Project Title: Upper Mississippi River Silver Carp Demographics

Geographic Location: Ohio River-IL/MO/KY, Headwaters Diversion Channel-MO/IL, Big Muddy River-IL/MO, Kaskaskia River-IL/MO, Meramec River-MO/IL, Pool 26-MO/IL, Pool 25-MO/IL, Pool 24-MO/IL, Pool 22-MO/IL, Pool 21-MO/IL, Pool 20-MO/IL/IA, Pool 19-IA/IL, and Pool 18-IA/IL along the main stem of the Upper Mississippi River.

Lead Agency: U.S. Fish and Wildlife Service (USFWS) Columbia Fish and Wildlife Conservation Office (FWCO), Edward Sterling and USFWS La Crosse FWCO, Yu-Chun Kao

Participating Agencies: USFWS Carterville FWCO

Statement of Need: Although Williamson and Garvey (2005) and Seibert et al (2015) quantified basic population and ecological characteristics of Silver Carp captured from the Mississippi River, a comprehensive baseline for their relative abundance and demographics along the Upper Mississippi River (UMR) has not yet been developed. Furthermore, quantifying annual fluctuations in the relative abundance and demographics of Silver Carp can provide insights into the status of their populations across a broad spatial scale. This, in turn, facilitates the assessment of management and control measures for this invasive species on an annual basis. This project was, therefore, designed to develop a 2021–2023 baseline of Silver Carp relative abundance and population demographics along the UMR main stem.

Project Objectives:

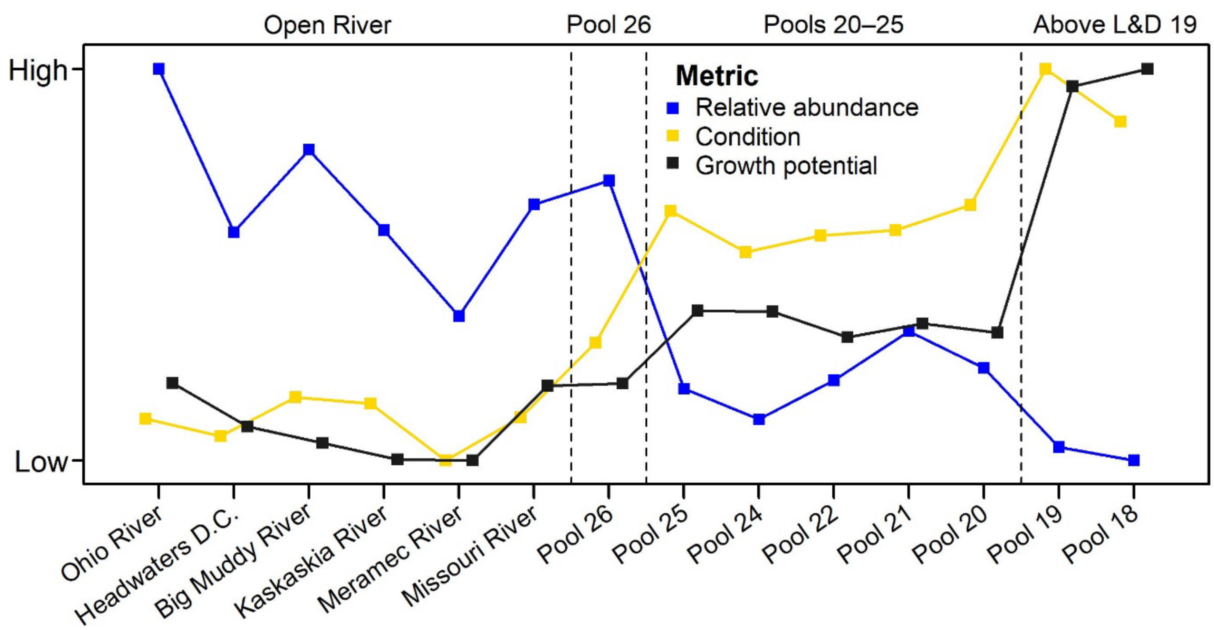
1) To assess the relative abundance, size structure, body condition, proportion of males, age structure and recruitment, and growth and mortality of Silver Carp in the UMR.
2) To define reasonable spatial units to investigate annual changes in Silver Carp relative abundance and demographics in the UMR.

Project Highlights:

- Established baseline SVCP demographic rates (I.e., Length, Weight, and Age structure, sex, condition, and growth) along a gradient of >430 river miles of the UMR utilizing standardized electrified dozer trawl sampling.
- Identified that SVCP abundance generally decreases from upstream to downstream locations.
- Identified that growth rate and condition of SVCP are negatively correlated with abundance.
- Pool 26 appeared to be a unique population where growth and condition were increased along with high abundance of SVCP.
- Large 2018-2019 cohorts were able to be tracked with age data in Pool 26 and Open River locations.

- A large 2016 cohort dominated the catch above LD 19, but new young cohorts (2020-2023) were identified above LD 19 with standard electrified dozer trawl sampling.
- We recommend continued management actions in the IMZ alongside increased management actions in Pool 26 and Open River locations.

Graphic summary for the 2021−2023 baseline UMR Silver Carp demographics



Methods:

Study area—The UMR extends from the headwaters in Minnesota to the confluence of the Ohio River and is characterized by 29 lock and dam (L&D) structures creating a series of navigation pools and an open river reach (Fremling et al. 1989). Contracted fishing and research funded through the UMR Invasive Carp Team (UMRICT) showed that densities of invasive Silver Carp below L&D 19 (Keokuk, IA) are considerably higher than those above the L&D. Furthermore, there is evidence of reproduction and recruitment below L&D 19 but reproduction is limited above it (WIU & ILDNR 2018; MDC 2017). These differences in Silver Carp population's likely result from low immigration to locations above L&D 19, which has a head height of 11.6 m at minimum flow. Except for movement through the lock chamber, L&D 19 is a barrier to upstream fish movement (Wilcox et al. 2004). This study focuses on 14 locations along the main stem of the UMR, which can be grouped into three reaches: (1) "above L&D 19", which includes Pools 18 and 19, (2) "pooled reach", which includes Pools 20–26, and (3) "open river", which includes six locations along the free-flowing section between the confluence of the Missouri River near St. Louis, MO to the confluence of the Ohio River near Cairo, IL (Figure 1; Table 1).

Site selection—Sample sites were selected using a random sampling design stratified by aquatic habitat type (Wilcox 1993). Habitats were classified into main channel border, side channel border, backwater, and tributary habitats, by using cover/use data sets from the Upper Mississippi River Restoration Program Long Term Resource Monitoring Element. Within each of the 14 sample locations, a minimum of 20 sites were selected. The number of sample sites allocated to each habitat type is proportional to the area of that habitat type within the sample location. Further details for sample site selection and history are given in our 2022 Report (Project: Upper Mississippi River Silver Carp Demographics, MICRA 2023).

Field collections—During 2021, surveys were conducted using the electrified dozer trawl (hereafter dozer trawl; Hammen et al. 2019) and the modified electrofishing technique (Bouska et al. 2017). These two methods were selected because of their effectiveness in capturing Silver Carp and their continued use throughout the Mississippi River Basin to monitor Silver Carp populations. Results of the 2021 surveys indicated that both methods were effective and captured a similar size distribution of Silver Carp. Catch rates were, however, higher when using the dozer trawl. Thus, we focused on dozer-trawl surveys in 2022 and 2023. At locations above L&D 19, where Silver Carp abundance is low, additional data for length, weight, sex, and age were collected from fisheries-dependent sampling of commercial gill-net catches.

All fish captured were enumerated by the lowest identifiable taxonomic level and measured for total length (TL; mm). Silver Carp with >250 mm TL were categorized as “stock-sized” (Phelps and Willis, 2013) and were weighed to establish the weight–length relationship. Sex was determined for stock-sized Silver Carp based on the presence or absence of pronounced ridges on the dorsal surface of pectoral fins, which indicates the fish is male or female, respectively (Wolf et al. 2018). Any Silver Carp for which exterior determination of sex was inconclusive were evaluated via internal examination.

