Patterns in spatial use and movement of Silver Carp among tributaries and main-stem rivers: insight from otolith microchemistry analysis

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Abstract Invasive Silver Carp (Hypophthalmichthys molitrix) have established populations throughout the Missouri River basin. The main-stem Missouri River has undergone a multitude of alterations, creating a channel with greater mean depths and velocities, limiting optimal habitat for Silver Carp. Tributaries to the Missouri River may provide refuge from the swift flows within the main-stem Missouri River and, therefore, may play a vital role in the lifecycle of Silver Carp throughout the basin. Understanding the spatial extent under which these invasive fish function in this large, open river system is crucial to inform management efforts. Here, we used otolith microchemistry of Silver Carp from the Kansas River, a major tributary to the Missouri River, to reconstruct environmental histories as a means to assess the proportions of resident (individuals who never left the Kansas River system) and transient (individuals who at some point occupied the Missouri River) individuals. Silver Carp within the Kansas River were predominantly residents (adults = 54%; juveniles = 65%) with the majority of reproduction coming from within the Kansas River itself. These results suggest removal efforts in the Kansas River may be effective means of managing this invasive fish species. Transient fish exhibited short durations of signatures indicative of the Missouri River (mean percent of data points for adults = 10% and juveniles = 36%), suggesting movements into the Missouri River were brief. These results highlight the importance of connectivity of tributary habitat among large rivers and provides important information for invasive species management.

Keywords Silver Carp · Microchemistry · Invasive species management · Missouri river · Connectivity · Tributary

Introduction

Silver Carp (Hypophthalmichthys molitrix) are an invasive species from eastern Asia that invaded U.S.A. waterways in the early 1980’s (Freeze and Henderson 1982; Conover et al. 2007; Lu et al. 2020). Since their introduction, Silver Carp expanded their range to encompass the majority of the Mississippi River Basin (Conover et al. 2007), including the lower...
Missouri River drainage where they expanded as far north as North Dakota (Hayer et al. 2014). The spatial extent under which Silver Carp occur in the Missouri River drainage is unclear because of the open nature and connectivity of this large river system. The lower Missouri River (downstream of Gavins Point Dam, SD) is devoid of dams leaving approximately 1,305 river kilometers (rkm) and numerous connections to tributaries open to immigration and emigration of Silver Carp. These open corridors, coupled with Silver Carp’s ability for long, longitudinal movements (DeGrandchamp et al. 2008; Coulter et al. 2016), has aided in range expansion into and throughout the lower Missouri River drainage.

Modifications for flood control and to maintain a navigable channel (wing dikes, levies, and bank stabilization structures) are extensive throughout the lower Missouri River. These modifications created greater mean depths and velocities while also limiting lateral connectivity with the river floodplain (Galat et al. 1998; Pegg et al. 2003; Steffensen and Mestl 2016). Consequently, limited optimal habitat exists for Silver Carp in the main-stem of the Missouri River because they prefer areas with lower velocities (DeGrandchamp et al. 2008; Calkins et al. 2012). Tributaries to the Missouri River, and limited habitat behind wing dikes, may provide refuge habitat for Silver Carp seeking to escape the high velocity flows of the Missouri River (Kolar et al. 2005). Additionally, tributaries may act as stepping-stones for longitudinal movement throughout the basin.

Longitudinal connectivity between populations influences biological processes (Pegg and Chick 2010), such as gene flow, and is facilitated by transient individuals within a population. Silver Carp populations are typically comprised of fish with individual-based movement patterns where some exhibit transient behaviors and others remain lifelong residents of a given area (Coulter et al. 2016; Prechtel et al. 2018). This life strategy promotes dispersal and the colonization of new areas while also ensuring that some individuals stay in suitable habitat (Coulter et al. 2016). Dichotomy in individual based movement patterns has been documented in other riverine fishes such as Common Carp Cyprinus carpio (Butler and Wahl 2010), many salmonids (Rodriguez 2002) and Guadalupe Bass Micropterus treculii (Perkin et al. 2010). Discerning the proportions of transient and resident individuals within Silver Carp populations can provide insight for management action (Prechtel et al. 2018). For example, populations comprised mostly of resident individuals would be ideal for removal efforts. Additionally, timing these removal efforts to coincide with periods of reduced movement distances (i.e., summer months) could be effective means for removing transient individuals (Prechtel et al. 2018).

