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Introduction and Need: Silver Carp (*Hypophthalmichthys molitrix*) populations and their effects on the Mississippi River ecosystem have been studied extensively since their introduction in the 1970s (Koel et al. 2000, Chick and Pegg 2001, Lohmeyer and Garvey 2009, Sampson et al. 2009, Seibert et al. 2015). Although Williamson and Garvey (2005) and Seibert et al. (2015) quantified basic population and ecological characteristics of Silver Carp captured in the Mississippi River, a comprehensive annual analysis of the population demographics and relative abundances of this species along a broad spatial gradient of the Mississippi River has not been conducted. Furthermore, updating these data with current demographic rate estimates can inform the status of Silver Carp populations on large spatial scales and help assess management and control measures through time. This study was, therefore, designed to collect baseline annual abundance and population demographic data to inform spatially explicit management of Silver Carp in the Upper Mississippi River.

Project Objective:

1. Quantify relative abundance, proportion of each sex, body condition, recruitment, growth, and mortality of Silver Carp in the Upper Mississippi River with the goal of informing management actions.

Methods:

Study area: The Upper Mississippi River (UMR) extends from the headwaters in Minnesota to the confluence of the Ohio River and is characterized by 29 lock and dam 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) suggest that densities of invasive Silver Carp downstream of Lock and Dam 19 (L&D 19; Keokuk, IA; RM 365) are considerably higher than those upstream of the dam. Furthermore, there is evidence of reproduction and recruitment below L&D 19 but reproduction is limited above this structure (WIU & IL DNR 2018; MDC 2017). These differences in Silver Carp populations likely result from low immigration to areas upstream of pool 19 because L&D 19 has a head height of 11.6 m at minimum flow and, except for movement through the lock chamber, is a barrier to upstream fish movement (Wilcox et al. 2004). This study focused on examining potential differences in demographic rates between pools 18-19 (hereafter referred to as “above L&D 19”), pools 20-26 (hereafter referred to as “pooled reach”), and the “open river reach” of the UMR, defined as the 314 km section of free-flowing river between the confluence of the Missouri River near St. Louis, MO to the confluence of the Ohio River near Cairo, IL (Figure 1).



Figure 1. The area sampled for Silver Carp during fall 2022. Sampling locations are designated as black and white areas and tributaries where sampling occurred are highlighted in red. The southernmost dam in the figure is located in the Kaskaskia River, whereas all other dams are in the mainstem Mississippi River.

Site selection: Sampling during fall 2021 was designed to characterize Silver Carp population demographics within large tributaries of the UMR under the assumption that their characteristics would be representative of the populations in the mainstem Mississippi River. Low water levels during the sampling period, however, required that many sites be relocated to the mainstem Mississippi River adjacent to tributary locations that could not be accessed (i.e., Cache River, Apple Creek, Meramec River, Cuivre River, Fabius River, Wyaconda River, Des Moines River, Skunk River, and Iowa River). These tributary sites were relocated to either main channel border or side channel border areas of the mainstem Mississippi River to ensure that all accessible habitats likely inhabited by Silver Carp were sampled. This sampling protocol allowed researchers to gather demographic information representative of the entire population.

Because of the challenges encountered during 2021 sampling, protocols were further adapted for 2022 sampling to include tributary and mainstem Mississippi River sites within each sampling location. To adequately describe demographic rates, all habitats where Silver Carp may be found were included for each sample location of the UMR. Mainstem sites included main channel border, side channel border, and backwater habitats. Tributary sites remained similar to the 2021 sampling protocol. Sample locations were identified as individual pools of the pooled reach of the UMR (i.e., pools 18-26), and 10-kilometer stretches of river centered around major tributary confluences in the open river reach of the UMR (i.e., Missouri, Meramec, Kaskaskia, Big Muddy, and Ohio rivers, and the Headwaters Diversion Channel).

Eight locations from 2021 were redefined for 2022 sampling because of their proximity to larger tributary mouth confluences or because they fell within a pooled reach. These locations were redefined by combining Apple Creek with the Big Muddy River location and including the Cache River in the Ohio River sampling location, the Cuivre River in Pool 26, the Salt River in Pool 24, the Fabius River in Pool 22, the Wyaconda River Pool 21, the Skunk River in Pool 19, and the Iowa River in Pool 18 (Figure 1). All 2021 sampling was encompassed in the larger 2022 sampling locations.

Sample sites for 2022 were selected using a random sampling design stratified by aquatic habitat type (Wilcox 1993). Habitats were classified by using cover/use data sets derived from the Upper Mississippi River Restoration Program Long Term Resource Monitoring element and include main channel border, side channel border, backwater, and tributary habitats. A minimum of 20 sites were selected within each sample location and were divided proportionally between four habitat complexes, assuming all habitat types were available in each sampling location. If certain habitats were not available in the sampling location (e.g., no tributaries available) the sample sites intended for that habitat were allocated among the other available habitats based on the proportionality of the available habitats within the sample location.

Field collections: During 2021, sampling was conducted using the electrified 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 describe Silver Carp populations. Results of the 2021 sampling indicate that both methods were effective and captured a similar size distribution of Silver Carp. Catch rates were, however, higher when using the electrified dozer trawl. Thus, 2022 sampling focused primarily on dozer trawling. Other gears were used to supplement catches in low-density areas or areas where the electrified dozer trawl could not be effectively deployed (e.g., areas with high flows).

Daytime electrified dozer trawling was conducted during August and September, 2022 to target Silver Carp. The late summer time period was chosen because water levels are relatively stable, and reproduction has a reduced effect on length-weight relationships. Additionally, annulus formation in otoliths occurs prior to this time (Thompson and Beckman 1995) and catch rates of Silver Carp are typically highest and most consistent during fall (Sullivan et al. 2017).

The electrified dozer trawl operation and specifications are described in Hammen et al. (2019). Briefly, five-minute transects were conducted along the contour of the shoreline from downstream to upstream as close to shore as possible without obstruction and where the net was completely submerged (net frame is 0.91 m high) at a boat speed of about 4.8 kph (3.0 miles/hr). For safety, dozer trawl sampling occurred only when nearshore currents were < 0.5 m/s (Guy et al. 2009).

All fish captured were identified to species, enumerated, and measured for total length (TL; mm). Fish > 250 mm TL were weighed because this was the primary interest of this project. Sex was determined for Silver Carp ≥ 250 mm TL (hereafter referred to as “stock-sized”; Phelps and Willis 2013) 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.

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

Supplemental fisheries-dependent sampling was used in locations above L&D 19 due to difficulty capturing Silver Carp using standardized gears. Data from fisheries-dependent sampling were not used for relative abundance metrics but were used for all subsequent demographic estimates (i.e., length distribution, length-weight relationship, relative weight, proportion of sex, age, and growth).

Lab processing: Otoliths collected from this sampling effort were aged by personnel from the Columbia, La Crosse, and Carterville FWCO's. One otolith per fish was prepared by sanding on a transverse plane until reaching the nucleus using a sequence of 600, 800 and 1000 grit sandpaper, and polished with lapping film. Prepared otoliths were mounted in putty, submerged in glycerol, illuminated with a fiber optic light, and viewed using a Nikon SMZ25 dissecting scope. 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 2/3 consensus (Maceina and Sammons 2006; Seibert and Phelps 2013). If no agreement was reached, readers reviewed the otolith until a minimum of 2/3 consensus was obtained (Maceina and Sammons 2006). If a 2/3 consensus could not be reached, the otolith was omitted from our dataset.

Data analysis: Catch-per-unit-effort (CPUE) was used as an index of the relative abundance of stock-sized Silver Carp for each of the 14 sample locations. CPUE was calculated as total catch of stock-sized Silver Carp per hour of standardized electrified dozer trawling. Only stock-sized Silver Carp were used for relative abundance estimates because they are assumed to be fully recruited to the population (Project: Invasive Carp Demographics, ICRCC-MRWG 2021).

The sex of each stock-sized Silver Carp was determined as described above and the proportion of male Silver Carp calculated by dividing the number of males by the total number sampled for each location. Additionally, relative weight, the ratio of observed weight to standard weight of a fish of a given TL, was used as an index of body condition. The standard weight was calculated using the empirical equation:

$$\log_{10} Ws = -5.15756 + 3.06842(\log_{10} TL),$$

where Ws represents the standard weight and TL is total length (Lamer 2015). Relative weight was then calculated as the ratio of observed weight to standard weight.

Using all Silver Carp sampled, growth, and mortality were estimated for each location. A von Bertalanffy (1938) model was used to estimate growth parameters using the equation:

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

Here, $L(t)$ is the mean fish length at age t , L_{∞} is the theoretical maximum fish length, K is the Brody growth coefficient, and t_0 is the age at which a fish's length is equal to 0.