At each sample location, lapilli otoliths were extracted from the first 100 Silver Carp captured, with a maximum of 20 Silver Carp per site. Following the first 100 collected, otoliths were extracted from any Silver Carp in an unfilled 50 mm length bin for growth analysis. For each length bin, a minimum of ten individuals was targeted.

Aging Silver Carp—Lapilli otoliths were aged by personnel from the USFWS Columbia, La Crosse, and Carterville FWCOs. One otolith per fish was prepared by sanding or sectioning each otolith to expose the transverse plane. Otolith preparation was finished with sandpaper using a sequence of 600, 800 and 1,000 grit sandpaper, and polished with lapping film. Sanded otoliths were mounted in putty, submerged in glycerol, illuminated with a fiber optic light, and viewed using a Nikon SMZ25 dissecting scope.

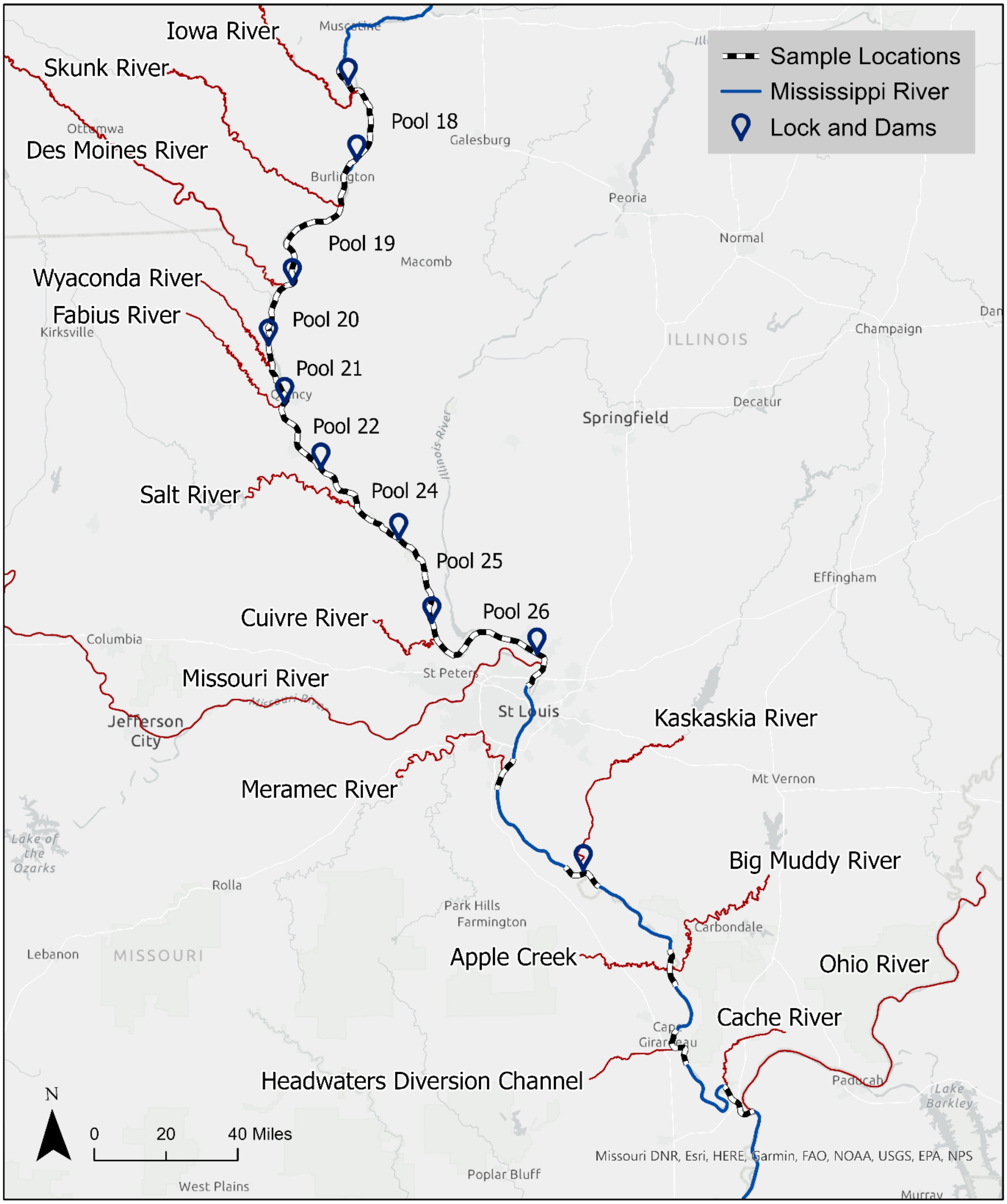


Figure 1. *The area sampled for Silver Carp during fall, from late July to September, 2021–2023. Sample locations are designated as black and white areas and tributaries where surveys were conducted are highlighted in red. The southernmost dam in the figure is located near the mouth of the Kaskaskia River, whereas all other dams are in the main stem Mississippi River.*

Sectioned otoliths were mounted to a slide, submerged in glycerol, and viewed using the illuminator light from beneath the slide. If the first otolith was unreadable, the second was similarly prepared and analyzed. Three readers aged each otolith independently, then a final age was recorded using a minimum of two-thirds consensus (Maceina and Sammons 2006; Seibert and Phelps 2013). If the consensus was not initially reached, the readers reviewed the otolith until an agreement was achieved (Maceina and Sammons 2006), which could result in a "no determination" (ND) age classification.

Data analysis—To assess the relative abundance of Silver Carp, we used dozer-trawl catch per unit effort (CPUE) of stock-sized Silver Carp as an index. Only stock-sized Silver Carp were used for this relative abundance index because they are assumed to be fully recruited to the survey gears (Project: Invasive Carp Demographics, ICRCC-MRWG 2021). By exclusively utilizing data from dozer-trawl surveys, we addressed the issues related to gear selectivity, ensuring that this index of relative abundance is comparable across locations and years.

To assess size structure, body condition, proportion of males, age structure and recruitment, and growth and mortality of Silver Carp in UMR, we analyzed data from dozer-trawl surveys, complemented by data from fisheries-dependent sampling at locations above L&D 19. Altogether, the data for Silver Carp at locations above L&D 19 comprised 74 individuals from dozer-trawl surveys and 78 individuals from fisheries-dependent sampling.

To assess size structure and body condition, we visualized the total length frequency of stock-sized Silver Carp across reaches and sample years and compared the relative weight (Wr) of all Silver Carp across sample locations. The relative weight is the ratio of observed weight to standard weight of a fish of a given TL. The standard weight was calculated using an empirical equation specific for UMR Silver Carp

$$Ws = CF \times \beta_1 \times TL^{\beta_2} \quad (1)$$

where *Ws* represents the standard weight, *CF* is a correction factor for logarithm transformation bias (Sprugel, 1983), *TL* is the total length, and β_1 and β_2 are parameters to be estimated by fitting this equation to data collected in 2021–2023. The correction factor was needed here because the parameters β_1 and β_2 were estimated by fitting the logarithm-linearized equation

$$\ln(Ws) = \ln(\beta_1) + \ln(\beta_2) \times TL \quad (2)$$

to data of stock-sized Silver Carp weighted by the inverse of the number of survey sites within each reach and year (i.e., a weighted simple linear regression model method; Zar 1999). This weighted approach was employed to ensure that each reach and year contributed equally to the overall analysis, without being biased by the difference in sample effort. This means that a larger sample size in any given reach and year was a reflection of its higher Silver Carp density in this analysis, rather than a result of higher survey effort.

The proportion of male Silver Carp was calculated by dividing the number of males by the total number of sexed individuals at each location. Although the investigations on the differences in size structure, age structure, and growth rates between sexes may be of some interest, they were not pursued in this project as they do not align with our primary objectives. The proportion *z*-tests (Zar 1999) were used to investigate whether the proportions of males were > 50% at a significance level of $\alpha = 0.05$ across sample locations and years.

To assess age structure and recruitment, we visualized the age frequency of stock-sized Silver Carp across reaches and sample years, with a goal to identify strong year classes. We also assessed catches of age-0 Silver Carp across locations and sample years, with a goal to identify potential spawning locations and strong cohorts.