Identifying environmental history of Silver Carp using otolith microchemistry may be a viable strategy to discern the proportions of transient and resident individuals in a population. Strontium (Sr) and Barium (Ba)–in ratios to Calcium (Ca)–are two common trace elements used in otolith microchemistry analyses (Whitledge et al. 2007, 2019; Zeigler and Whitledge 2010; Crook et al. 2013; Carlson et al. 2016). Specifically, these trace elements were used to identify natal origins of Silver Carp captured in the Illinois River (Norman and Whitledge 2015) and urban Chicago fishing ponds near the Illinois River (Love et al. 2019). Here, we used otolith microchemistry to reconstruct the environmental history of Silver Carp captured in the Kansas River to determine the proportion of resident and transient individuals. Additionally, we aimed to quantify tributary (e.g., Kansas River) versus main-stem Missouri River occupancy durations of transient Silver Carp within the Kansas River. These data will provide insight into movement patterns of Silver Carp between the Missouri River and the Kansas River habitats and help to determine if removal efforts would be effective at reducing abundance of Silver Carp in the Kansas River.

**Methods**

**Study area**

The Kansas River is a large tributary to the Missouri River (Fig. 1) with origins at the confluence of the Smoky Hill and Republican rivers (Quist and Guy 1999) in Kansas, where it then flows 274 km (Makister and Paukert 2008) to its confluence with the Missouri River near Kansas City, Kansas. Discharge in the Kansas River basin is controlled by 18 federal reservoirs and over 13,000 small impoundments (Quist et al. 1999). The main-stem of the Kansas River has three major barriers, the Topeka Weir in Topeka, Kansas at river-kilometer (rkm) 141, Bowersock
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Dam in Lawrence, Kansas at rkm 84, and the Johnson County Weir in Edwardsville, Kansas at rkm 24 (Fig. 1). Bowersock Dam is a low-head hydropower dam (Quist and Guy 1999) and is the largest of the three barriers that can impede upstream longitudinal movements of riverine fishes (Eitzman et al. 2007; Dean et al. 2022), including Silver Carp (Werner et al. 2022). Our study area was the lower half of the Kansas River from the Topeka Weir, in Topeka, Kansas to the confluence with the Missouri River. We divided the Kansas River into three distinct segments associated with the three barriers on the main-stem of the Kansas River. Segment 1 is between the confluence with the Missouri River and the Johnson County Weir (24 rkm), Segment 2 is between the Johnson County Weir and Bowersock Dam (60 rkm), and Segment 3 is between Bowersock Dam and the Topeka Weir (57 rkm). No Silver Carp have been detected upstream of Bowersock Dam in Segment 3 (Werner et al. 2022). We also included a 22 rkm segment of the Missouri River and a 29 rkm segment of the Wakarusa River from its confluence with the Kansas River to the Clinton Reservoir Dam for otolith and water data collection.

Microchemistry data collection

We collected water samples in autumn 2018, winter 2019, and summer 2019 to assess spatiotemporal variations in water trace element concentrations (Ciepiela and Walters 2019). We gathered water samples from the Kansas River (Topeka Weir to
the confluence with the Missouri River; n = 25 total samples) during all three sampling events. Sampling locations in the Wakarusa River (below Clinton Reservoir to the confluence with the Kansas River; n = 5 total samples) and Missouri River (16 km upstream of the confluence to 7 km below the confluence with the Kansas River; n = 7 total samples) were added to the winter 2019 and summer 2019 sampling events for a total of 37 samples collected. Some sampling locations in the Kansas River were not collected during high water events in 2019 due to dangerous water conditions. We collected water samples using a syringe filtration technique from 13 sites across the three river systems (Kansas River = 9 sites, Wakarusa River = 2 sites, Missouri River = 2 sites) (Fig. 1) following protocols outlined in Spurgeon et al. (2018). We rinsed a 250 ml bottle a minimum of three times before collecting each water sample. We then rinsed a syringe filter and used it to filter 15 ml of water into a cleaned and rinsed collection bottle. We stored the sample bottles in a cool, dark location until we sent them to the lab for analysis. We analyzed samples for Strontium (Sr), Barium (Ba), Magnesium (Mg), and Calcium (Ca) at the University of Southern Mississippi’s Center for Trace Analysis. Data were reported as the molar concentration for each trace element and converted to element:Ca (mmol/mol) ratios (e.g., Sr:Ca, Ba:Ca, and Mg:Ca) (Whitledge et al. 2019).