Annual natural mortality (M) was empirically estimated using the updated Pauly (1980) mortality estimator described in Then et al. (2015) which is defined as:

$$M = 4.118K^{0.73}L_{\infty}^{-0.333},$$

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

All analyses were performed in R 4.1.2 (R Core Team 2021) and were visualized using the ggplot2 package (Wickham 2016).

2022 Project Highlights:

- Three regional Fish and Wildlife Conservation offices coordinated to collect 1,962 Silver Carp throughout the Upper Mississippi River, of which:
 - 1,700 Silver Carp were captured using the standardized electrified dozer trawl.
 - 1,369 fish were aged using lapilli otoliths.
 - Sampling during 2022 spanned > 430 river miles (RMs), and the data suggest:
 - Higher densities of smaller (< 600 mm TL) Silver Carp in the open river reach.
 - Similar age structure among all UMR locations, but increased growth and larger Silver Carp in the pooled reaches.
 - The most upstream location with evidence of recruitment (young stock-sized fish < age-5) was Pool 22 during 2021 (Fabius River, RM 323). Overall, there was little to no evidence of early life stages upstream of Pool 26 (RM 237)
 - No age-0 Silver Carp were collected during 2022.
 - Relative abundance in the pooled reach (RM 237–RM 437) was lower than that of the open river reach (RM 0–RM 237), and very few Silver Carp were captured upstream of L&D 19.
 - Relatively high densities of Silver Carp and evidence of recruitment in Pool 26 are suggestive of a source population. Relatively fast growth and high condition, however, are suggestive of a sink population in this pool. Taken together, these characteristics suggest that Pool 26 is likely a transition area between the open river reach and pooled reach.
 - Improved sampling protocols (i.e., random-stratified design) facilitated data collection from multiple habitat types, providing data with decreased catch rate variability and more accurate location-specific length structure for each Silver Carp population.

Results and Discussion:

Herein, we update 2021 summary results with fall 2022 data collected by the USFWS Columbia, La Crosse, and Carterville FWCs. These data have been shared among offices and are available for informing management decisions and future demographic data collections aimed toward refining management recommendations.

A total of 375 5-minute electrified dozer trawl transects were conducted during fall 2022 (Table 1). These sampling efforts yielded 1,700 stock-sized Silver Carp from 14 study locations in the UMR.

Table 1. Summary data for Upper Mississippi River locations sampled during fall 2022. For each location, the river miles (RM; RM = 0 at the confluence of the Ohio River), number of 5-minute transects (N), total catch of Silver Carp, mean and standard error (SE) of catch-per-unit-effort of stock-sized Silver Carp number/hr, and total length (TL) range of Silver Carp is presented.

Location	RM	N	Total catch	Mean (SE) stock CPUE (number/hr)	TL range (mm)
Pool 18	410-437	56	4	0.85 (0.41)	907-1050
Pool 19	365-410	81	4	0.60 (0.36)	447-948
Pool 20	343-365	21	85	48.49 (17.0)	590-815
Pool 21	325-343	20	84	50.40 (11.89)	600-908
Pool 22	301-325	22	83	45.27 (10.7)	530-770
Pool 24	273-301	22	68	35.90 (8.69)	658-840
Pool 25	242-273	20	70	41.91 (7.51)	490-810
Pool 26	203-242	20	239	141.60 (29.34)	279-800
Missouri River	191-198	20	139	83.40 (23.82)	364-854
Meramec River	157-164	20	157	95.95 (35.56)	467-901
Kaskaskia River	114-120	13	133	122.77 (32.07)	335-735
Big Muddy River	73-79	20	241	144.59 (30.47)	528-857
Headwaters Diversion Channel	46-52	20	172	104.20 (28.34)	427-1110
Ohio River	0-8	20	221	139.68 (40.69)	573-920
Summary	0-437	375	1700	75.39 (19.78)	279-1110

Relative abundance: Silver Carp CPUEs varied among study locations and within river reaches during 2021, with some CPUEs very high (e.g., Kaskaskia River; mean CPUE = 284/hr, SE = 50/hr), and some very low (e.g., Ohio River; mean CPUE = 48.6/hr, SE = 21/hr; Figure 2). During fall 2022, CPUEs varied less within river reaches (i.e., open river reach, pooled reach, above L&D 19) and were all about 100/hr for the six open river locations, about 50/hr for the six pooled reach locations, and about 1/hr for the two locations above L&D 19 (Figure 2). The only exception was Pool 26 which was the only pooled location with a CPUE > 100/hr and had the second highest relative abundance of any location sampled (mean CPUE = 141.6/hr, SE = 29/hr; Figure 2). These data suggest a greater relative abundance in the open river reach of this project (i.e., between the Ohio River and Missouri River) compared to pooled reaches upstream of Pool 26. Catches of Silver Carp above L&D 19 were extremely low (Table 1), likely due to reduced immigration from below L&D 19 which has been identified as a barrier to fish passage (Larson et al. 2017, Whitley et al. 2019). Similarly, the reduction in relative abundance in the pooled reach when compared to the open river reach suggests that dams impact the ability of Silver Carp to migrate upstream (Figure 2). Lastly, the greater stability in within-sample location CPUEs in 2022 relative to 2021 may result from the increased sampling effort. During 2022, at least 20 standardized electrified dozer trawl transects were performed at each sample location, whereas 2021 sampling only conducted 10 standardized electrified dozer trawl transects along with 10 modified electrofishing transects at each location (not used for CPUE metrics).

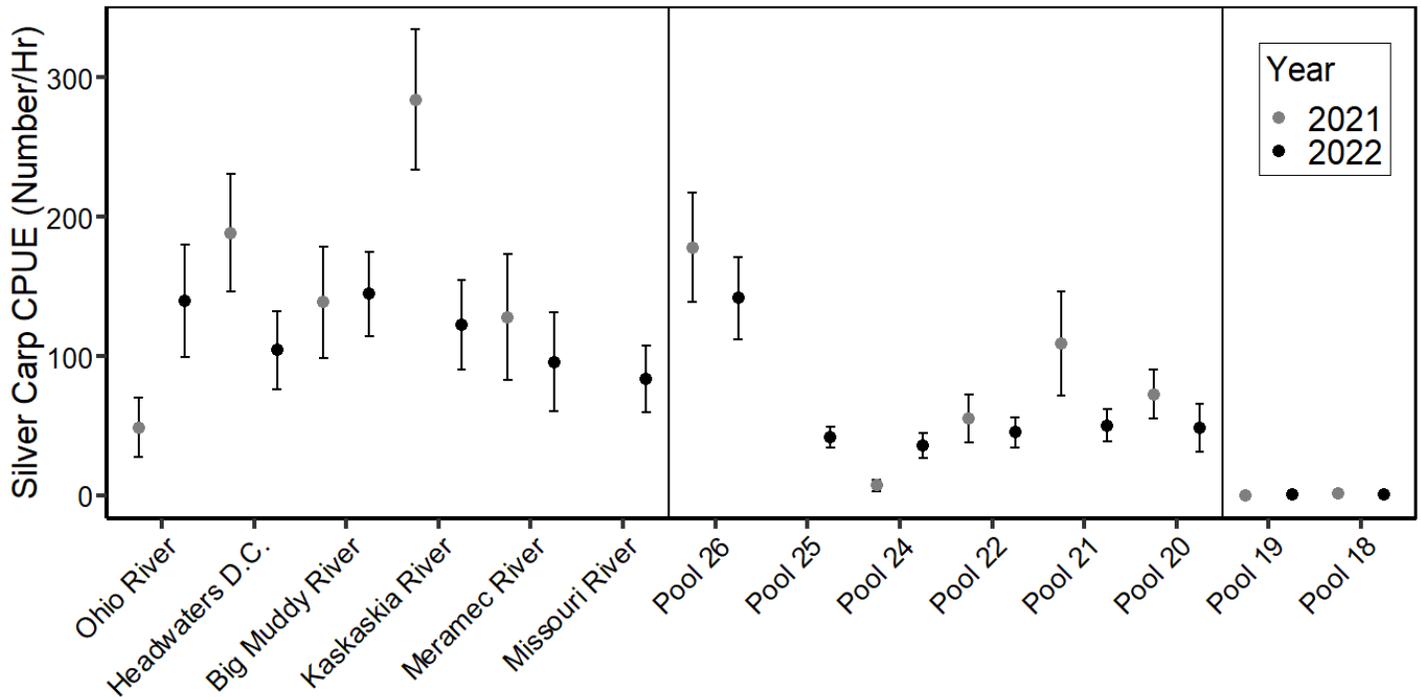


Figure 2. Location-specific mean stock-sized catch-per-unit-effort of Silver Carp (number/hr) during 2021 (gray points) and 2022 (black points). Error bars represent standard error. All fish were sampled using standardized electrified dozer trawl. Vertical black lines separate locations of Upper Mississippi River; the Ohio River-Missouri River (left) is the open river reach, Pool 26-Pool 20 (middle) is the pooled reach, and Pool 19-Pool 18 (right) is above Lock & Dam 19.