To assess growth and mortality, we estimated parameters in the von Bertalanffy (1938) growth model by fitting it with our length-at-age data. Data of age-0 and age-1 individuals were excluded due to the large sample size and large variation in TL (N = 3,973; range = 20–303 mm) and the small sample size (N = 8), respectively. The model was expressed as

$$L(t) = L_\infty \times \left[1 - e^{-K\times(t-t_0)}\right] \quad (3)$$

where $L(t)$ is the mean fish length at age t, L_∞ is the theoretical maximum fish length, K is the Brody growth coefficient, and t_0 represents the adjustment for the difference between the integer age, determined by counting annuli, and the actual age at which the carp was captured. To estimate the parameters L_∞, K, and t_0, we used a nonlinear mixed model approach. Specifically, L_∞ and K were modeled as mixed-effects variables, incorporating fixed effects that are constant across locations and random effects that are specific to each location or reach. Conversely, t_0 was modeled as a fixed-effects variable, ensuring consistency across all locations. This approach is justified by the fact that all fish hatch roughly at the same time and are then captured roughly at the same time each year. For example, should all fish hatch in June and be captured in September, the estimate of t_0 would approximate 0.3 across all locations. The estimates of L_∞ and K were later used to empirically estimate the natural mortality rates (M), by location and by reach, following the updated Pauly (1980) equation described in Then et al. (2015)

$$M = 4.118 \times K^{0.73} \times L_\infty^{-0.333} \quad (4)$$

where L_∞ (in cm) and K are growth parameters from the von Bertalanffy growth model.

Based on available information, we endeavored to identify the appropriate spatial unit within UMR for investigating how Silver Carp demographics vary from one unit to another and change over time. While the lock and dam structures provided a basis for treating each reach as a spatial unit, we regarded this as a starting point. We considered a spatial unit appropriate if Silver Carp within it exhibit similar relative abundance across sample locations. Consequently, we used a general linear model approach (Zar, 1999) to analyze whether a finer spatial resolution is necessary to describe changes in the CPUE (*CPUE*) of stock-sized Silver Carp across years. These models were expressed as

$$ln(CPUE + \delta) \sim Year + Location \quad (5)$$

where δ is a small positive value added to *CPUE* to avoid undefined ln(0), which was defined as half of the minimal positive CPUE, *Year* represents sample year, and *Location* represents sample location. Both *Year* and *Location* were included in the model as categorical variables. We deemed a study unit as appropriate if the general linear model showed that *Location* is not significant at an $\alpha = 0.05$ level.

All analyses were performed in R 4.3.1 (R Core Team 2023).

Results and Discussion

Herein, we update 2021–2022 summary results with fall 2023 data collected by the USFWS Columbia, La Crosse, and Carterville FWCOs. These data have been shared among offices and are available upon requests through the lead agencies. Overall, dozer-trawl surveys were conducted at a total of 359 sites during fall 2023 (Table 1). These efforts resulted in the collection of 1,837 Silver Carp (1,833 stock-sized) from 14 sample locations in the UMR.

Table 1. *Summary of sample effort (number of dozer-trawl survey sites; N), Silver Carp catch, and range of Silver Carp total length (TL) of dozer-trawl surveys across the 14 sample locations (Location) in the Upper Mississippi River during fall 2023. Note that river mile was set to 0 at the confluence of the Ohio River.*

Location	River Miles	N	Total Catch	Stock-sized	TL Range (mm)
Pool 18	410–437	29	0	0	–
Pool 19	365–410	34	61	58	90–850
Pool 20	343–365	27	76	76	575–826
Pool 21	325–343	25	77	77	600–825
Pool 22	301–325	25	45	45	619–819
Pool 24	273–301	25	43	43	627–856
Pool 25	242–273	23	60	60	631–850
Pool 26	203–242	24	204	203	158–780
Missouri River	191–198	25	307	307	407–900
Meramec River	157–164	17	341	341	480–930
Kaskaskia River	114–120	16	244	244	480–765
Big Muddy River	73–79	22	189	189	510–863
Headwaters Diversion Channel	46–52	20	89	89	550–880
Ohio River	0–8	47	101	101	576–1,004
Summary	0–437	359	1,837	1,833	90–1,004

Relative abundance—Silver Carp CPUE varied spatially and temporally during 2021–2023. Variability of CPUE values across sample locations was expected due to the large spatial extent and population fragmentation from dams. Variability within sample locations across years is likely due to fluctuating catchability between surveys. Fluctuations in catchability can be largely attributed to water levels changing annually. For example, extremely low water made surveys at the Ohio River and Headwaters Diversion Channel difficult in 2023, resulting in abnormally low catch rates.

Although variability existed among sample locations and years, clear patterns among river reaches were evident in Silver Carp relative abundance. Over the three years of surveys, the general trend in Silver Carp CPUE was about 100/hr or higher at locations within the open river reach, about 50/hr or lower at locations in the pooled reach except Pool 26, where CPUE was generally above 100/hr, and about 1/hr at the two locations above L&D 19 (Figure 2). There were several exceptions to these trends, including the low CPUE observed in a couple locations and years in open river locations, the high CPUE in 2021 at Pools 20 and 21, and the high CPUE in 2023 at Pool 19. We note that the low CPUE in the open river reach were likely associated with reduced catchability in low water conditions while the relatively high CPUE in Pool 19 in 2023 was due to the relatively large catch of a putative age-0 cohort.

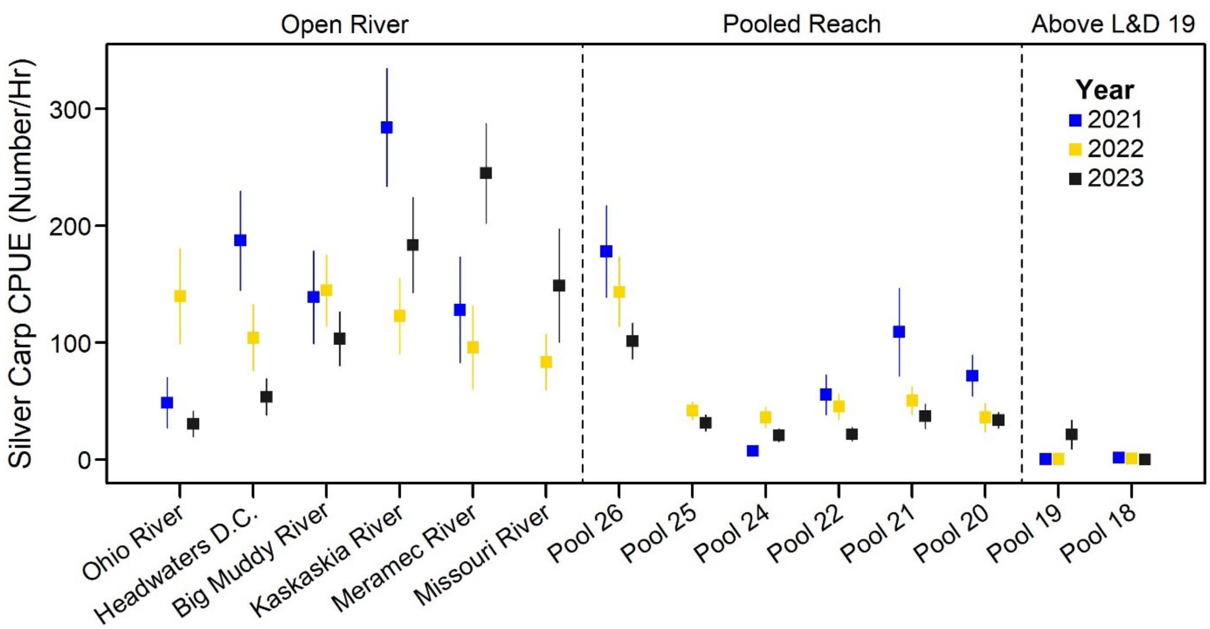


Figure 2. *Location-specific mean stock-sized catch-per-unit-effort of Silver Carp (number/hr) in the Upper Mississippi River during 2021–2023. Error bars represent one standard error. All fish were sampled using the dozer trawl. Vertical dashed lines separate locations into reaches of the Upper Mississippi River.*

These data suggest a greater relative abundance of Silver Carp in the open river reach and Pool 26 compared to locations above L&D 25 (Figure 2). Catches of Silver Carp above L&D 19 were extremely low, likely due to reduced immigration from below L&D 19 (Larson et al. 2017; Whitledge et. al 2019). Likewise, the lower relative abundance at Pools 20–25 compared to Pool

26 and the open river reach indicates that dams may impede the migration and recruitment of Silver Carp.