We collected juvenile and adult Silver Carp from Segments 1 and 2 of the Kansas River and from the Wakarusa River in May to August of both 2018 and 2019 using a combination of electrofishing gears and mini-fyke nets (e.g., Werner et al. 2022). We extracted both lapilli otoliths from a minimum of 25 Silver Carp in Segments 1 and 2 of the Kansas River (otoliths from fish captured in the Wakarusa River were included in the total tally for Segment 2) during June, July, and August in 2018 and 2019. We analyzed one otolith from the first 25 individual fish collected from each segment in each month in 2018. In 2019, we were able to be more selective of which otoliths we used because we captured more fish in each segment (e.g., Werner et al. 2022); therefore, we selected otoliths that were devoid of cracks and other imperfections. We collected otoliths from only adult Silver Carp (>400 mm) in 2018, whereas in 2019 we collected otoliths from both juvenile Silver Carp (<400 mm) and adult Silver Carp for a total of 300 otoliths selected for laser ablation. The majority of otoliths from juvenile Silver Carp were collected in Segment 1 because juveniles were rare in Segment 2 (Werner et al. 2022). Additionally, we aimed to select otoliths for microchemistry analysis based on spatiotemporal variations on when they were collected to account for variation that may occur in trace element signatures over both time and space. We extracted otoliths by making an incision through the top of the skull into the cranial cavity and collected the otoliths using non-metallic tweezers. Then, we cleaned the otoliths of flesh and placed them in 2 ml polyethylene vials until they were prepared for ablations in the lab (Table 2).

We washed the otoliths with deionized water and allowed them to dry for 24 h. We then embedded the otoliths in epoxy (Epoxicure Epoxy Resin and Hardener, Beuhler Inc., Lake Bluffs, Illinois) and sectioned them across the transverse plane through the nucleus using a Buehler IsoMet low speed saw. We sanded otolith sections using 1,500 and 3,000 grit sandpaper and polished them to reveal annuli using 3 µm lapping paper. We then rinsed the sectioned otoliths in deionized water, adhered them to microscope slides with double sided tape, and stored them until microchemistry analysis. We analyzed the trace element composition of the otoliths using a Thermo X-Series2 inductively coupled plasma mass spectrometry coupled with a Teledyne-CETAC Technologies LSX-266 laser ablation system. Ablations (beam diameter = 20 µm, scan rate = 5 µm/sec., laser pulse rate = 5 Hz) began approximately 100 µm on one side of the nucleus, ablated completely through the nucleus, to the adjacent edge of the otolith. We analyzed a standard developed by the U.S. Geological Survey (USGS) (MACS-3, CaCO3 matrix) every 15–20 samples to adjust for instrument drift using procedures outlined by Whitledge et al. (2019). Otolith microchemistry data were converted to molar concentrations for each element and reported as element:Ca (mmol/mol) ratios (e.g., Sr:Ca, Ba:Ca, and Mg:Ca) using calcium as the internal standard and the stoichiometric concentration of calcium in aragonite Calcium Carbonate (CaCO3) (Whitledge et al. 2019).

We primarily focused on Sr:Ca ratios to classify the environmental history of Silver Carp because these trace elemental ratios have a robust and well-documented relationship with ambient water chemistry and are commonly used in microchemistry analysis.
of Silver Carp otoliths (e.g., Norman and Whitledge 2015; Whitledge et al. 2019; Love et al. 2019). Specifically, lapilli otoliths are analyzed for their Sr:Ca ratios because they are usually composed of the aragonite polymorph of CaCO$_3$ (Whitledge et al. 2019). Aragonite has a higher affinity for Sr compared to other polymorphs such as vaterite and calcite (Campana 1999; Melancon et al. 2005; Pracheil et al. 2019). A combination of Sr:Ca, Ba:Ca, and Mg:Ca ratios were used as an indicator for vaterite otoliths (Mg:Ca > 0.4 mmol/mol, Ba:Ca < 0.004 mmol/mol, and Sr:Ca < 0.1 mmol/mol) (Whitledge et al. 2019). We did not use Mg in any further reconstruction of environmental history because metabolic processes more heavily regulate Mg than Sr or Ba (Thomas et al. 2017; Hüssy et al. 2020). Any otoliths identified to be composed of vaterite were excluded from the analysis as well as otoliths with extremely high Sr:Ca values (e.g., erroneous errors in excess of realistic values such as > 10 mmol/mol).