Length structure: Silver Carp length structures were similar among locations within river reaches and were thus combined for visualization (Figure 3). Silver Carp captured during 2021 ranged from 20 to 970mm TL (mean = 91 mm TL, SE = 3.38 mm), and catches across locations were dominated by individuals < 200 mm TL (N = 4,049, 74%). Due to the highly skewed nature of the length structure when including all Silver Carp, sub-stock-sized individuals (< 250mm TL) were removed from length structure visualization (Figure 3). Silver Carp < 200mm TL were detected at eight locations during 2021, primarily in the open river reach (Ohio River, N = 870, Headwaters Diversion Channel, N = 1835, Big Muddy River N = 839, Kaskaskia River, N = 1, Meramec River, N = 58, Pool 26, N = 445, and the Pool 24, N = 1). No sub-stock-sized individuals were captured during 2022.

During 2022, captured Silver Carp ranged from 279 to 1,110 mm TL (mean = 654 mm TL, SE = 2.31 mm). No detections of sub-stock-sized Silver Carp and no detections of age-1 fish captured during 2022 (see age structure; Figure 7) may be an indication that the 2021 year class did not successfully recruit to the population.

Length distributions of stock-sized Silver Carp during 2021-2022 varied between river reaches. The mean length of stock-sized Silver Carp in the open river reach was 610 mm TL (SE = 3.72 mm), 647 mm TL (SE = 6.72 mm) in the pooled reach, and 882 mm TL (SE = 8.70 mm) in locations above L&D 19. Differences in the length distributions of stock-sized Silver Carp in the pooled and open river reaches of the UMR could result from dams reducing movement among these reaches as well as density-dependent growth in the open river reach (Figure 3).

Fishery-dependent sampling, which was used to supplement catches from standardized surveys in locations above L&D 19 sampled a similar length structure to those caught with standardized sampling. Those fish were, therefore, included in estimates of demographic rates.

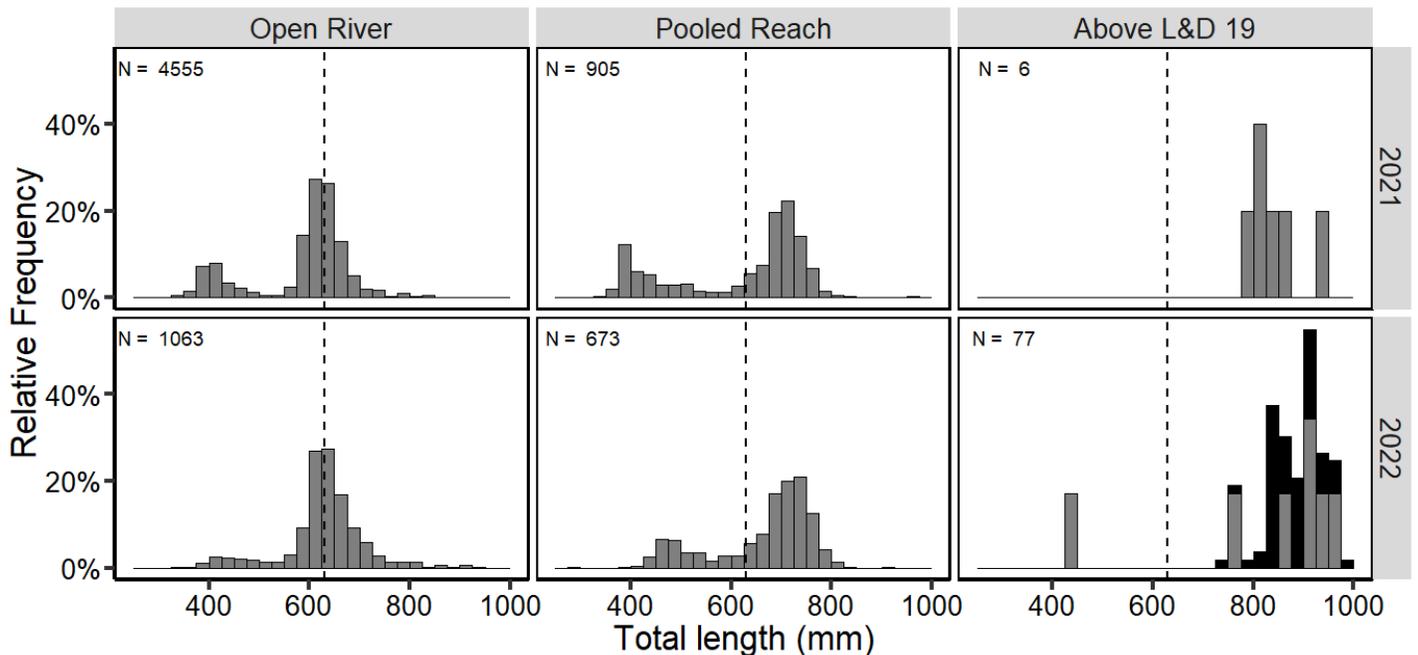


Figure 3. Reach-specific relative length-frequency histograms and total pooled catches of Silver Carp sampled using electrified dozer trawl from all locations of the Upper Mississippi River during 2021 and 2022. Length data also include fish captured with standardized modified electrofishing during 2021. Commercial gill-net data were used for length distribution in low-density areas above L&D 19 during 2022, which were stacked and indicated in black. Vertical dashed lines represent the overall mean TL (630mm TL) of all stock-sized Silver Carp sampled during 2021 and 2022.

Body Condition: Length-weight relationships indicate that the rate at which Silver Carp increase in weight per unit length is higher in the pooled reach and above L&D 19 relative to the open river reach (Figure 4). The length-weight relationships did not differ between the pooled reach and areas above L&D 19 (Figure 4).

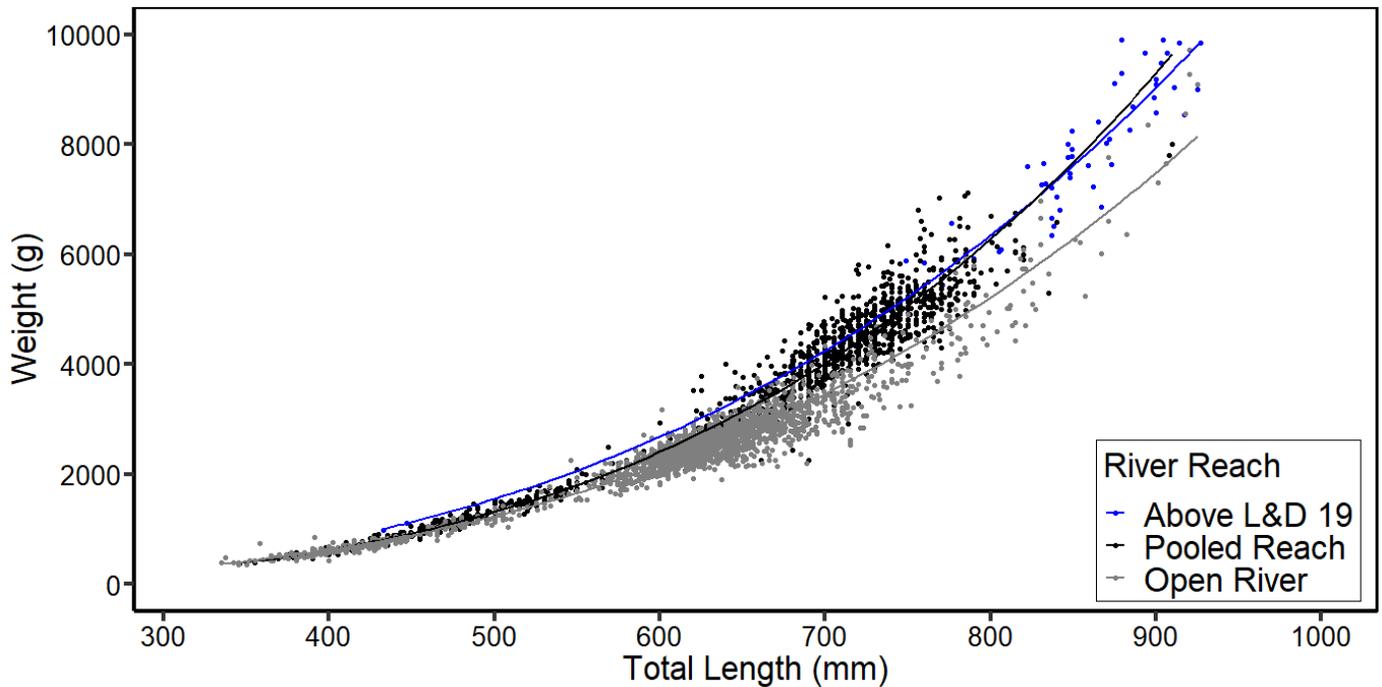


Figure 4. Reach-specific total length (mm) versus wet weight (g) relationships for stock-sized Silver Carp. Gray points represent Silver Carp captured in the open river reach, black points the pooled reach, and blue points in locations above L&D 19 using the electrified dozer trawl during fall 2021-2022. Each line represents the fitted length-weight relationship for each area. Samples above L&D 19 were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill-net catches.