Size structure—In 2023, the mean TL of Silver Carp captured in dozer-trawl surveys was 625 mm (SE = 2.5 mm, range = 90–1,004 mm). This is similar the mean (640 mm, SE = 2.3 mm, range = 279–1,110 mm) in 2022, but much larger than the mean (161 mm, SE = 3.3 mm, range = 20–970 mm) in 2021. The relatively low mean TL of Silver Carp observed in 2021 could be attributed to the large proportion of sub-stock-sized individuals with TL ≤ 250 mm (79%, N = 3,962). These individuals were detected at five locations, predominantly in the open river reach (Ohio River, N = 841, Headwaters Diversion Channel, N = 1,829, Big Muddy River N = 836, Meramec River, N = 57, and Pool 26, N = 399). In contrast, no sub-stock-sized individuals were captured in 2022, and only 4 were captured in 2023.

During 2021–2023, length distributions of stock-sized Silver Carp exhibited similarities within but showed variations between reaches (Figure 3). The mean TL of stock-sized Silver Carp were 613 mm (SE = 1.5 mm, range = 335–1,110 mm) in the open river reach, 662 mm (SE = 2.9 mm, range = 279–970 mm) in the pooled reach, and 388 mm TL (SE = 28.3 mm, range = 253–1,050 mm) at locations above L&D 19. The low mean TL of Silver Carp observed at locations above L&D 19 was due to the 57 putative age-0 individuals with TL ≤ 302 mm captured in 2023. These individuals accounted for a large proportion of the total captured (80%; total N = 71) in the three years. After excluding these putative age-0 individuals, the mean TL of stock-sized Silver Carp became 850 mm (SE = 9.9 mm, range = 447–1,050 mm) at locations above L&D 19.

Given the small number of Silver Carp captured in dozer-trawl surveys, supplementary data obtained from individuals captured via commercial gillnetting at locations above L&D 19 in 2022 (N = 69) and 2023 (N = 9) were integrated into the visualization (Figure 3). These Silver Carp were all stock-sized, with mean TL of 888 mm (SE = 0.9 mm, range = 749–1,028 mm) in 2022 and 917 mm (SE = 5.7 mm, range = 805–969 mm) in 2023. Note that no commercial samples were collected in 2021.

Body condition—In 2021–2023, length–weight relationships indicate that the rate at which Silver Carp increase in weight per unit length is higher in the pooled reaches above L&D 26 relative to the open river reach (Figure 4). In addition to the general trend that fish in the open river exhibit reduced condition relative to the pooled reaches, several emaciated Silver Carp were observed in the open river reach sites in 2023. Emaciated Silver Carp indicate that densities may be high enough in the open river reach that fish competing for food, space, and other resources may be beginning to experience physical atrophy.

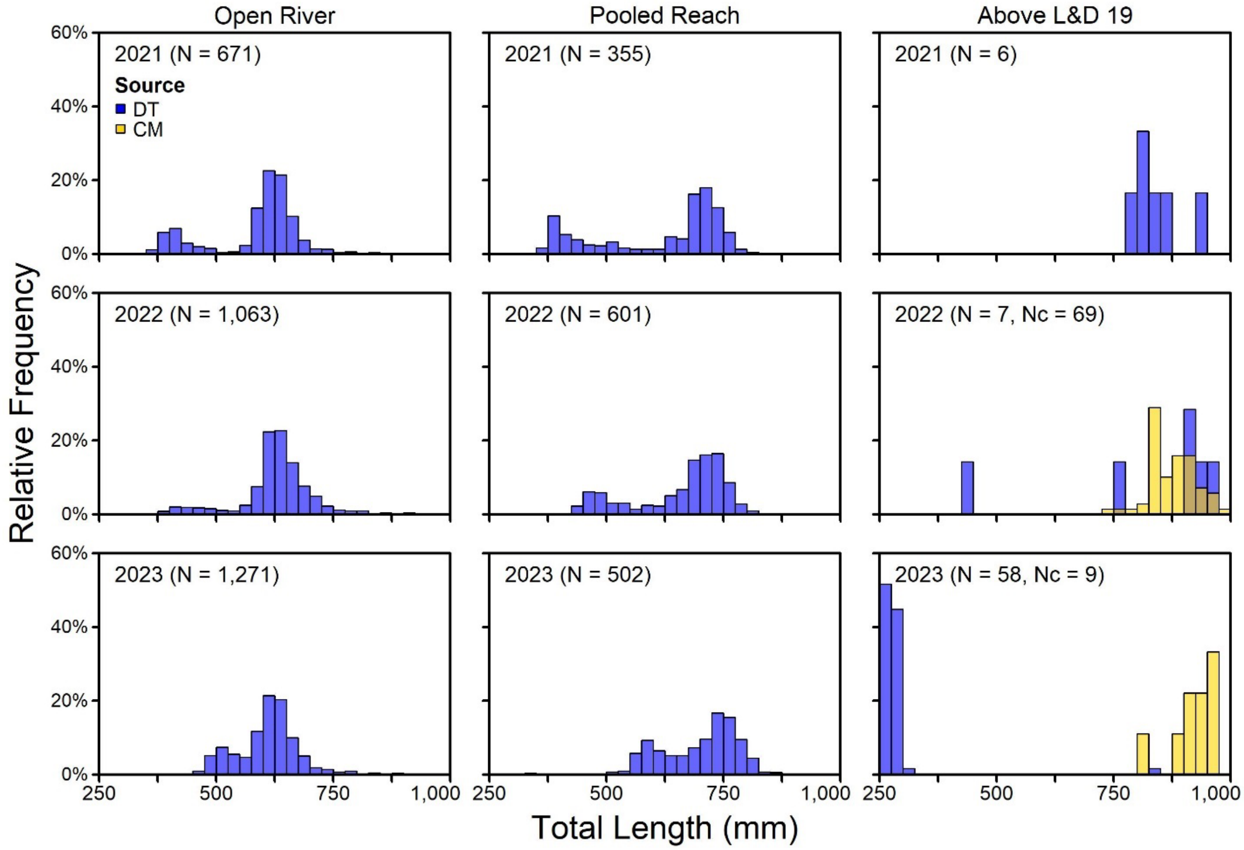


Figure 3. *Reach-specific relative length-frequency histograms of stock-sized (total length > 250 mm) Silver Carp from electrified dozer-trawl surveys (DT, with a sample size of N) in the Upper Mississippi River during 2021–2023. Supplementary data from sampling commercial gill-net catches (CM, with a sample size of Nc) were included for low-density locations above L&D 19 during 2022–2023.*

We also examined variation in body condition (i.e., relative weight) of stock-sized Silver Carp among sample locations. Based on data collected from dozer-trawl surveys in 2021–2023, the standard weight for the UMR Silver Carp was estimated as

$$Ws = CF \times \beta_1 \times TL^{\beta_2} = 5.945075 \times TL^{3.088313} \times 10^{-6} \quad (6)$$

where TL is total length in mm and Ws is standard weight in g. As described in Methods section, β_1 and β_2 were estimated by fitting the linear model equation (2) to data of 4,519 stock-sized Silver Carp using a weighted simple linear regression model method (Zar 1999). The model has a coefficient of determination (R^2) of 0.97, corresponding to a CF of 1.000064 to adjust for logarithm transformation bias (Sprugel 1983). The estimated values of β_1 and β_2 were 5.944694 $\times 10^{-06}$ and 3.088313, respectively. Employing equation (6) means that a Silver Carp with a relative weight of one is considered to have an average condition compared to other Silver Carp of the same size in the UMR during 2021–2023.