**Data analysis**

We used otoliths collected from Silver Carp captured from Segment 2 of the Kansas River and from the Wakarusa River in 2018 to characterize the relationship between water and otolith microchemistry signatures in the Kansas and Wakarusa rivers. During low flow events—such as those in 2018—the Johnson County Weir was a barrier to upstream movement between Segment 1 and Segment 2 (Werner et al. 2022; Dean et al. 2022). Isolation of Silver Carp in Segment 2 for an extended period (e.g., > 3 months) likely facilitated trace elemental equilibrium in the signatures (e.g., Macdonald and Crook 2010). Additionally, movement rates of Silver Carp are lower during low flow events (DeGrandchamp et al. 2008; Calkins et al. 2012; Coulter et al. 2016; Prechtel et al. 2018), likely limiting movement between the mainstem Kansas River and its tributaries. We characterized the relationship between water and otolith microchemistry signatures in the Missouri River using ablation data from Silver Carp captured in isolated backwaters of the Missouri River (n = 13). Missouri River Silver Carp otolith data were provided by the Center for Fisheries, Aquaculture, and Aquatic Sciences at Southern Illinois University – Carbondale (Norman and Whitledge 2015). We isolated trace elemental ratio data at the edge of the selected otoliths (~30 µm) to characterize the relationship between water and otolith signatures in the Kansas, Missouri, and Wakarusa rivers (Norman and Whitledge 2015; Spurgeon et al. 2018). These data were used in the following tests and model construction.

We grouped water samples and otoliths by river of sample collection and assessed differences using univariate and multivariate methods. Tests of normality (i.e., Shapiro–Wilk tests [Shapiro and Wilk 1965]) indicated water and otolith microchemistry data deviated from normality, thus we proceeded with non-parametric tests. We used a permutated multivariate analysis of variance (perMANOVA) (Anderson 2001) to examine the differences in otolith and water trace elemental signatures between river systems, adjusting the P-value using the Bonferroni method for pairwise comparisons (α = 0.05/3 = 0.0167). We then used a Kruskal–Wallis test (Kruskal and Wallis 1952) followed by a post hoc Dunn’s test (Dunn 1964) to examine pair-wise differences in water and otolith trace elemental signatures between river systems, adjusting the P-value for multiple comparisons using the Holmes method.

We used a recursive partitioning modelling approach to separate trace elemental signatures in Silver Carp otoliths between river systems. We built the recursive partitioning tree using the rpart package (Thernau et al. 2019) in program R (R Core Team 2020). Recursive partitioning trees aim to split the data into homogeneous groups to increase the homogeneity of the elements (i.e., trace elemental ratios) within groups (i.e., rivers) (Dinov 2018). We used a splitting criterion based on the Gini impurity index (e.g., Spurgeon et al. 2018) and selected the tree within one standard error to the tree with the lowest cross-validated error (Spurgeon et al. 2018; Thernau et al. 2019). We then used the resulting partitioning tree to predict the trace elemental threshold that distinguished each river. We classified individual Silver Carp captured in the Kansas River and Wakarusa River as “transient” if they had signatures indicative of the Missouri River or “resident” if they lacked those signatures.

We determined the proportion of transient adult and juvenile Silver Carp in Segments 1 and 2 in both 2018 and 2019. Additionally, we determined the proportion of transient Silver Carp that were male and female by examining the gonads of each individual to examine sex-specific movement patterns. We then isolated ablation data from the nucleus of the otolith
by measuring the diameter of the nucleus and extracting data pertaining to that segment of the ablated transect to determine the proportion of Silver Carp in the Kansas River with natal origins from the Missouri River. We also enumerated movement events between the Missouri River and other water bodies. We classified movement events as a shift in trace element data to signatures indicative of the Missouri River at any point along the ablated transect. We also aimed to quantify the percent of time each transient fish spent in the Missouri River versus other adjacent water bodies in the drainage to gain insight on habitat use by Silver Carp in the basin. To do so, we calculated the percent of Sr:Ca data points indicative of the Missouri River (i.e., percent of points in each spike; Fig. 5) for each transient fish. We then plotted this value for each individual by its total length.

Results

Water chemistry

Multivariate comparisons among rivers indicated water trace elemental signatures (i.e., the combination of Sr:Ca and Ba:Ca ratios) differ between the Kansas River and Wakarusa River ($F = 74.3, r^2 = 0.726, P = 0.003$), Kansas River and Missouri River ($F = 24.1, r^2 = 0.445, P = 0.003$), and Wakarusa River and Missouri River ($F = 41.1, r^2 = 0.804, P = 0.012$). Univariate comparisons indicate water Sr:Ca ratios ($\chi^2 = 22.5, P < 0.001$) and Ba:Ca ratios ($\chi^2 = 13.9, P < 0.001$) differ among rivers. Pair-wise comparisons revealed that water Sr:Ca ratios were higher in the Kansas River than both the Missouri River ($Z = 3.14, P = 0.003$) and the Wakarusa River ($Z = 4.09, P < 0.001$). However, water Sr:Ca ratios were similar between the Wakarusa River and the Missouri River ($Z = 1.13, P = 0.26$). Water Ba:Ca ratios were similar between the Kansas River and Missouri River ($Z = -1.6, P = 0.111$). Water Ba:Ca ratios were lower in the Wakarusa River than either the Kansas River ($Z = 3.01, P = 0.005$) or the Missouri River ($Z = 3.68, P < 0.001$) (Fig. 2).