We also examined variation in fish condition (i.e., relative weight) among sample locations by estimating standard weight using the equation developed by Lamer (2015) and converting to relative weight. Relative weight standards are often generated using a 75th-percentile regression line approach (Murphy et al. 1991). However, the Silver Carp relative weight equation was developed using a 50th-percentile approach (Wege and Anderson 1978, Lamer 2015), which defines a fish in average condition as having a relative weight of one. We expected that fish from locations in the pooled reach would exhibit higher relative weights when compared to fish from the open river reach due to increased resource availability and less intraspecific competition resulting from lower fish densities (Figure 2). Consistent with our expectations, spatial patterns in relative weight mirrored patterns in relative abundance (Figure 5). Median relative weight values were < 1 in open river locations and, except for Pool 26, were > 1 in pooled reach locations. These results indicate that overall condition was higher in the pooled reach locations relative to open river locations (Figure 5). Again, Pool 26 appeared to be a transition area between open river locations and pooled locations with a median relative weight near one.

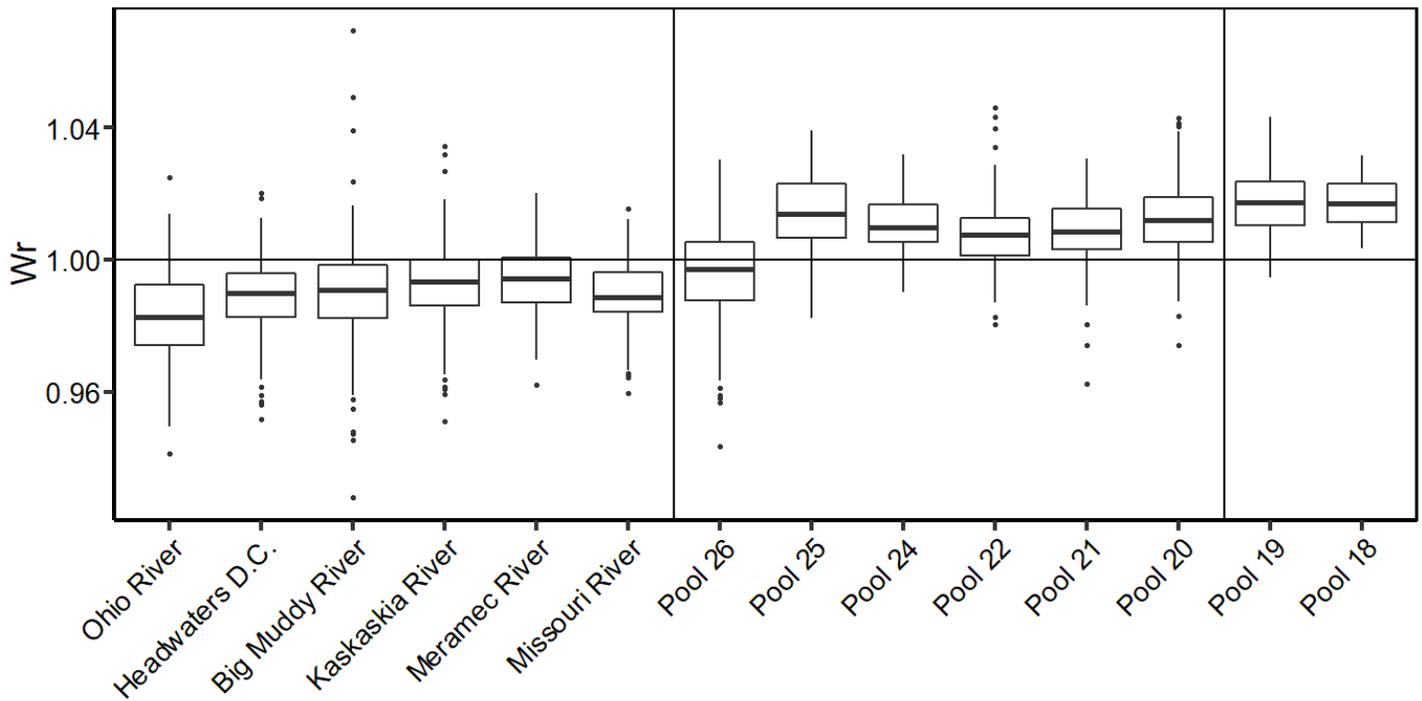


Figure 5. Location-specific boxplots of individual stock-sized Silver Carp relative weights (W_r). The vertical black lines indicate the separations between the open river reach (left), pooled reach (middle), and locations above L&D 19 (right). Fish were sampled using the electrified dozer trawl during fall 2021-2022. Samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill-net catches for areas above L&D 19.

Sex proportions: The sex of all stock-sized Silver Carp captured was determined using pectoral spine analysis (Wolf et al. 2018) or internal examination. Exploited fish populations can be male dominated due to size-based sexual dimorphism and size-biased harvest that preferentially removes large-bodied individuals (e.g., Fenberg and Roy 2008) which, for many fish species, are more likely to be female (Parker 1992), although Silver Carp have not been documented to exhibit sexual dimorphism. Analysis of 2021-2022 age data revealed differences between male and female growth patterns. Specifically, males had lower growth potential in all age samples (i.e., $L_\infty = 704$ mm, $K = 0.351$, $t_0 = -0.499$) relative to females (i.e., $L_\infty = 732$ mm, $K = 0.342$, $t_0 = -0.318$). However, the locations sampled in the UMR are not highly exploited except for those above L&D 19 (MICRA 2019). Therefore, we expected to see relatively equal proportions of male and female Silver Carp across all sample locations below L&D 19. In general, observations were consistent with expectations (i.e., the proportion of each sex was near 50% for all locations). These data provide baseline sex proportion information across the UMR to test for potential shifts in Silver Carp population sex structure in response to harvest.

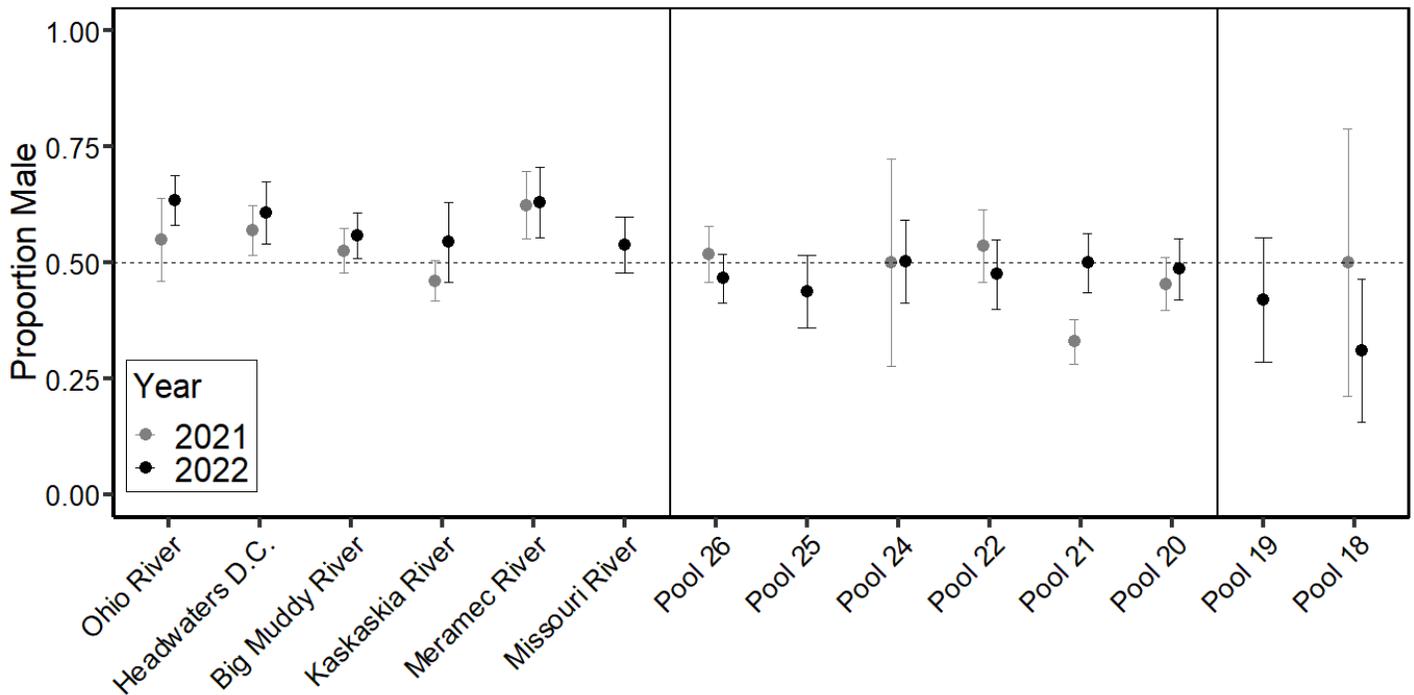


Figure 6. Location-specific means and standard errors describing the proportion of male Silver Carp in the total catch. The vertical black lines indicate the separation between the open river reach (left), pooled reach (middle), and locations above L&D 19 (right). Fish were sampled using the electrified dozer trawl during fall 2021-2022. Samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill-net catches in areas above L&D 19.