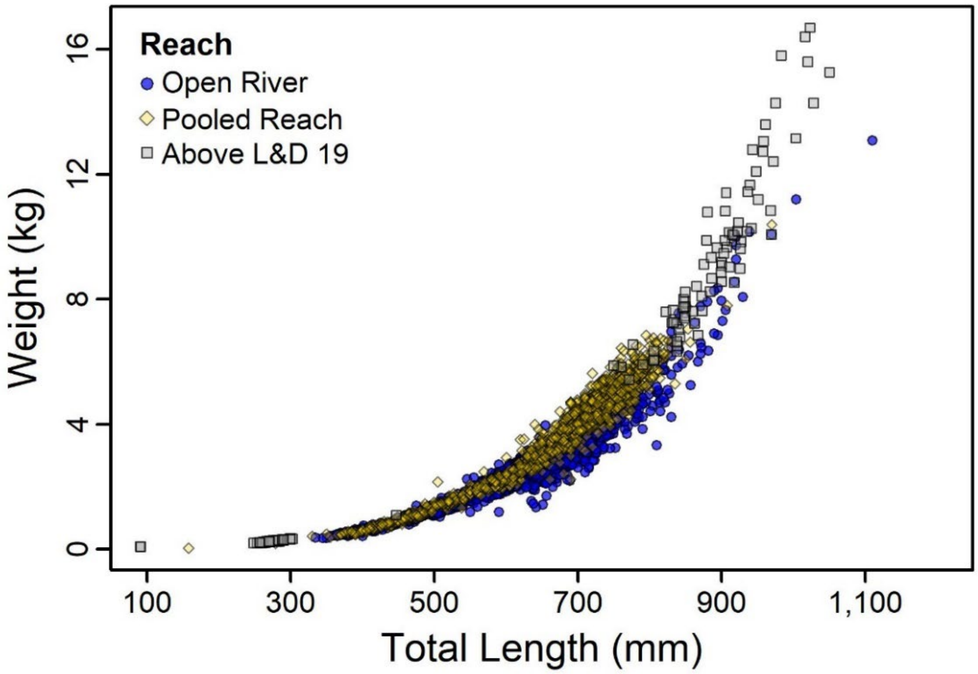


Figure 4. *Reach-specific total length (mm) versus wet weight (g) relationships for Silver Carp captured in the Upper Mississippi River during 2021–2023. The majority of fish were from electrified dozer-trawl surveys (N = 4,523), with complementary fish from fisheries-dependent sampling (N = 79) at locations above L&D 19.*

We found that Silver Carp from locations at the pooled reaches exhibited higher relative weights compared to those from the open river reach (Figure 5). This is possibly due to increased resource availability and less intraspecific competition resulting from lower fish densities (Figure 2). Mean relative weights were < 1 in open river locations and, except for Pool 26, were > 1 in pooled reach locations. Pool 26 appeared to be a transition area between open river locations and pooled locations with a mean relative weight > 1 in 2022 and 2023.

Proportion of males—In at least one year during 2021–2023, the proportion *z*-tests (Zar 1999) showed that the proportions of males were significantly > 50% ($P < 0.05$) in four locations in the open river reach but significantly < 50% in three locations in the pooled reach (Figure 6). Notably, the Ohio River location was the only one where the proportions of males were significantly > 50% in all three years during 2021–2023. Additionally, while the proportion tests did not show significant results, the proportion of males were generally > 50% at locations above L&D 19. More research is required to investigate the differences in sex ratios across the UMR reaches. These data also provide baseline sex proportion information across the UMR, which can be used to test for potential shifts in Silver Carp population sex structure in response to harvest or migration.

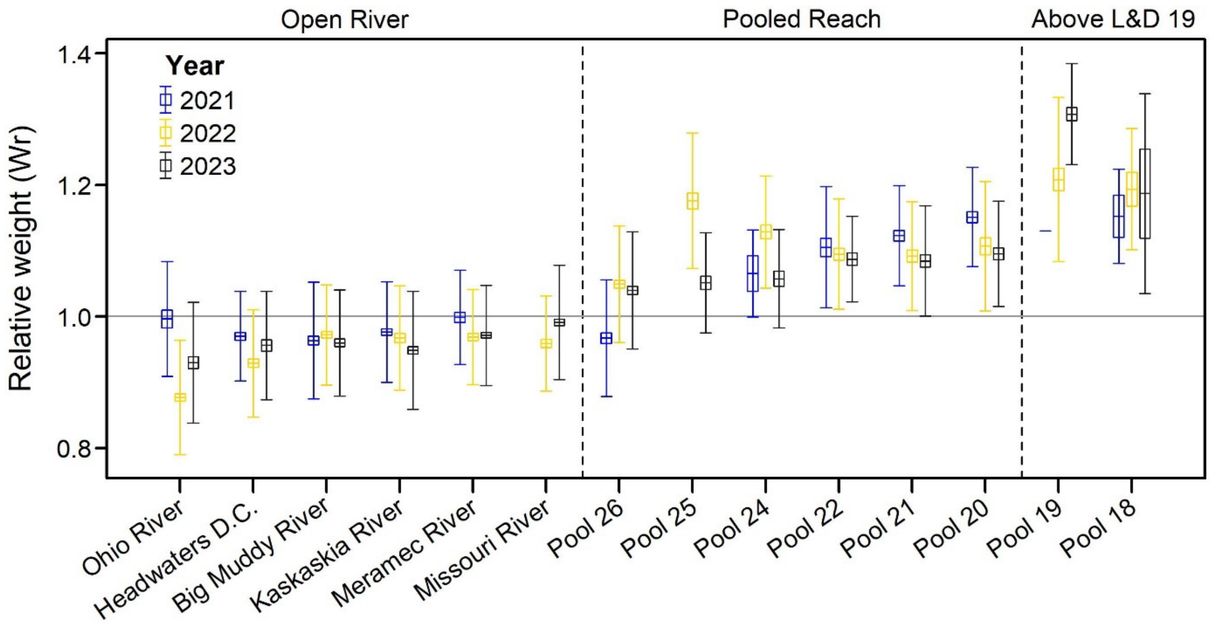


Figure 5. *Location-specific relative weights (Wr) of stock-sized Silver Carp in the Upper Mississippi River during 2021–2023. In each location, the horizontal line represents the mean Wr, the box covers mean ± SE, and the error bar represents mean ± SD. Vertical dashed lines separate locations into reaches of the Upper Mississippi River. The majority of fish were from electrified dozer-trawl surveys (N = 4,523), with complimentary fish from fisheries-dependent sampling (N = 79) at locations above L&D 19.*

Age structure and recruitment variability—We aged 681, 1,200, and 1,017 Silver Carp in the years 2021, 2022, and 2023, respectively. Most of these Silver Carp were from dozer-trawl surveys (N = 2,825), with complementary fish from fisheries-dependent sampling (N = 73) at locations above L&D 19.

Age-frequency histograms (Figure 7) suggest variable recruitment of Silver Carp during the last 12 years with strong and weak cohorts represented across reaches. We identified strong 2018 and 2019 cohorts in the open river reach and Pool 26. Specifically, in the 2021–2023, the 2018 and 2019 cohorts represented 16% and 58% of aged Silver Carp from the open river reach and Pool 26, respectively. These strong cohorts coincide with other studies that have documented a large 2018 cohort in the lower Illinois River, which intersects the UMR in Pool 26 (ICRCC 2021; Figure 1), and a large 2019 cohort in the Missouri River which intersects the UMR south of Pool 26 (MICRA 2021; Figure 1). Another strong 2016 cohort was depicted at locations above L&D 19 (seven years old in 2023; Figure 7). While egg-carrying females have been caught multiple times in our surveys, there was no clear evidence for any of 2021 and 2022 cohorts recruiting into age 1 at locations above L&D 19 from our data. In summary, these data provide strong evidence showing that the Silver Carp populations in the UMR are dominated by a few strong cohorts. More research is needed to understand the ecosystem (biological and environmental) factors and cross-sub-basin movement dynamics leading to the formation of strong cohorts.