Water Sr:Ca and Ba:Ca ranges reported here from the Missouri River (Fig. 2) overlap with ranges reported by Whitlege et al. (2019) and incorporate a mean Sr:Ca concentration in the Missouri River downstream of the Kansas-Missouri confluence reported by Phelps et al. (2012). Additionally, Phelps et al. (2012) reported a Sr:Ca value of 3.5 mmol/mol in the Kansas River, which falls within the 1.5 interquartile range of Sr:Ca concentrations reported here (Fig. 2).

Otolith chemistry

We used data from the edge of the otoliths collected from a total of 73 adult Silver Carp with a mean total length of 671 mm (sd = 46 mm) to classify the relationship between water and otolith microchemistry in the Kansas River (n = 59) and Wakarusa River (n = 14), and data from the edge of the otoliths from 13 adult Silver Carp from the
Missouri River. Additionally, we used this subset of data, and further randomly divided it, to train (Kansas River: \( n = 48 \), Wakarusa River: \( n = 11 \), Missouri River: \( n = 9 \)) and test (Kansas River: \( n = 11 \), Wakarusa River: \( n = 3 \), Missouri River: \( n = 4 \)) the recursive partitioning tree model for the following, larger analysis. Multivariate tests among rivers of capture indicated otolith trace elemental signatures did not differ between otoliths collected from the Kansas River and Wakarusa River (\( F = 7.47, r^2 = 0.095, P = 0.027 \)), but did differ between otoliths collected from the Kansas River and Missouri River (\( F = 84.6, r^2 = 0.547, P = 0.003 \)), and the Wakarusa River and Missouri River (\( F = 75.5, r^2 = 0.751, P = 0.003 \)). Univariate tests indicate otolith trace elemental signatures differed among rivers of capture in both Sr:Ca ratios (\( \chi^2 = 38.8, P < 0.001 \)) and Ba:Ca ratios (\( \chi^2 = 34.5, P < 0.001 \)). Pair-wise comparisons revealed Sr:Ca ratios were higher in otoliths collected from the Missouri River than otoliths collected from either the Kansas River (\( Z = −5.05, P < 0.001 \)) or the Wakarusa River (\( Z = 6.06, P < 0.001 \)). Additionally, Sr:Ca ratios were higher in otoliths collected from the Kansas River than otoliths collected from the Wakarusa River (\( Z = 2.65, P = 0.008 \)). Barium:Calcium ratios were higher in otoliths collected from the Missouri River than otoliths collected from either the Kansas River (\( Z = −5.86, P < 0.001 \)) or the Wakarusa River (\( Z = 3.48, P < 0.001 \)). However, Ba:Ca ratios did not differ between otoliths collected from the Kansas River and Wakarusa River (\( Z = −1.27, P = 0.127 \)) (Fig. 3).

The recursive partitioning tree correctly classified 100% of fish collected in the Kansas River, 50% in the Missouri River, and 0% in the Wakarusa River. However, all fish collected from the Wakarusa River were classified as fish from the Kansas River (Table 1). Thus, our model could only be used to

Table 1  Classification matrix for Silver Carp collected from Segment 2 of the Kansas River and from the Wakarusa River in 2018, and from isolated backwaters of the Missouri River used to build and test the recursive partitioning tree

| Predicted       | Sampled          |
|-----------------|------------------|
|                 | Kansas river | Missouri river | Wakarusa river |
| Kansas river    | 11           | 2             | 3              |
| Missouri river  | 0            | 2             | 0              |
| Wakarusa river  | 0            | 0             | 0              |

Fig. 3  Comparison of otolith microchemistry signatures (~30 \( \mu \text{m} \) of data isolated from the edge of the otolith) from Silver Carp captured from Segment 2 of the Kansas River in 2018, the Wakarusa River in 2018, and isolated backwaters of the Missouri River. The horizontal solid line within the box represents the median value, upper and lower limits of the box are quartile ranges, and whiskers are 1.5 interquartile range. Points represent data outside of the 1.5 interquartile range. Median otolith Sr: Ca and Ba: Ca ratios do not differ between rivers that bear the same letter above the box plot. The dashed horizontal line on the Sr: Ca plot represents the threshold between the Kansas and Missouri River (2.082 mmol/mol Sr:Ca)
distinguish between the Kansas River and the Missouri River (Sr:Ca > 2.082 mmol/mol was indicative of the Missouri River; Fig. 3). Ba:Ca was the most influential variable in our model (variable importance score = 57) followed by Sr:Ca (variable importance score = 43). The inclusion of Ba:Ca in the model did not refine the model enough to be able to further distinguish between the Wakarusa River and the Kansas River and between the Wakarusa River and the Missouri River. Additionally, Ba:Ca data were more erratic with numerous erroneous data points across all individuals while the Sr:Ca data were more consistent. Therefore, we exclusively used Sr:Ca ratios in environmental history reconstruction.

