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Research Article

Population characteristics of silver carp from the source of their North American introduction in the Lower Mississippi River

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Abstract

Silver carp, *Hypophthalmichthys molitrix*, escaped into the Lower Mississippi River (LMR) over 50 years ago, established reproductive populations, and spread across much of the Mississippi River Basin. Demographic rates of silver carp are needed to inform decisions on control and management of this invasive species, but have not been published for the LMR. The purpose of this paper is to report silver carp age and growth estimates from fish collected in riverine (mainstem) and backwater (lake) habitats in the LMR during the period 2011–2019, to compare our results with populations from other geographic areas in the Upper Mississippi River drainage, and to evaluate latitudinal and habitat differences in demographic parameters. Silver carp gained weight with increasing length similarly throughout the lower and upper basin. However, annual growth rates were higher in the LMR compared to northern rivers including the Illinois, Wabash, Missouri, and Middle Mississippi rivers. In the LMR, regression analyses demonstrated that females were heavier in lakes than males or females in the mainstem and that females in lakes had the lowest instantaneous mortality (-0.186). Maximum age was 8 and 10 years for females and males, respectively. The largest male weighed 13.8 kg with a total length of 1022 mm, and was 7 years old. The largest female weighed 16.0 kg with a total length of 1034 mm TL, and was 7 years old. Rapid growth rates, larger sizes, and lower mortality in the LMR, in combination with limited commercial fishing, extensive river-floodplain connectivity, and vast amounts of spawning areas, ensure that LMR silver carp will continue to act as a source of fast-growing invasive individuals for other reaches and other rivers throughout the Mississippi River Basin.

Key words: Latitudinal gradients, recruitment, mortality, age, growth, mainstem channel, oxbow lakes, backwater

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Introduction

Silver carp, *Hypophthalmichthys molitrix*, are one of the most widely cultured fish in the world and are now found in 88 countries and territories including the United States (Kolar et al. 2005; Cai et al. 2017). This invasive species is native to rivers flowing into the Pacific Ocean from Vietnam to Russia (21°N to 54°N) (Laird and Page 1996; Xie and Chen 2001; Froese and Pauly 2021). Silver carp were introduced into Arkansas, USA during 1973 to control algal blooms in wastewater treatment plants and aquaculture facilities (Henderson 1978; Freeze and Henderson 1982), eventually escaping into surrounding states (Kelly et al. 2011). Populations expanded throughout the Lower Mississippi River during the 1990s and 2000s (Eggleton et al. 2024). With dispersal rates of up to 64 river km per day (DeGrandchamp et al. 2008) and a maximum reported upstream distance traveled of over 1100 km from the Yazoo River System in Mississippi to Pool 26 on the Upper Mississippi River (Stafford 2024), populations have expanded to most of the Mississippi River system (Kolar et al. 2005; Conover et al. 2007; Coulter et al. 2016).

Silver carp can weigh over 27 kg, grow to over 1 m total length, and live up to 20 years in their native range of Southeast Asia (Conover et al. 2007; Nico et al. 2005). Maximum ages of silver carp reported in the Mississippi River drainage are much lower ranging from 5 to 6 years including the Middle Mississippi River between the confluence of the Missouri and Ohio Rivers (Williamson and Garvey 2005), and the Illinois River (Irons et al. 2011). Hayer et al. (2014) reported a maximum age of 5 years in tributaries to the Missouri River, but 10 years after the invasion front, maximum age was 14 years although growth rates had decreased (Harms et al. 2024). Sullivan et al. (2020) also found that maximum silver carp age decreased with increasing latitude in the Upper Mississippi River system whereas recruitment was less stable for populations with higher relative abundance estimates and where carp were first detected ≥20 years ago. Ridgway and Bettoli (2017) indicated that growth tends to increase at lower latitudes. They sampled the lowermost reservoirs on the Tennessee River (Kentucky Lake) and Cumberland River (Lake Barkley) and reported a maximum total length and age of 1005 mm and 13 years for silver carp, respectively. They also reported that silver carp had faster growth rates than for other populations reported around the globe, with age 3 females and males attaining mean total lengths of 782 and 807 mm, respectively.

Growth rates of silver carp in the Lower Mississippi River mainstem (LMR), which extends from the mouth of the Ohio River to the Gulf of Mexico, have not been previously reported despite the fact that they originated in Arkansas and the LMR represents the center of population abundance and a primary dispersal route. The LMR provides unlimited spawning sites in flowing reaches and extensive backwaters and lakes with high productivity for rearing (Varble et al. 2007; Pongruktham et al. 2010). The availability of spawning and foraging habitat in the LMR sustains population expansion throughout the valley. Information on population structure is needed throughout the range of the species for management and control strategies implemented by the Invasive Carp Regional Coordinating Committee (https://invasivecarp.us/about-ICRCC.html, accessed May 2024) and state fish conservation agencies. Therefore, the objectives of this paper are to compare silver carp age and growth in the LMR to other geographic areas in the Mississippi River Basin, to evaluate latitudinal differences in demographic rates, and to compare growth rates of males and females in the LMR between mainstem and adjacent floodplain lakes.