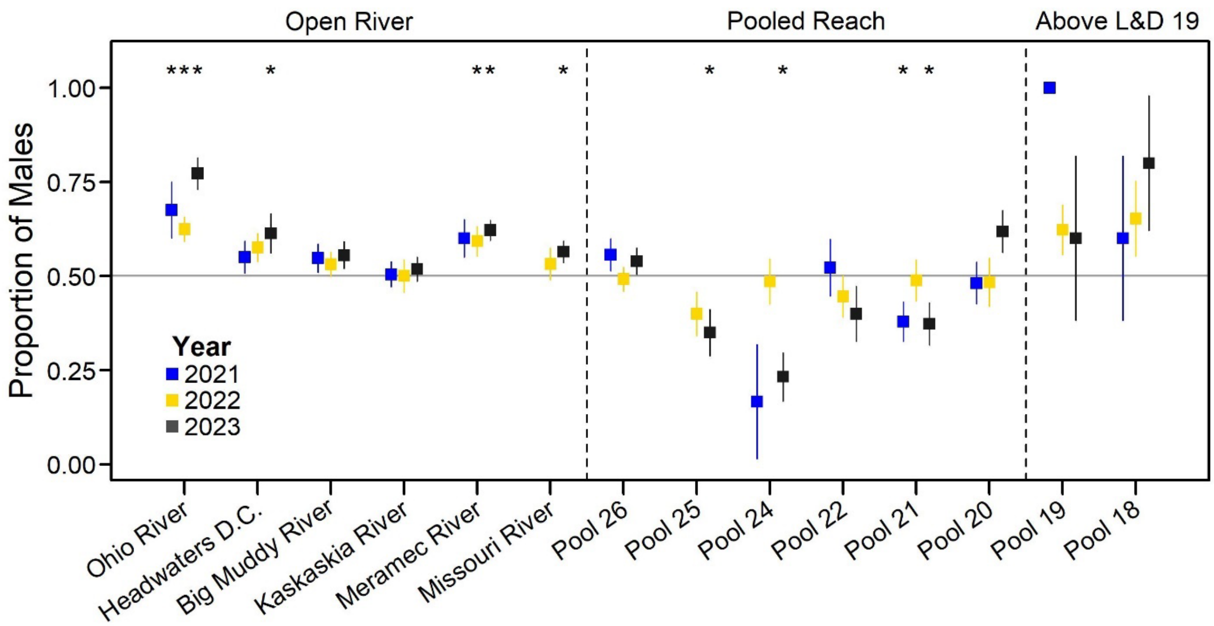


Figure 6. *Location-specific mean proportions of stock-sized male Silver Carp in the Upper Mississippi River during 2021–2023. Error bars represent one standard error. Asterisks denote that the mean proportions significantly deviate from 0.5, with a significance level of α = 0.05 based on proportion z-tests (Zar 1999). Vertical dashed lines separate locations into reaches of the Upper Mississippi River. The majority of fish were from electrified dozer-trawl surveys (N = 4,461), with complementary fish from fisheries-dependent sampling (N = 78) at locations above L&D 19.*

A total of 426 of aged Silver Carp were one–four years old at the time of capture in 2021–2023. Among them, 213 (50%) were from the open river reach and 177 (42%) were from Pool 26. This implies that the recruitment is hindered at the locations above L&D 25. Indeed, insufficient flow or distance for egg drift can result in ineffective spawning and recruitment of Silver Carp (George and Chapman 2013). Additionally, high flow velocity without main stem barriers in the open river reach allows adequate drift distance for developing eggs, increasing the probability of a successfully hatch (Sullivan et al. 2018). Further monitoring of these, and subsequent, year classes will inform spatial and temporal changes in the age structure of the Silver Carp population and may provide evidence supporting the hypothesis that reduced flows and insufficient drift distance caused by dams in the pooled reach hinder egg survival and reduce recruitment of Silver Carp in the Upper Mississippi River.

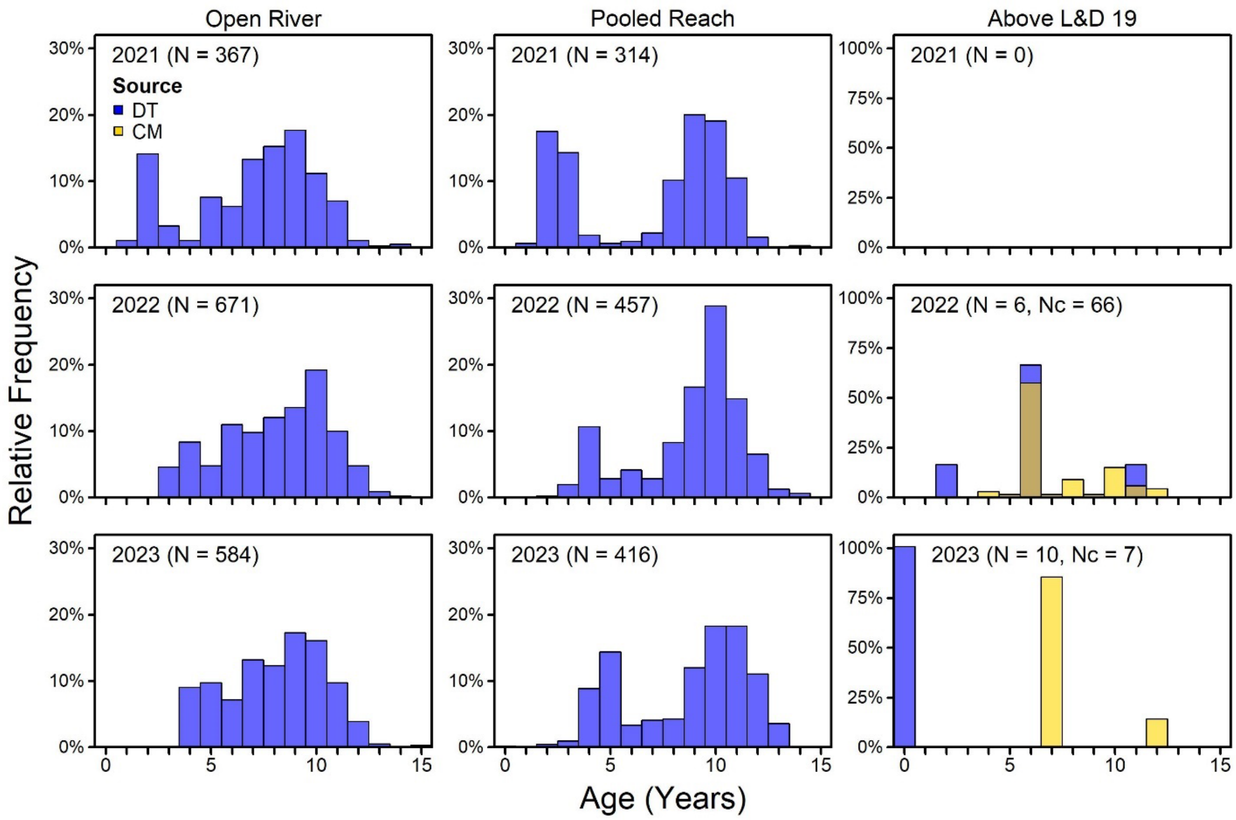


Figure 7. *Reach-specific relative age-frequency histograms of Silver Carp from electrified dozer-trawl surveys (DT, with a sample size of N) in the Upper Mississippi River during 2021–2023. Supplementary data from sampling commercial gill-net caches (CM, with a sample size of Nc) were included for low-density locations above L&D 19 during 2022–2023.*

The catch rates of age-0 Silver Carp were variable across years and locations. We did not age all sub-stock-sized (TL ≤250 mm) Silver Carp but assumed the unaged sub-stock-sized Silver Carp to be age 0. This aligns with other studies showing that mean TL of Silver Carp at age one is around 250 mm (Project: Invasive Carp Demographics, ICRCC-MRWG 2021). In 2021, 3,962 sub-stock-sized Silver Carp were captured at five locations, predominantly in the open river reach (Ohio River, N = 841, Headwaters Diversion Channel, N = 1,829, Big Muddy River N = 836, and Meramec River) and in Pool 26 (N = 399). The largest among them had a TL of 180 mm, suggesting that they were all age-0 Silver Carp. In contrast, no sub-stock-sized individuals were captured in 2022, and only 4 were captured in 2023 (three in Pool 19 and one in Pool 26). However, the TL of 54 among the 57 putative age-0 Silver Carp captured in Pool 19 in 2023 were stock-sized, with TL of 253–302 mm. Nine of these putative age-0 Silver Carp, despite being stock-sized, were aged and were confirmed to be age 0. The largest among these aged individuals had a TL of 290 mm, indicating a high likelihood that all 57 of putative age-0 Silver Carp were indeed age 0.