The vaterite polymorph of CaCO₃ was not detected in any of the otoliths analyzed, however, 24 otoliths were left out of the analysis due to reported erroneous values that exceeded realistic values. There were no indications that cracks or other imperfections in the otoliths interfered with laser ablation results.

We reconstructed environmental histories of 276 (n = 239 adult; n = 37 juvenile) Silver Carp with approximately 46% of adults and 35% of juveniles classified as transient individuals. The proportion of transient individuals among sampling years and segment of capture for adult Silver Carp was consistently 45%–49%, except in Segment 1 (downstream of the Johnson County Weir; Fig. 1) during 2019 where the proportion of transients was approximately 22%. Juvenile Silver Carp were predominantly residents in 2019 with approximately 65% of individuals sampled lacking trace elemental ratios indicative of the Missouri River (Table 2). About 57% (n = 37) of transient fish we identified sex for were male and approximately 43% (n = 28) were female.

Approximately 17% (n = 19) of transient adult Silver Carp had natal origin signatures indicative of the Missouri River, 10 of which were captured in Segment 1 and the remaining 9 were captured in Segment 2. Approximately 46% (n = 6) of transient juvenile Silver Carp had natal origin signatures from the Missouri River. Five were captured in Segment 1 and one was captured in Segment 2. Overall, approximately 9% (n = 25) of all fish sampled for microchemistry analysis had natal origins predicted to be from the Missouri River (Table 3).

A single movement event into the Missouri River was most common for both adult (n = 82) and juvenile (n = 10) transient Silver Carp. Two movement events occurred less often for adults and juveniles. Approximately 22% of transient adults (n = 24) and 23% of transient juveniles (n = 3) exhibited two movement events. Three movement events were exceedingly rare in adults (n = 3) while no juveniles captured exhibited three movement events (Table 3).

Transient juvenile Silver Carp exhibited a greater percent of points above the Missouri River threshold (i.e., percent of points in each spike) than transient adult Silver Carp. The percent of points above the Missouri River threshold for adults was less than 30% for the majority of the individuals, ranging from approximately 2% to 36% of points. Juveniles were more erratic, ranging from approximately

| Segment 1 | Segment 2 | Segments Combined |
|-----------|-----------|------------------|
| Adult Silver Carp | 49% (n = 69) | 49% (n = 72) | 49% (n = 141) |
| 2018 | 22% (n = 18) | 45% (n = 80) | 41% (n = 98) |
| 2019 | 44% (n = 87) | 47% (n = 152) | |
| Years Combined | N/A (n = 0) | N/A (n = 0) | N/A (n = 0) |
| Juvenile Silver Carp | 34% (n = 32) | 40% (n = 5) | 35% (n = 37) |
| 2018 | 34% (n = 32) | 40% (n = 5) | |
| 2019 | N/A (n = 0) | N/A (n = 0) | N/A (n = 0) |
| Years Combined | N/A (n = 0) | N/A (n = 0) | N/A (n = 0) |

| Number of movement events | Natal origins from the Missouri River |
|---------------------------|-------------------------------------|
| 1 | 2 | 3 |
| Adult Silver Carp | 25 | 12 | 1 | 10 |
| Segment 1 | 57 | 12 | 2 | 9 |
| Segment 2 | 9 | 2 | 0 | 5 |
| Juvenile Silver Carp | 1 | 1 | 0 | 1 |

Table 2 Percent transient adult and juvenile Silver Carp in Segment 1 and Segment 2 of the Kansas River, and in both segments combined in 2018 and 2019. Total number of fish analyzed for otolith microchemistry are in parenthesis.

Table 3 Number of transient adult and juvenile Silver Carp captured in the Kansas River that exhibit 1, 2, and 3, movement events into the Missouri River for each segment. Natal origins from the Missouri River is the number of transient individuals with Missouri River Sr:Ca signatures at the nucleus of the otolith.
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10% to 71% of points. Overall, there was a negative relationship between the percent of points above the Missouri River threshold and total length (Fig. 4).