Study sites

The LMR mainstem sites included six locations extending from the mouth of the Ohio River (river kilometer, Rkm 1534) downstream to near the mouth of the Mississippi River at the Gulf of Mexico (Rkm 32) (Fig. 1). However, the majority of collections in the mainstem occurred between Rkm 686 and Rkm 1516. Collections from the Bonnet Carré Spillway were entrained silver carp originating directly from the Mississippi River and considered mainstem inhabitants (Killgore et al. 2022). Three floodplain water bodies in the batture (leveed floodplain) of the LMR were sampled. These included two oxbow lakes, Desoto (34.081264; -90.504757) and Horn (34.583692; -90.092179), both connected to the Mississippi River via tie channels. The third water body was Forest Home Chute (32.455749; -90.028080), a long, narrow, side channel that runs parallel to the main channel of the Mississippi River near Rkm 719-729 (Ochs et al. 2019). It is mostly lentic, similar to oxbow lakes, and connects to the mainstem periodically.

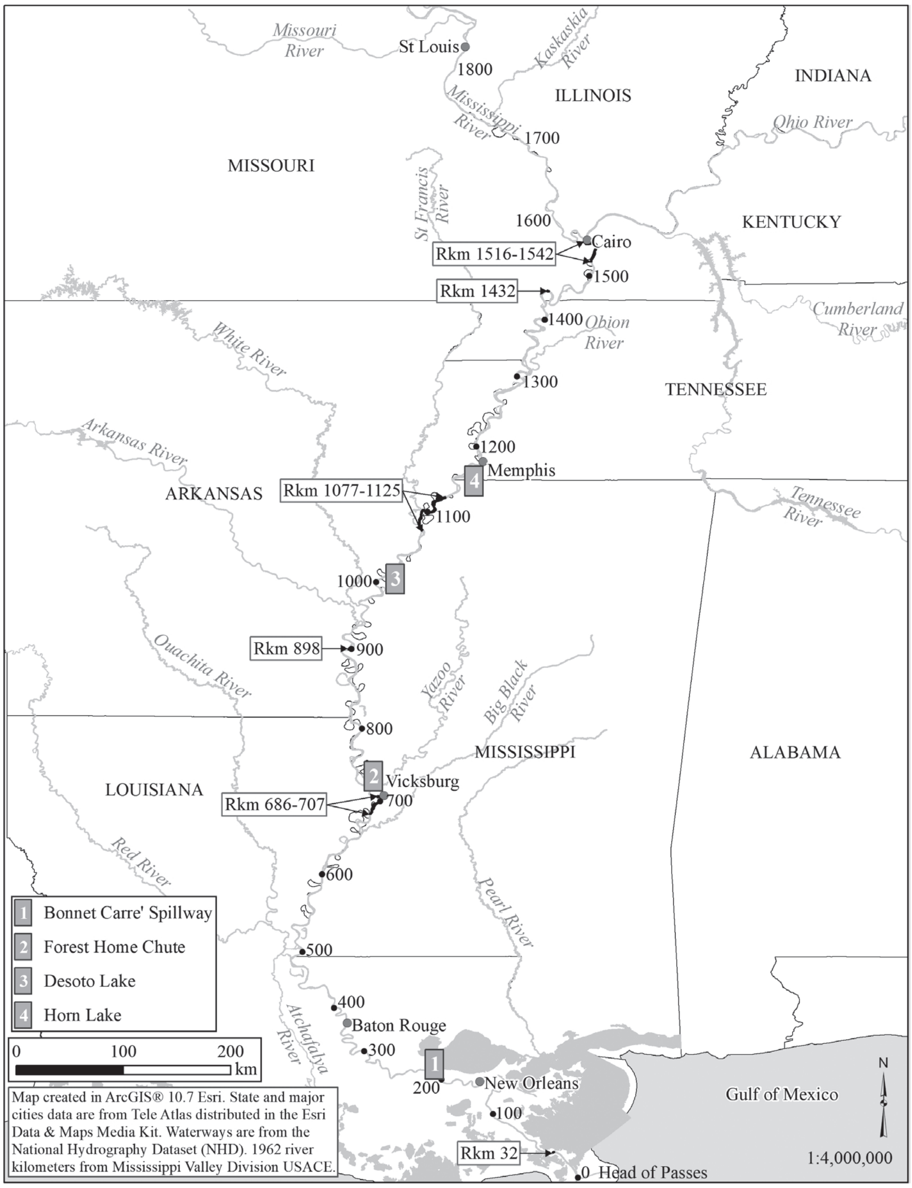

Figure 1. Capture locations of silver carp in the Lower Mississippi River (LMR) from 2011-2019. Boxed river kilometers (Rkm) indicate mainstem sampling reaches. Lakes indicated by boxed numbers 1-4. Samples were collected from Fort Jackson (Rkm 32, 29.2130N, -89.2722W) upstream to the near the mouth of the Ohio River (37.0053N, -89.1765W).