Recruitment variability, growth, and mortality: Age data are critical for estimating vital rates (i.e., recruitment, growth, and mortality rates) in fish populations. Vital rates are factors that can drive shifts in a population through time and are necessary for parameterizing stock assessment models as well as other types of population models that help inform and evaluate management efforts (Hilborn and Walter 1992; Jackson 2007). Age structures (lapilli otoliths) were collected from 1,062, and from 1,369 Silver Carp during 2021 and 2022, respectively. Fish were sampled using standardized electrified dozer trawling along with supplemental non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill net catches where necessary to meet sample size requirements (about 100 individuals per sample location).

Age-frequency histograms suggest variable recruitment of Silver Carp during the last 12 years with strong and weak cohorts represented in each population (Figure 7). Although inconsistent among river reaches, we were able to detect strong year classes from age-frequency histograms (Figure 7). Specifically, we identified strong 2018 and 2019 cohorts in the open river reach as well as portions of the pooled reach. These strong cohorts coincide with other studies 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). Except for the 2018 and 2019 year classes, the population appears to be dominated by older Silver Carp (about 7-10 years; 2011-2014 year classes) at all sample locations. Furthermore, with the exception of Pool 26, which accounted for nearly all of the fish in the pooled reach < 5 years old, larger numbers of younger (< 5 years) Silver Carp were captured in the open river reach compared to the pooled reach locations (Figure 7). We suspect that spawning and/or recruitment is hindered in pooled reaches. 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 mainstem 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 spawning events and reduce recruitment of Silver Carp in the Upper Mississippi River.

Age data from above L&D 19 depicted a relatively large 2016 cohort (age-6 in 2022; Figure 7). This is interesting because there is evidence that those fish spawned above L&D 19 and that they recruited to the population. Although the pooled reaches may be primarily a migrant population, infrequent spawning and recruitment events appear to occur.

Age-0 Silver Carp were detected at eight locations during 2021, primarily in the open river reach (i.e., Ohio River, N = 870, Headwaters Diversion Channel, N = 1835, Big Muddy River N = 839, Kaskaskia River, N = 1, Meramec River, N = 58, Pool 26, N = 445, and Pool 24, N = 1). These fish were omitted for the purposes of comparing age frequencies due to their aggregated distribution and abundance which would inhibit reasonable comparisons of age frequencies among locations. No age-0 or age-1 fish were captured during 2022, which provides evidence of variable recruitment across years (Rothschild 2000). Although over 4,000 age-0 fish ranging from 20-180 mm TL were captured during 2021, there were no age-1 Silver Carp captured in 2022 and no indication that the 2021 cohort successfully recruited to the population. Silver Carp were assumed to be age 0 if < 200 mm TL. Other studies that have shown that mean length at age 1 for Silver Carp is around 250 mm TL or greater (Project: Invasive Carp Demographics, ICRCC-MRWG 2021).

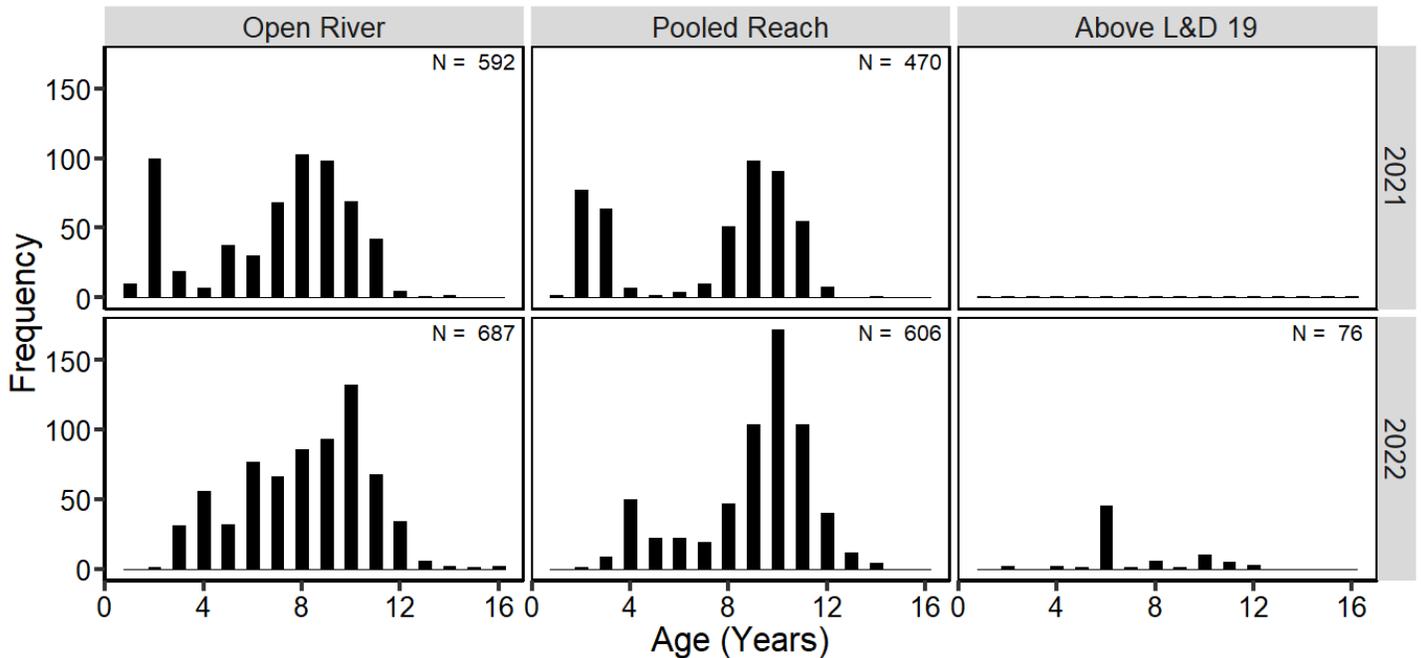


Figure 7. Reach-specific age frequency histograms for Silver Carp captured using electrified dozer trawl from all locations of the Upper Mississippi River during 2021 and 2022. Age samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill-net catches.

Recruitment variability indices rely on accurate age data that can characterize year class strengths through time. Due to high variability in length-at-age estimates for Silver Carp, we did not calculate recruitment variability indices. The presence of rare, large cohorts and frequent small year classes, however, provides evidence that Silver Carp do not recruit annually to the populations in the UMR.

Location-specific von Bertalanffy growth models were used to estimate the maximum theoretical lengths (L_{∞}) and Brody growth coefficients (K) for Silver Carp captured in the UMR during fall 2021-2022 (Table 2). These models suggest that L_{∞} values are consistently higher in the pooled reach locations (i.e., Pool 26-Pool 18) relative to the open river locations (i.e., Ohio River-Missouri River; Table 2), indicating increased growth potential in the pooled reaches, which may be linked to density-dependent resource availability (Table 2). The Brody growth coefficient (K), or the rate at which fish attain this theoretical maximum length (L_{∞}), is, however, variable (Table 2). Fish in the open river reach typically attain their location-specific theoretical maximum length earlier than those in the pooled reach. Such shifts in growth potential in response to changes in fish density have been documented in other studies (Lorenzen and Enberg 2002) and suggest that continued monitoring of growth could provide insight into density-dependent growth responses to harvest and removal efforts in the future (see Coulter et al. 2018). It is important to note that age structure collection varied among locations. Ohio River, Pool 22, Pool

20 and Pool 18 had missing younger (age < about 4-5) age classes which resulted in inaccurate K or t_0 estimates for those locations (Table 2). All parameter estimates were included in this report because L_∞ values were reasonable for all locations and helped provide preliminary evidence for growth variability between the open river reach and pooled reach locations.

