditions (i.e., slow-moving habitats with consistent depths >1 m). Despite catch rates being consistently higher with the dozer trawl in our system, catch was highly variable. Additional evaluations of gear efficiency would be beneficial before adopting this gear as a standardized long-term monitoring assessment tool. When specialized gears like the dozer trawl are not available or effective for a specific study area, managers may consider different methods of conventional electrofishing. Additionally, incorporating a suite of gears, such as mini-fyke nets (Collins et al. 2017; Gibson-Reinemer et al. 2017), may be necessary to sample a broader range of fish sizes. Although mini-fyke net catch rates were not high, they did provide utility in monitoring for juvenile Silver Carp and locating areas and habitat where juvenile Silver Carp occurred.

We failed to detect the presence of Silver Carp upstream of Bowersock Dam over the course of this study, indicating that Silver Carp either are not found upstream of Bowersock Dam or occur in low densities. Bowersock Dam is a known barrier for other fishes, such as Blue Sucker *Cycleptus elongates* (Eitzmann et al. 2007) and Blue Catfish *Ictalurus furcatus* (Dean 2020), and could be a barrier to Silver Carp as well.

Differences in catch rates between segments 1 and 2 for both adult and juvenile Silver Carp could be facilitated by multiple factors, including by the Johnson County Weir functioning as a partial barrier impeding constant continuity between segment 2 and the Missouri River during periods of lower flows. A rise in river stage has been shown to cue movement of adult Silver Carp (DeGrandchamp et al. 2008) upstream in the spring (Coulter et al. 2016), likely providing opportunities to traverse the barrier when river stage is conducive for fish passage. However, this barrier drastically limits or completely blocks upstream passage during low-water periods. Juvenile Silver Carp have reduced swimming and burst swimming speeds (Hoover et al. 2012) that may limit the river velocities that they are able to navigate. The higher flows required to traverse this barrier could prove difficult for juvenile Silver Carp to navigate, creating a water velocity barrier. Therefore, we hypothesize that passage of juvenile Silver Carp over the Johnson County Weir may be limited compared with their adult counterparts.

The low catch rates of juveniles and lack of any age-0 Silver Carp in segment 2 may be due to various abiotic and biotic factors. In ideal conditions, Silver Carp eggs drift for approximately 30 h before hatching (Chapman and George 2011), after which larval Silver Carp are capable of swimming vertically and reaching suitable nursery habitat (George and Chapman 2013). This is ample time for drift to carry Silver Carp eggs spawned in segment 2 downstream and into segment 1 or into the Missouri River in nearly all river conditions because segment 2 is short at only 60 km. However, during low-water years, such as 2018, segments 1 and 2 are nearly disconnected with a near-stagnant pool forming upstream of the Johnson County Weir, creating conditions where the majority of larval Silver Carp and eggs would not likely drift downstream into segment 1. Therefore, we hypothesize that reproduction may also be limited in segment 2 because we failed to detect any age-0 Silver Carp in segment 2 in 2018 but were able to capture them in segment 1 during the same year.

Segment 1 likely provides important spawning and nursery habitat for Silver Carp in the Kansas River. Although the presence of larval Silver Carp in this system has never been investigated, unpublished results from otolith microchemistry analysis indicate that production is occurring in the Kansas River (Werner 2020). Age-0 Silver Carp have been shown to occur at higher densities in areas with slower moving waters (e.g., Haupt and Phelps 2016), such as those observed in segment 1 in 2018. Indeed, Silver Carp could be using tributaries of the Missouri River like the Kansas River as nursery habitats, seeking refuge from the high-velocity currents typical of the Missouri River. Future work to describe recruitment patterns in relation to abiotic conditions throughout the lower Missouri River basin would be beneficial for understanding Silver Carp populations throughout the Missouri River basin.

Body condition varied at both spatial and temporal scales, where Silver Carp had lower weights at a given length in 2019 than in 2018. River discharge was drastically different between sampling years. Discharge in 2018 was consistently at 42 m^3/s during the sampling season. Discharge was sporadic in 2019 with multiple high-water events, the largest of which was approximately 2,800 m^3/s. High flows could have been an additive stressor on these fish, requiring a greater metabolic demand to navigate increased river velocities. Additionally, turbidity in the Kansas River was higher in 2019 than in 2018. Elevated turbidity and flows in large rivers can lead to decreases in gross primary production by decreasing light transmittance and respiration. High-velocity flows inhibit the buildup of autotroph biomass and reduce residence time (Glibert et al. 2014; Bernhardt et al. 2018; Hosen et al. 2019). Reduced food availability coupled with higher metabolic demand likely contributed to the reduced condition of Silver Carp in 2019. Gravid females likely had a negligible influence on measures of condition because we found no effect of sex on length–weight relationships.

The differences in length–weight relationships between segments in 2018 may relate to the differences in catch rates because segment 2 likely exhibited decreased rates of intraspecific competition. Food consumption rates have been shown to exhibit a curvilinear relationship with population density, where populations with greater abundances have reduced consumption rates resulting in reduced condition and growth rates (Amundsen et al. 2007).

Tributaries to the Missouri River system, such as the Kansas River, may be important for completing life history stages, particularly for life stages that require conditions not typically found within the main stem of the Missouri River. Low-velocity habitats have been reduced by channelization in the main-stem Missouri River (Jacobson et al. 2009), possibly increasing the importance of tributaries to Silver Carp, providing access to alternative habitats (e.g., refugia, low velocity, vegetation). Segment 1 of the Kansas River could be a recruitment source for Silver Carp in upstream segments of the Kansas River and could also be contributing to the Missouri River basin population (Werner 2020). Additional research to examine recruitment sources for Silver Carp captured in the Missouri River would provide important information for understanding Silver Carp metapopulation dynamics.

A key consideration for aquatic nuisance species management is removal to reduce population density and monitoring areas at the greatest risk of invasion (Kolar et al. 2010). Removal efforts have been shown to reduce densities of invasive carp *Hypophthalmichthys* spp. by 40% in the upper Illinois River (MacNamara et al. 2016) and could help reduce population densities of Silver Carp within the Kansas River, particularly near the confluence of the Missouri River. Focusing removal efforts on segment 1 would provide the most benefit as catch rates were highest in this segment. Monitoring in segment 3 of the Kansas River should be continued to detect early invasion before Silver Carp are able to become established. Investigating how Silver Carp utilize the vast tributary networks in the Missouri River basin will provide a greater holistic understanding of the importance of various habitats throughout the basin. Such information is invaluable when formulating and implementing a basinwide control plan.

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