**Discussion**

Examination of otolith trace elemental signatures may be a useful tool in reconstructing environmental histories and predicting natal origins of Silver Carp in the Kansas River and Missouri River systems. Our study indicated the population within the Kansas River is comprised of predominantly residential individuals, having a consistent signature indicative of the Kansas River throughout the life-span of the fish. Therefore, recruitment from within the Kansas River system is regularly occurring without connectivity to additional river systems. Segment 1 may be of particular importance for reproduction as most juvenile Silver Carp were documented in this reach (Werner et al. 2022). Segment 1 has an average depth less than 1.5 m and is characterized by low velocity flows (Eitzmann and Paukert 2010). These habitat conditions are typically where age-0 Silver Carp are found at higher densities (e.g., Haupt and Phelps 2016) and are habitats commonly used as nursery grounds (Kolar et al. 2005; Conover et al. 2007; Milardi et al. 2017).

River fish communities have been found to contain both stationary (i.e., resident) and mobile individuals, where the proportion of mobile fish approximate 25–30% (Radinger and Wolter 2014). Mobile fish are an important component in riverine systems, facilitating dispersal, recolonization, and gene flow (Booth et al. 2013; Radinger and Wolter 2014; Peacock et al. 2016). In addition, differential movement patterns within a population have been described for invasive species dispersal. Stratified diffusion is where both short and long-distance dispersers coexist, helping to facilitate rapid invasion of new habitats and increasing genetic diversity (Hengeveld 1989). Long-distance dispersers help to identify new habitat patches, whereas, short dispersers use local habitat to increase density through reproduction and recruitment. Silver Carp in the Kansas River appears to follow the stratified diffusion model, where approximately 40–50% of individuals were considered mobile. The high proportion of mobile individuals in this system indicates high dispersal capabilities and invasion risk for areas further upstream and in connected drainages.

Our data show that about 20% of all transient adult and juvenile Silver Carp in the Kansas River had natal origin signatures indicative of the Missouri River. Natal origins of the other 80% of the transient individuals were not identified because of the lack of microchemistry data throughout the basin. These results are noteworthy because Deters et al. (2013) documented the highest drifting egg densities in the main-stem Missouri River while samples collected in tributaries (e.g., Lamine River, Bonne Femme Creek, Perch Creek, Moniteau Creek, Moreau River, and Osage River) had significantly lower densities. However, Camacho et al. (2020) documented egg production in tributaries to the upper Mississippi River. This provides evidence that tributary habitats can be used for reproduction and is likely a function of select habitat availability. Therefore, it is likely that select tributaries throughout the Missouri River basin—such as the Kansas River—may be sources of reproduction and recruitment for Silver Carp. Identifying these sources throughout the basin would provide information as to where control efforts should be focused. Additionally, these data could reveal source-sink dynamics between the main-stem Missouri River and adjacent systems.
Transient Silver Carp exhibited trace elemental signatures indicative of the Missouri River for relatively short durations (e.g., Fig. 5). These results indicate that transient Silver Carp occupied the Missouri River for less time compared to other systems (Fig. 4). Brief occupancy (i.e., <30% of data points on the ablated transect) in the Missouri River is likely influenced by the lack of optimal habitat available for Silver Carp. Additionally, higher velocity flows in the Missouri River (e.g., Pegg et al. 2003) prevents the buildup of autotrophic biomass and reduces residence time (Hosen et al.; 2019), limiting food availability for Silver Carp in this system. Areas with lower velocities, like the Kansas River and areas behind wing dikes, may provide habitat with higher resource availability as well as refuge from the swift flows within the main channel (e.g., DeGrandchamp et al. 2008; Calkins et al. 2012; Coulter et al. 2016).

A few of the transient Silver Carp we analyzed had trace elemental signatures that indicated multiple movement events through the Missouri River. These results suggest the Missouri River may function more as a movement corridor for Silver Carp as they migrate between areas of suitable habitat. Further research on movement patterns of Silver Carp throughout the Missouri River basin is needed to test this hypothesis because management of these invasive fish may be better suited focusing on the multitude of tributary habitats throughout the Missouri River drainage rather than the main-stem Missouri River. Movement events into the Missouri River are likely induced by a variety of factors. For example, increased movement rates as a response to a rise in river flood stage has been documented for adult Silver Carp (Peters et al. 2006; DeGrandchamp et al. 2008; Coulter et al. 2016). Increased movement rates could facilitate movement events into the Missouri River as transient individuals seek new habitats (Prechtel et al. 2018). Additionally, broad scale upstream movements occurring in the spring typically occur as Silver Carp stage for spawning events (Coulter et al. 2016). Brief forays into the Missouri River could occur as Silver Carp seek suitable spawning habitat located in the Missouri River itself or other tributaries in the basin.