Age data were also combined into river reaches (i.e., open river reach, pooled reach, and above L&D 19) to depict the overall differences between larger meta-populations that appear to have similar characteristics (e.g., length structure, condition, and growth) (Table 3). Reach-specific growth models show the trend in increasing growth potential values from the open river reach ($L_\infty = 667$ mm TL), to pooled reach ($L_\infty = 761$ mm TL), to above L&D 19 ($L_\infty = 925$ mm TL) (Table 3; Figure 8).

Empirical mortality estimates depict a range of annual natural mortality (M) estimates among locations in the UMR (Table 2). Values from the updated Pauly (1980) mortality estimator (Then et al. 2015) depict a range of annual natural mortality from 0.37-0.66 per year. M was not estimated for Ohio River, Pool 22, Pool 20 and Pool 18 because of the unreliable estimates of K from the von Bertalanffy model. Generally, natural mortality was higher in the open river reach ($M = 0.56$ per year) relative to the pooled reach ($M = 0.38$ per year; Table 3) which is consistent with our expectations and may suggest high densities and, therefore, greater intraspecific competition results in increased mortality of Silver Carp.

Table 2. Life history parameters of Silver Carp at each study location of the Upper Mississippi River; L_∞ , K , and t_0 parameters are von Bertalanffy (1938) growth coefficients, and the M parameter is the annual natural mortality estimate from the updated Pauly (1980) empirical equation (Then et al. 2015). Fish were captured with the electrified dozer trawl during fall 2021 and 2022 and age samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill-net catches.

Location	L_∞ (cm)	K (per year)	t_0 (years)	M (per year)
Ohio River	693	0.67	-0.087	NA
Headwaters D.C.	669	0.508	-0.134	0.62
Big Muddy River	655	0.489	-0.15	0.61
Kaskaskia River	652	0.363	-0.604	0.49
Meramec River	643	0.472	-0.221	0.60
Missouri River	674	0.406	0.92	0.52
Pool 26	700	0.3	-0.57	0.42
Pool 25	778	0.272	-0.516	0.37
Pool 24	759	0.33	-0.166	0.43
Pool 22	814	0.138	-4.332	NA
Pool 21	754	0.301	-1.274	0.41
Pool 20	727	0.807	1.865	NA
Pool 19	922	0.637	0.989	0.66
Pool 18	1154	0.069	14.133	NA

Table 3. Life history parameters of Silver Carp at each river reach of the Upper Mississippi River; L_{∞} , K , and t_0 parameters are von Bertalanffy (1938) growth coefficients, and the M parameter is the annual natural mortality estimate from the updated Pauly (1980) empirical equation (Then et al. 2015). Fish were captured with the electrified dozer trawl during fall 2021 and 2022 and age samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gill-net catches.

River Reach	L_{∞} (cm)	K (per year)	t_0 (years)	M (per year)
Open River	667	0.437	-0.163	0.56
Pooled Reach	761	0.277	-0.551	0.38
Above L&D19	925	0.598	-0.916	0.63

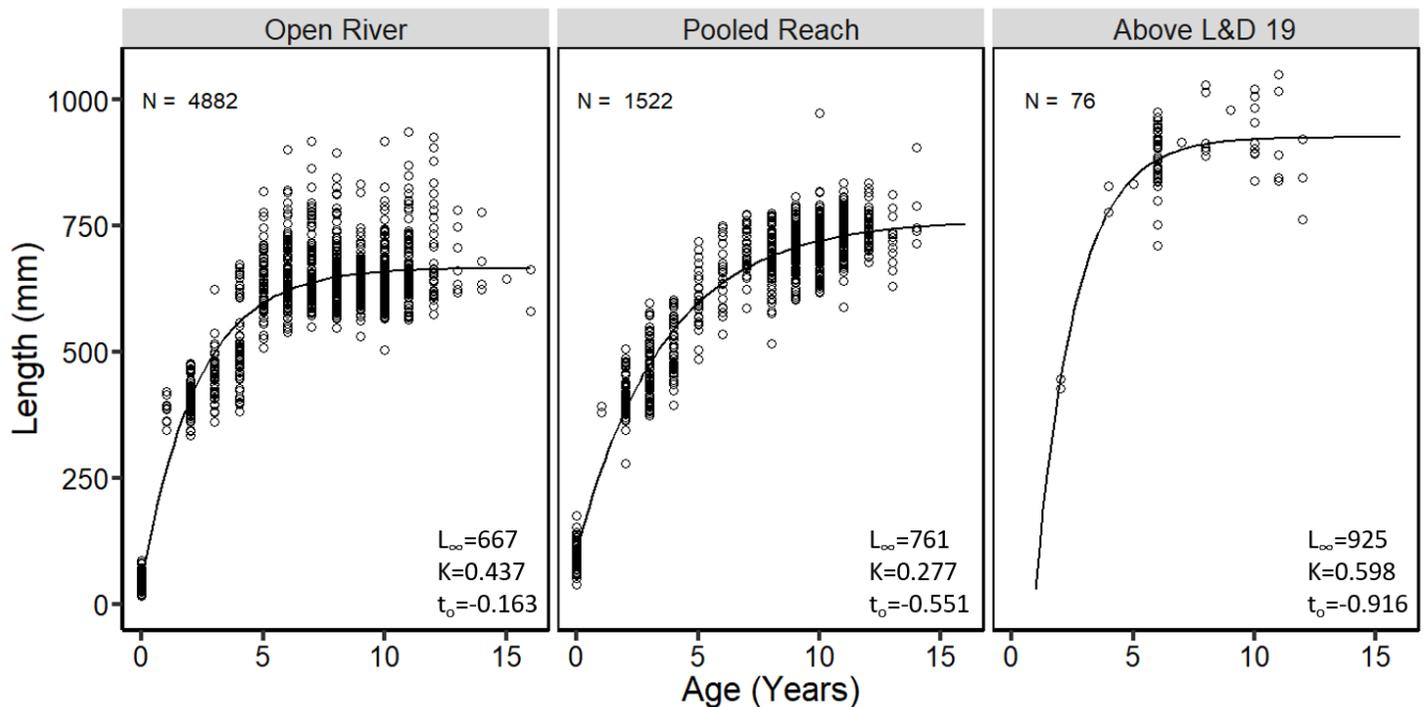


Figure 8. Reach-specific von Bertalanffy growth models depicting mean length-at-age for Silver Carp captured using electrified dozer trawl from all locations of the Upper Mississippi River during 2021 and 2022. Age samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gillnet catches.

Pool 26 of the Upper Mississippi River: Results from Pool 26, the lowermost pooled reach location, deviated from the overall pattern of increased densities, reduced condition, and reduced growth in the open river reach relative to pooled reaches. Silver Carp length distributions were left-shifted relative to other pooled reach locations but right-shifted relative to open river reach locations (Figure 9). Pool 26 was also the only location in the pooled reach where large numbers of Silver Carp < 600 mm TL were captured and the only location in the pooled reach with an indication of recruitment. The latter is supported by a large cohort growing from about 400 mm TL to about 500 mm TL from 2021 to 2022 (Figure 9).