There are at least two plausible explanations for these variable catch rates. First, the recruitment may vary across locations and years (Rothschild 2000). As previously discussed, egg survival might be hindered at locations above L&D 25 and large cohorts did not occur often in the UMR (Figure 7). Second, the aggregated distribution of these age-0 fish could contribute to their low catchability, which, in turn, resulted in sampling bias when some or all aggregations were missed in surveys. Although, considering that age-0 fish captures were in close proximity to one another, it is unlikely that sampling efforts were insufficient to detect age-0 cohorts if they were in an appreciable number.

Finally, we highlight the high growth rates of age-0 Silver Carp observed in Pool 19 in 2023. Given that Silver Carp in the UMR usually hatch during the summer, a group of individuals reaching a TL of about 275 mm by fall is indicative of a growth rate approaching the highest levels previously recorded only in controlled aquaculture settings, where Silver Carp were provided unlimited food (Cremer and Smitherman 1980). While there is presently no evidence of successful Silver Carp recruitment at the locations above L&D 19 after the strong 2016 cohort, the high growth rate observed in Pool 19 and the warm winter of 2023 suggest the potential for their successful recruitment into a strong year class.

Growth and mortality—Location-specific maximum theoretical lengths (L_∞) and Brody growth coefficients (K) of the von Bertalanffy growth model were estimated using a nonlinear mixed-model approach by fitting the model to Silver Carp length-at-age data in the UMR during 2021–2023 (Table 2). The estimates of L_∞ were highest in locations above L&D 19, followed by locations in the pooled reach, with the lowest estimates in locations of the open river reach. However, the estimates of Missouri River and Ohio River locations were close to the estimates of Pool 26. The estimates of K were generally higher at the locations above L&D 19 and in the open river reach, although the lowest estimate was from the Missouri River location in the open river reach. Together, these estimates indicate that fish in the open river reach typically attain their location-specific theoretical maximum length earlier than those in the pooled reaches. The higher growth potential in the pooled reaches may be linked to density-dependent resource availability (Lorenzen and Enberg 2002), suggesting that continued monitoring of growth could provide insight into long-term density-dependent growth responses to harvest and removal efforts in the future (see Coulter et al. 2018).

Empirically estimated natural mortality rates ranged from 0.381 to 0.595 per year across our sample locations in the UMR (Table 2). Generally, natural mortality rates were higher in the open river locations than the pooled locations, although the lowest estimate was from the Missouri River location in the open river reach. While this trend reinforced the notion of lower per-capita resource availability in the open river reach, it is important to note that these empirical estimates should be interpreted with caution, considering them as rough approximations rather than accurate values derived from designed sampling and analysis.

Table 2. *The estimates of life history parameters of Silver Carp at each study location of the Upper Mississippi River. The estimates of the maximum theoretical lengths (L_∞) and Brody growth coefficients (K) of the von Bertalanffy growth model (equation (3)) were corresponding to a t0 estimate of −0.490. The natural mortality rates (M) were estimated using the updated Pauly (1980) empirical equation (equation (4); Then et al. 2015). The majority of fish were from electrified dozer-trawl surveys (N = 2,808), with complementary fish from fisheries-dependent sampling (N = 73) at locations above L&D 19.*

Location	N	L_∞ (mm)	K (Year^{-1})	M (Year^{-1})
Pool 18	26	954.6	0.401	0.463
Pool 19	53	941.1	0.400	0.464
Pool 20	188	747.6	0.404	0.506
Pool 21	227	754.8	0.362	0.465
Pool 22	167	744.0	0.330	0.437
Pool 24	117	764.3	0.360	0.461
Pool 25	128	764.8	0.336	0.438
Pool 26	357	707.9	0.313	0.427
Missouri River	223	705.9	0.267	0.381
Meramec River	280	647.5	0.411	0.537
Kaskaskia River	291	648.2	0.371	0.498
Big Muddy River	292	660.9	0.413	0.535
Headwaters D.C.	286	673.9	0.457	0.572
Ohio River	246	708.2	0.494	0.595

The UMR spatial units—Our general linear model (GLM) analysis showed that the dozer-trawl CPUE of stock-sized Silver Carp were not significantly different between locations above L&D 19 ($P = 0.402$) but were significantly different across locations in the pooled reach ($P < 0.001$) and in the open river reach ($P < 0.001$). The significant CPUE difference across the pooled reach locations was driven by the CPUE in Pool 26. Upon excluding the data from Pool 26, the GLM analysis showed that the difference in the CPUE across pooled reach locations became non-significant ($P = 0.118$). The significant CPUE difference across the open river reach locations was driven by the CPUE in the Ohio River and Headwaters Diversion Channel locations in 2023, when extremely low water made dozer-trawl surveys difficult. Upon excluding the data from these surveys, the GLM analysis showed that the difference in the CPUE across open river reach locations became marginally non-significant ($P = 0.059$). Thus, there may be reason to consider four spatial units—above L&D 19, Pools 21−25, Pool 26, and open river—in the UMR for monitoring the annual changes in Silver Carp relative abundance and demographics. The disparities in Wr (Figure 5), length frequency (Figure 8), age frequency (Figure 9), and von

Bertalanffy growth parameters (Table 3) between Pool 26 and Pools 21−25, as well as between Pool 26 and the open river reach, further underscore the necessity of this separation.

Table 3. *The estimates of life history parameters of Silver Carp across spatial units of the Upper Mississippi River. The estimates of L∞ and K of the von Bertalanffy growth model were corresponding to a t0 estimate of −0.297. Refer to Table 2 for the explanations of table contents.*

Spatial Unit	N	L_∞ (mm)	K (Year^{-1})	M (Year^{-1})
Above L&D 19	79	946.8	0.412	0.474
Pools 20−25	827	754.9	0.362	0.465
Pool 26	357	699.3	0.341	0.456
Open river	1,618	674.3	0.385	0.504