We can distinguish habitat use between the Kansas River and Missouri River because of differences in water and otolith trace elemental signatures. However, otolith trace elemental signatures of the Wakarusa River and Kansas River were too similar to distinguish use between these two water bodies, even with the incorporation of multiple trace elements (e.g., Sr:Ca and Ba:Ca). The paucity of water and otolith microchemistry data throughout the Missouri River basin limited our analysis to only between the Kansas and Missouri rivers. Water chemistry signatures have been classified for the Platte River in Nebraska (e.g., Phelps et al. 2012; Spurgeon et al. 2018) and throughout the main-stem of the Missouri River below Gavins Point Dam, SD (e.g., Phelps et al. 2012; Norman and Whitledge 2015; Porreca et al. 2016; Spurgeon et al. 2018; Whitledge et al. 2019). However, other tributaries in the Missouri River drainage remain to be analyzed. Classification of these other tributaries will lead to insights in movement and recruitment sources of Silver Carp throughout the Missouri River basin.

Fig. 5 Example of ablation data from three Silver Carp captured from the Kansas River that exhibit trace elemental signatures indicative of the Missouri River. The horizontal line represents the threshold between the Kansas and Missouri Rivers (Sr:Ca = 2.082 mmol/mol) where signatures above the line are from the Missouri River. The shaded region is data that corresponds to the nucleus of the otolith (i.e., natal origins). Fish number 180208–2 had natal origin signatures from the Missouri River as well as another movement event with signatures from the Missouri River later in life. Fish 180,236–18 and 190,241–8 both have movement events with signatures from the Missouri River.
Additional otolith trace elemental signatures need to be characterized throughout the Missouri River drainage (Hüssy et al. 2020). Our results demonstrate that the relationship between otolith and water signatures may not always be a positive linear relationship (Figs. 2 and 3) and instead may resemble a logistic curve. Models built by Norman and Whitledge (2015) predicted otolith Sr:Ca ratios for Silver Carp captured from the Kansas River would be centered around 3.6 mmol/mol. However, we observed consistent values of approximately 1.5 mmol/mol (Fig. 3). These differences could be explained by contamination, instrumental miscalibration, or procedural errors. However, the predicted otolith Sr:Ca values for the Wakarusa (~ 1.65 mmol/mol) is within the 95% confidence intervals of the observed values (Fig. 3), indicating these errors were negligible. Biotic and abiotic factors such as salinity, temperature, oxygen, ontogeny, food and growth, and maturation can influence how trace elements are incorporated into the crystal lattice (Campana 1999; Norman and Whitledge 2015; Sturrock et al. 2015; Hüssy et al. 2020). One of these factors, or a combination of such, could have caused the negative relationship between otolith and water Sr:Ca values we observed in the Kansas River. Although these factors do not exert a strong influence on the biomineralization process of otolith formation (Hüssy et al. 2020), they could influence physiological processes governing trace element uptake and transport.

The Kansas River affords a unique opportunity for direct management and possible reduction of Silver Carp abundance because of the higher proportion of resident individuals. For example, removal efforts may be a viable option in the Kansas River and should focus on Segment 1 because this reach is likely where reproduction is occurring and where Silver Carp catch rates were the highest (Werner et al. 2022). Timing removal efforts to coincide with periods when Silver Carp are least active, such as during the late summer and early fall months (DeGrandchamp et al. 2008; Coulter et al. 2016), could have impacts throughout the Missouri River basin by removing a larger portion of transient individuals (Prechtel et al. 2018). Gears targeting all size groups, such as the electrified dozer trawl (Hammen et al. 2019; Werner et al. 2022), should be used to maximize effort (Tsehaye et al. 2013), particularly during years when age-0 Silver Carp are confined to Segment 1 (e.g., Werner et al. 2022).

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Author contributions J P. W – Contribution to conception and design, acquisition of data, and analysis and interpretation of the data. Drafting the article and final approval. Q J. D – Contribution to conception and design, acquisition of data, and interpretation of the data. Revising the article critically for important intellectual content, and final approval. M A. P – Contribution to conception and design and interpretation of the data. Revising the article critically for important intellectual content, and final approval. M J. H – Contribution to conception and design and interpretation of the data. Revising the article critically for important intellectual content, and final approval.

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Data availability All datasets analyzed during the current study are available from the corresponding author on request.

Code availability All the R code used for this study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing or conflicts of interest.

Ethical approval Data collected for this study were in compliance with Institutional Animal Care and Use Committee ID 1271. Collection of specimens was in accordance with Scientific Collectors permit SC-104–2018 issued by the Kansas Department of Wildlife, Parks and Tourism.

Consent to participate Not applicable.

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