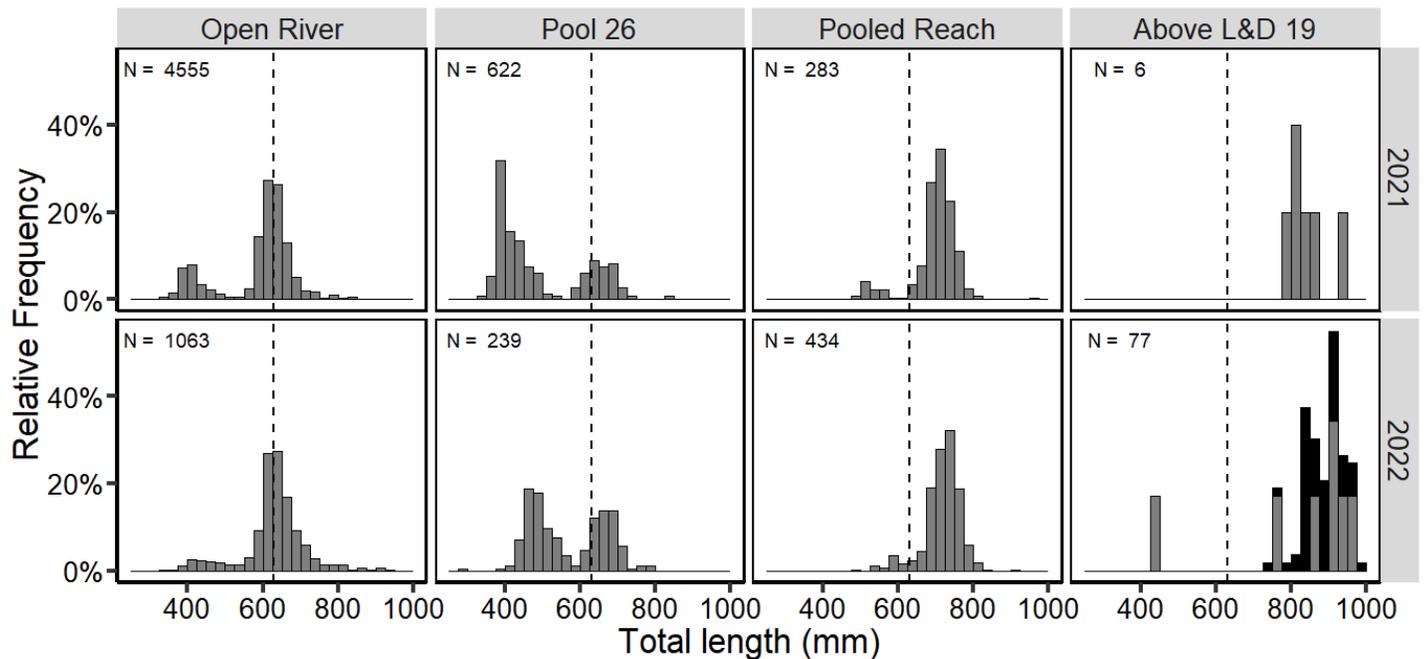


Figure 9. Reach-specific relative length-frequency histograms (Pool 26 separated from the pooled reach) and total pooled catches of Silver Carp sampled using electrified dozer trawl from all locations of the Upper Mississippi River in 2021 and 2022. Length data also includes fish captured with standardized modified electrofishing during 2021. Commercial gill-net data were used for length distribution in low-density areas above L&D 19 during 2022 and are indicated in black. Commercial harvest is indicated in black. The vertical dashed line represents the overall mean TL (630 mm TL) of all stock-sized Silver Carp sampled during 2021 and 2022.

Likewise, the condition of Silver Carp captured in Pool 26 was somewhat higher than that of fish captured in open river reach locations, but lower than that of fish captured in pooled reach locations (Figure 5). The age structure of Pool 26 Silver Carp also mirrored the observed length structure of these fish with high numbers of young fish observed in Pool 26 relative to other pooled reach locations (Figure 10). Within the pooled reach, the large 2018 and 2019 cohorts were only observed in Pool 26, suggesting that recruitment may occur within Pool 26, but may be hindered in all other pools.

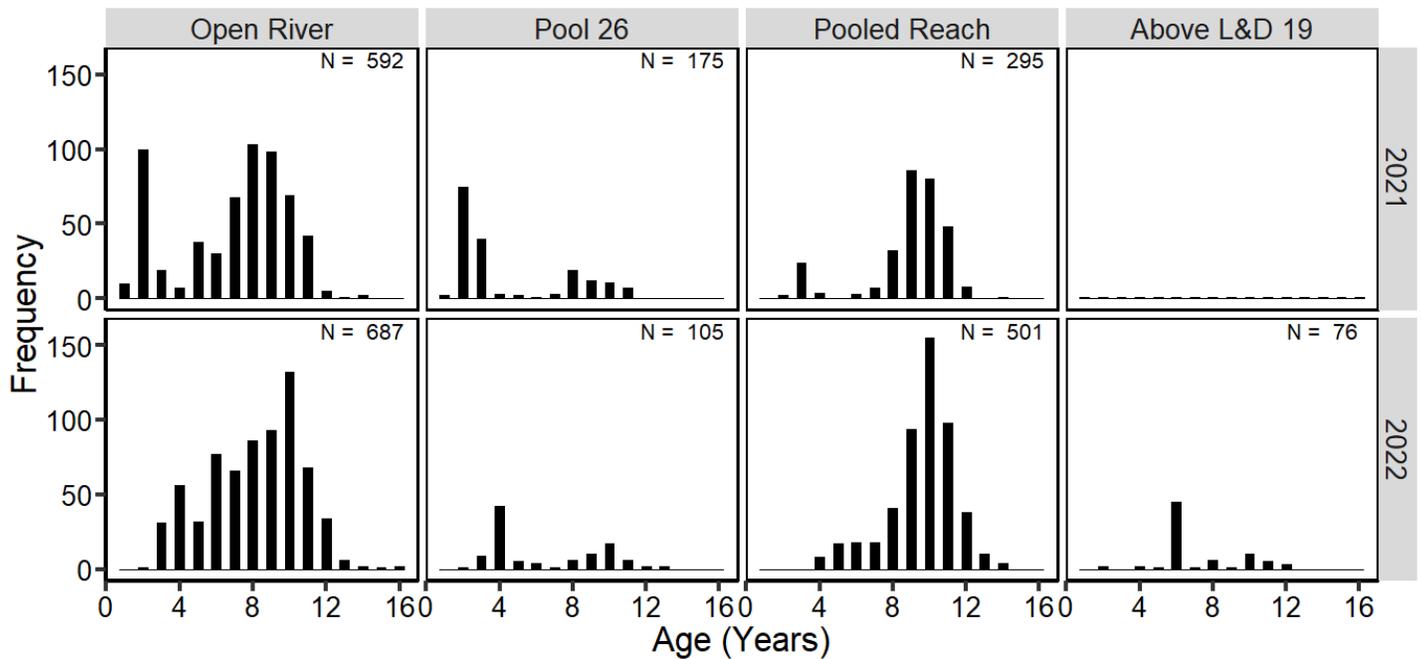


Figure 10. Reach-specific age frequency histograms (Pool 26 separated from the pooled reach) for Silver Carp captured using electrified dozer trawl from all locations of the Upper Mississippi River during 2021 and 2022. Age samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gillnet catches in areas above L&D 19.

Growth differed in Pool 26 relative to other pooled reach and/or open river reach locations (Figure 11). The L_{∞} of Silver Carp captured in Pool 26 was 700 mm TL whereas no open river reach location had a $L_{\infty} > 700$ mm TL, and no other pooled reach location had a $L_{\infty} < 725$ mm TL (Table 2). Collectively, Silver Carp population demographics in Pool 26 appear to be unique in relation to all other locations sampled within the UMR. It is the only pooled location with evident recruitment and increased densities relative to other pooled locations. However, condition and growth appear to align more with upper pools that have reduced densities and increased growth. These results suggest that the Pool 26 population may be a transition area or a desirable location for Silver Carp, where populations can thrive in high densities without reduced resource availability. The physical attributes of Pool 26 are unique because it is the lowermost pooled location and has a major tributary, the Illinois River, intersecting the pool. These unique physical characteristics of Pool 26 could affect resource availability, immigration, and emigration of Silver Carp within the pool and may contribute to the atypical demographics observed in relation to other UMR locations.

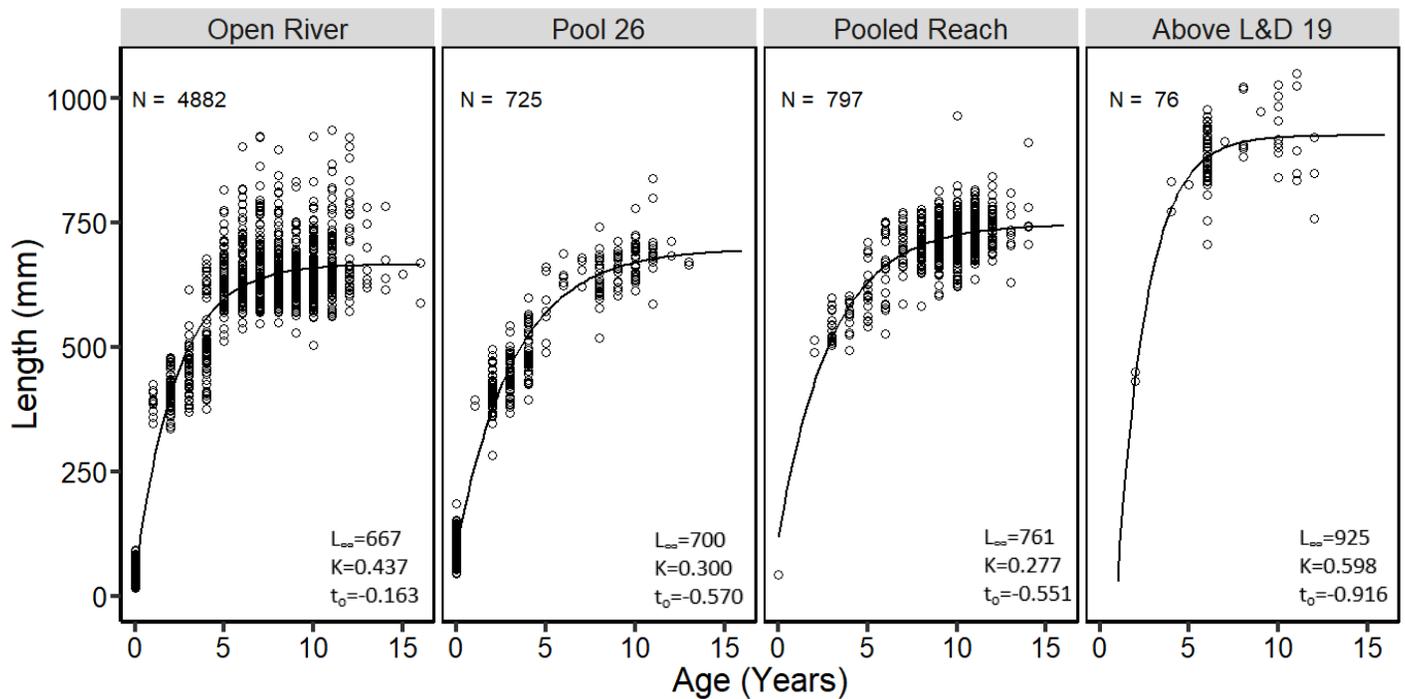


Figure 11. Reach-specific von Bertalanffy growth models (Pool 26 separated from the pooled reach) depicting mean length-at-age for Silver Carp captured using electrified dozer trawl from all locations of the Upper Mississippi River during 2021 and 2022. Age samples were supplemented with non-standardized electrified dozer trawl collections, modified electrofishing collections, and gillnet catches.