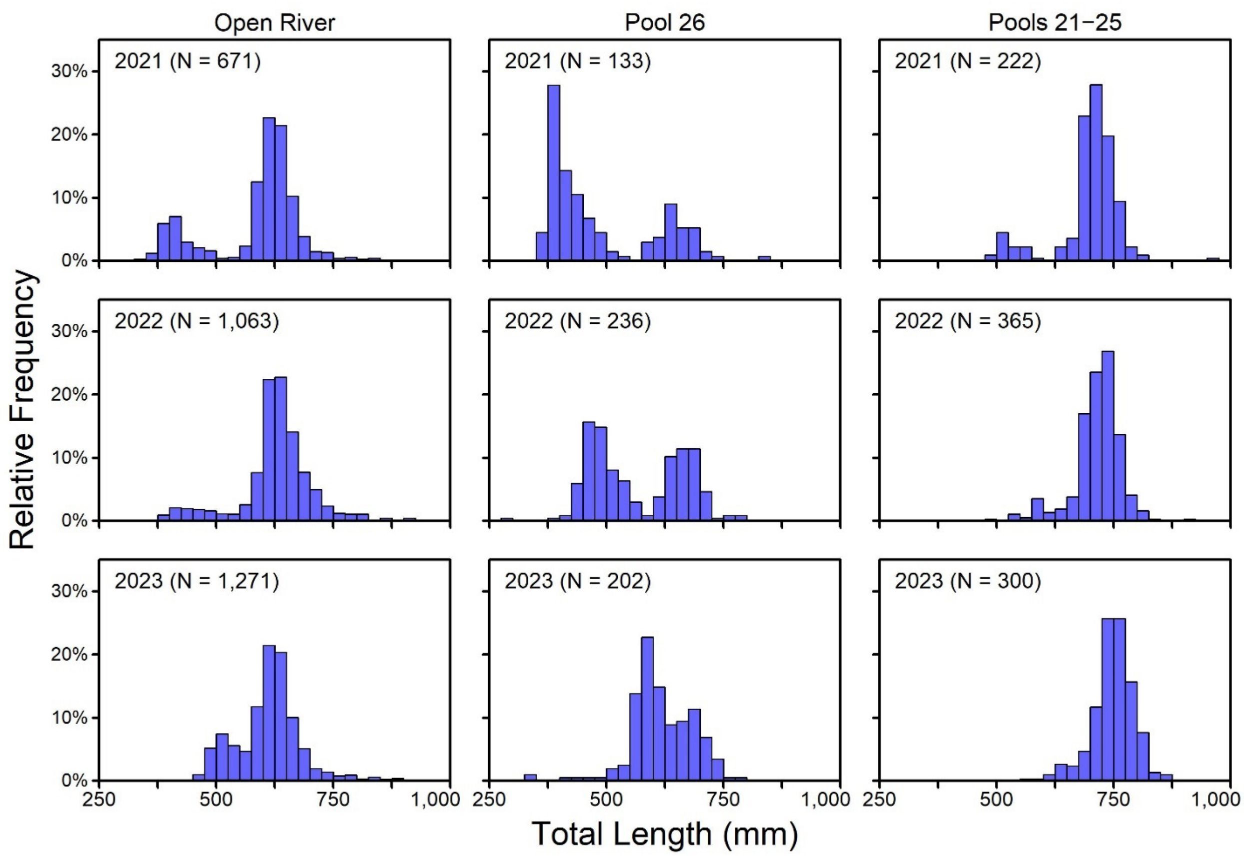


Figure 8. *Relative length-frequency histograms of Silver Carp from electrified dozer-trawl surveys in the open river reach, Pool 26, and Pools 20−25 of the Upper Mississippi River during 2021–2023.*

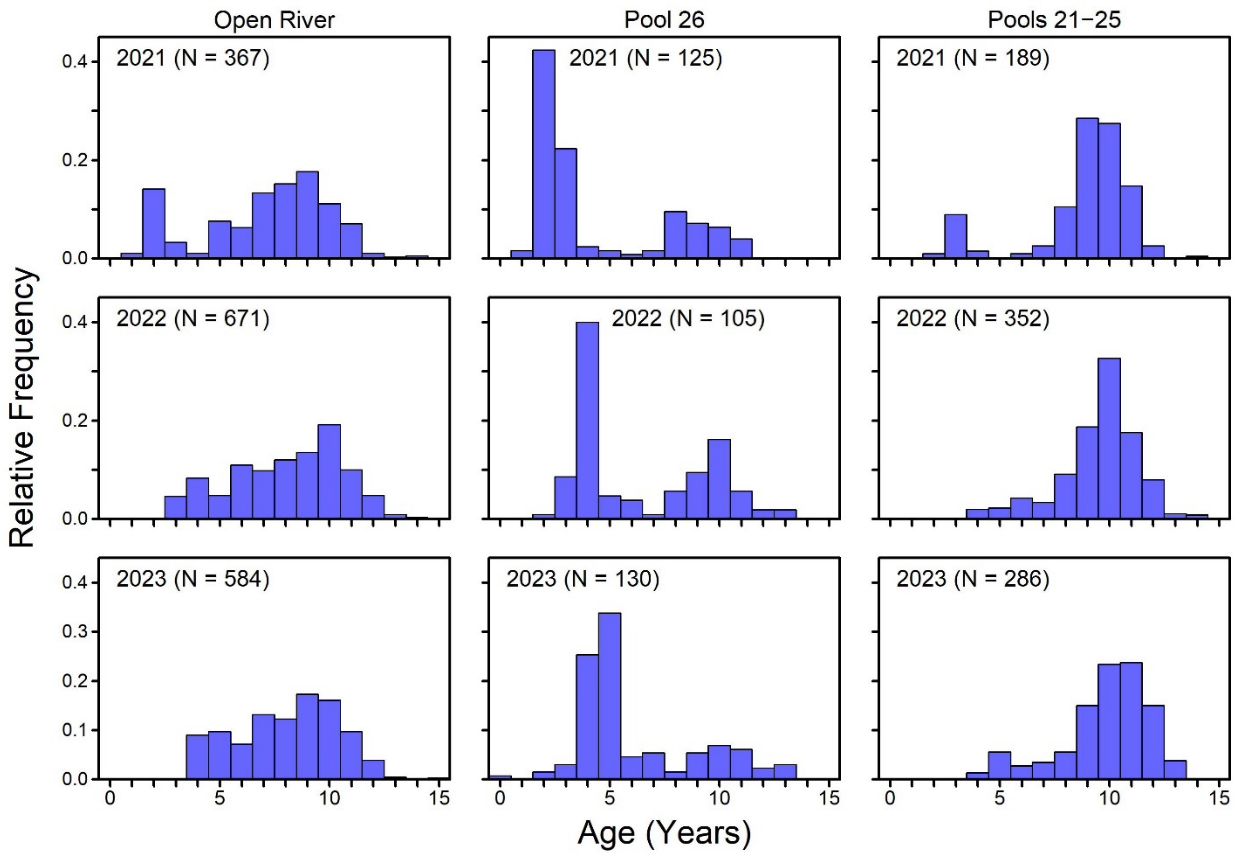


Figure 9. *Relative age-frequency histograms of Silver Carp from electrified dozer-trawl surveys in the open river reach, Pool 26, and Pools 20−25 of the Upper Mississippi River during 2021–2023.*

Recommendation:

1. The monitoring of Silver Carp relative abundance and demographics should be continued and adjusted every three to five years in response to knowledge about this invasive species gained through this monitoring effort.
2. After the first three years, our recommendation for Silver Carp monitoring is to monitor Silver Carp in four spatial units: above L&D 19, Pools 20−25, Pool 26, and the open river reach. The numbers of sample sites within each spatial unit should be adjusted accordingly, which means that the effort should be increased in Pool 26 but may be decreased in the other locations.
3. For management actions, we recommend continued removal efforts at the Intensive Management Zone (IMZ) above L&D 19, the primary removal efforts in the UMR, together with increased efforts in Pool 26 and the open river reach. The higher relative abundance and more frequent strong cohorts suggest a high risk of Silver Carp persistently migrating into the

pooled reaches from Pool 26 and the open river reach, which raises concerns about the potential establishment of self-recruiting Silver Carp populations in IMZ and its upstream locations.

4. The insights we gained over the past three years have revealed several research needs.
   4.1. The Silver Carp populations in the UMR were dominated by a few strong cohorts. These include the 2018 and 2019 cohorts in the open river reach and Pool 26 and the 2016 cohort at locations above L&D 19. More research is needed to understand the biological and environmental factors, as well as cross-sub-basin movement dynamics, leading to the formation of these strong cohorts.
   4.2. The recruitment of Silver Carp appeared to be hindered in the pooled reaches. Further research is needed to evaluate the hypothesis that reduced flows and insufficient drift distance caused by dams hinder egg survival and reduce recruitment of Silver Carp in the UMR.
   4.3. The condition and relative abundance of Silver Carp appeared to be negatively correlated. However, further research is still needed for developing a quantitative relationship between changes in the relative weight and relative abundance. One specific question that should be addressed by the research includes estimating the sample sizes required for precise estimates of relative weight and dozer-trawl CPUE of Silver Carp within an appropriate spatial scale.
   4.4. The male to female ratios were different across our sample locations in the UMR. However, the sex ratio of Silver Carp is an area that has been under studied. More research is needed to investigate the differences in sex ratios across the UMR reaches and whether this ratio can be used as an indicator of Silver Carp abundance and/or movement.
5. Findings in this report can be used as a 2021−2023 baseline of Silver Carp relative abundance and demographics in the UMR for future research. This includes a UMR standard weight equation:

$$Ws = 5.945075 \times TL^{3.088313} \times 10^{-6}$$

where *TL* is total length in mm and *Ws* is standard weight in g. A Silver Carp with a relative weight of one is considered to have an average condition compared to other Silver Carp of the same size in the UMR during 2021–2023.

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