Habitat-specific length comparisons: Adaptations to protocols from 2021 to 2022 included a randomized sampling approach stratified by habitats within each sample location of the UMR primarily to account for low water levels within tributaries. However, adapting to a mainstem sampling approach with tributaries included as a habitat classification allowed direct comparisons of mainstem and tributary habitats, which were predicated on the assumption that length distributions from tributary habitats were representative of mainstem populations.

A two-sample Kolmogorov-Smirnov (K-S; Zar 1999) test was used to determine whether the length distribution of Silver Carp captured at mainstem sites was similar to that of Silver Carp captured at tributary sites. The null hypothesis is that the mainstem and tributary samples are from the same population (i.e., distribution). Six tributaries were selected for analysis based on adequate transects completed ($N > 15$). The results of the two-sample K-S tests indicated statistically different length distributions between mainstem and tributary populations in the Big Muddy River ($P = 0.014$), Headwaters Diversion Channel ($P = 0.003$), Kaskaskia River ($P = 0.019$), Fabius River (Pool 22, $P < 0.001$), and the Cuivre River (Pool 26, $P = 0.002$) (Figure 12). However, the Pool 24 mainstem and Salt River tributary sites shared a similar distribution of sizes ($P = 0.144$). Overall, tributary samples appeared to have positively skewed length distributions, and mainstem samples had negatively skewed length distributions (Figure 12).

These results underscore the importance of sampling all available habitats where Silver Carp may be found when collecting demographic data because data collected from only one habitat type may misrepresent the entire population of interest and bias demographic estimates.

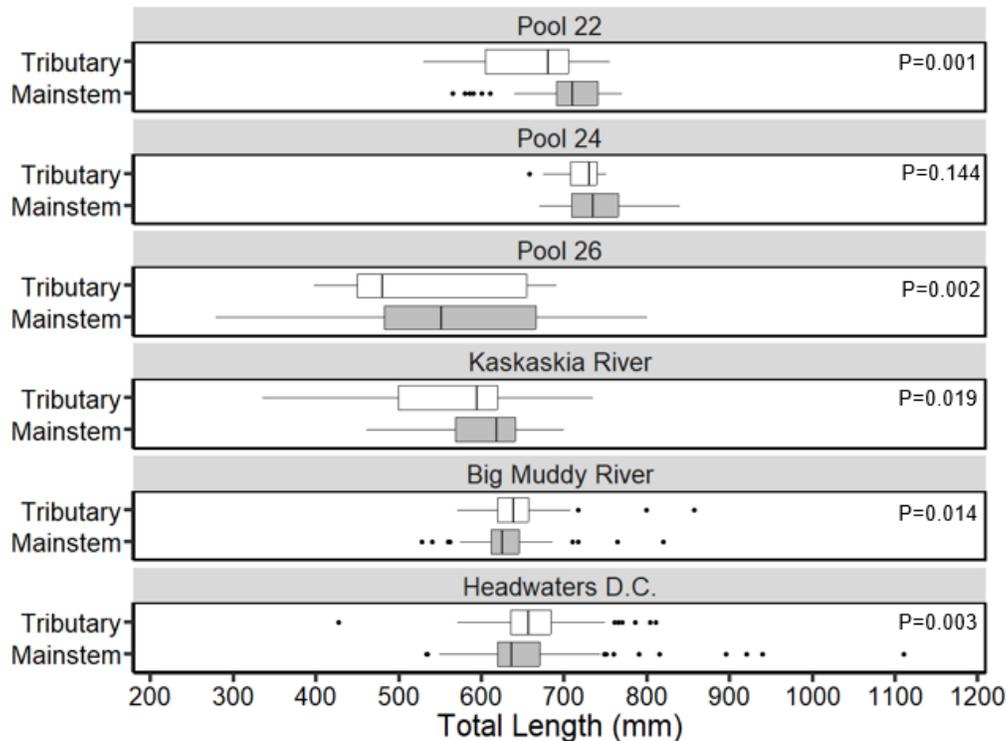


Figure 12. Length distributions of Silver Carp for individual sampling locations. For each boxplot the vertical line represents the median Silver Carp length, the lower and upper hinges correspond to the 25th and 75th percentiles, whiskers represent data between the largest and smallest values outside of the inter-quartile range, black points are the associated outliers. All fish were captured with the electrified dozer trawl during fall 2022.

Recommendations:

Biological systems are inherently complex and respond unpredictably, especially large riverine systems such as the Upper Mississippi River (Coulter et al. 2018). Furthermore, flow alterations, dams, training structures, and other river modifications add additional complexity to these systems (Poff et al. 1997; Garvey et al. 2010). Collection of high-quality demographic data enables managers to predict factors (e.g., temperatures, barriers, flow regimes, harvest, etc.) that affect Silver Carp populations and provide baseline metrics to measure population responses to future management or harvest events. Herein, we described results from a two-year study using fisheries-independent sampling to obtain demographic information of UMR Silver Carp. Initial observations of Silver Carp populations along a gradient of > 430 river miles of the UMR suggests patterns that may help managers better combat this invasive species. For example, relative abundance, size structure, condition, and population dynamics depict three potential

meta-populations of Silver Carp within the UMR. In the open river reach, Silver Carp were generally more abundant, smaller, in poorer condition, had smaller theoretical maximum sizes, and evident recruitment. These factors are consistent with “source” population dynamics (Crowder et al. 2000). In contrast, Silver Carp in the pooled reach, specifically upstream of Pool 26, exhibited lower abundance and were larger, in better condition, had larger theoretical maximum sizes, and had little to no evidence of consistent recruitment, consistent with “sink” population dynamics (Crowder et al. 2000). Furthermore, the extremely low relative abundances of Silver Carp above L&D 19 suggest that dams are acting as barriers to Silver Carp passage along the UMR and confirm that L&D 19 is a major barrier to fish movement (Larson et al. 2017, Whitley et al. 2019).

Although no recruitment indices were calculated, trends in year class strength throughout the sample locations depict variable recruitment throughout the UMR. Mortality indices indicate variable overall mortality throughout the UMR with higher mortality in areas of greater density and lower mortality in areas of lower density. Interestingly, Silver Carp in Pool 26 appear to exhibit unique demographic rates not similar to any other location sampled. Pool 26 appears to have evidence of a source population with evident recruitment and high densities. However, this pool still maintains increased condition and growth relative to the downstream populations in the open river reach. Data collected during 2021 and 2022 provides evidence that Pools 25-18 may be mostly comprised of migrant populations due to few captures of young (< age 4) fish or recruitment. Pool 26 appears to be the most upstream location with evidence of large recruitment classes in the UMR. These somewhat unusual demographics of Silver Carp in Pool 26 suggest that this is a transitional area that may be supporting upstream populations through immigration. It is important to note that successful recruitment above L&D 19 was documented during 2016, and those populations are composed of many of the individuals from that year-class although no annual spawning and recruitment have been documented since 2016.

We recommend coordinating monitoring with management and harvest of Silver Carp throughout the UMR to inform and evaluate management efforts within an adaptive management framework. Continued monitoring through fisheries-independent sampling will provide demographic rates (i.e., length, weight, sex, age, relative abundance) of Silver Carp to explore alternative harvest scenarios using model-based tools. We recommend standardized sampling, such as the approach described herein, to quantify Silver Carp population demographics throughout the Mississippi River that may have utility for providing basin-wide management recommendations. Finally, we recommend further investigation into the demographic anomalies observed in Pool 26 to determine factors affecting Silver Carp dynamic rates and the utility of this location for management efforts.

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