Methods

To characterize the large-scale variation in silver carp length at age and their growth performance throughout the vast LMR, we relied on samples collected opportunistically as part of various investigations at the U.S. Army Engineer Research and Development Center in Vicksburg, MS. Four gear types were used to collect silver carp. Gill nets produced 65% of the total catch, electrofishing 23%, hoop nets 3%, and the remaining 9% were jumpers that landed in one of our survey boats. Most gill nets were multifilament with 10.2 cm bar mesh, 91 m long, and 2.4 m deep. A 46 by 2.4 m trammel net with 6.3 cm square mesh was also used. Silver carp from Horn Lake were by-catch of commercial fishing during the 2011 paddlefish *Polyodon spathula* harvest which used 12.7 cm bar mesh. Boat electrofishing was generally operated as pulsed direct current, 60 Hz, and approximately 5 to 7 mean amps read from a Smith-Root GPP unit®. Hoop nets were 1.2 m diameter opening, 7 hoops, 4.6 m long, and 7.6 cm square mesh.

All silver carp collected were euthanized, and immediately after, fish were measured for total length to the nearest 1 mm and for weight to the nearest 10 g. Gonads were examined to determine sex. The leading pectoral fin rays were removed, labeled, and stored for subsequent aging. To prepare for aging, fin rays were sectioned along the basal portion of the ray to a thickness of approximately 0.70 mm using a Buehler Isomet® saw with a diamond wafering blade. Aging involved counting annuli on the sectioned rays while viewed under transmitted light with an Olympus SZX16® zoom stereomicroscope, equipped with an Olympus DP72® camera system and cellSens® imaging software. Two readers agreed in advance about what constituted an annular mark and independently aged each fish by counting annual marks. Opaque zones viewed under reflected light were counted as annuli. When a discrepancy occurred (about 45% of the time, 36% of those with a difference of 1 year), a consensus age was assigned if agreement could be reached; otherwise, the rays were discarded. The percent agreement and a coefficient of variation (CV) were calculated to document precision differences among agers (Campana 2001). Fin rays have been used in other silver carp studies (Kamilov 1985; Williamson and Garvey 2005; Seibert and Phelps 2013). Stuck et al. (2015) documented high agreement (78%) of fin rays with lapilli otolith in silver carp, but cautioned that fin rays can underestimate age, typically by 1 year.

We examined weight-length and mortality curves using linear methods, and growth curves using nonlinear methods. The relation between total body weight (W; g) and total length (L; mm) is represented by a logarithmic curve typically applied with a $\log_{10}$ transformation of W and L:

$$log_{10} W = b_0 + b_1 \cdot log_{10} L \tag{1}$$

where b_0 is an intercept parameter and b_1 is a slope parameter that describes weight increase relative to length increase. To test for potential differences in weight-length relations between habitats and between genders, equation 1 was expanded into an analysis of covariance to include habitat type (*H*: main channel = 0, lakes = 1), and fish gender (*G*: male = 0, female = 1):

$$log_{10} W = b_0 + b_1 \cdot log_{10} L + b_2 \cdot log_{10} L \cdot H + b_3 \cdot log_{10} L \cdot G + b_4 \cdot log_{10} L \cdot H \cdot G \tag{2}$$

where b_0 is an intercept parameter, b_1 tests for an effect of length on weight, b_2 tests for an effect of habitat on the length-weight model, b_3 tests for an effect of gender on the length-weight model, and b_4 tests if an effect of habitat on the length-weight model depended on gender, or if an effect of gender depended on habitat.

The relation between number of fish (N) and age (years) is represented by a logarithmic curve that is typically linearized with a $\log_e$ transformation of N (i.e., catch curve):

$$log_e N = b_0 + b_1 \cdot age \tag{3}$$

where b_0 is an intercept parameter and b_1 is a slope parameter that represents the instantaneous rate of annual mortality. To test for potential differences in mortality between habitats and between gender equation 3 was expanded to include habitat type and fish gender:

$$log_e N = b_0 + b_1 \cdot age + b_2 \cdot age \cdot H + b_3 \cdot age \cdot G + b_4 \cdot age \cdot H \cdot G \tag{4}$$

where b_0 is an intercept parameter, b_1 tests for an effect of age on number, b_2 tests if b_1 is influenced by habitat, b_3 tests if b_1 is influenced by gender, and b_4 tests if any effect of gender on b_1 depends on habitat, or any effect of habitat depends on gender. Equations 1–4 were fit with the GLM procedure (SAS 2020).

Length at age data were used to estimate von Bertalanffy growth coefficients (von Bertalanffy 1938) with the original model parameterization (Cailliet et al. 2006) and using a nonlinear model:

$$L_t = L_\infty - (L_\infty - L_0) \cdot e^{-Kt} \tag{5}$$

where L_t is the length at age t in years, L_∞ is the mean asymptotic length, L_0 is the length at time zero (i.e., hatching), K is a growth coefficient, and e is the exponent for natural logarithms. L_0 was fixed as 5.1 mm based on estimates published by Chapman and George (2011). Equation 5 was expanded to test for potential differences in growth characteristics between habitats and between fish gender:

$$\begin{aligned} L_t = {} & [L_\infty + (b_1 \cdot H) + (b_2 \cdot G) + (b_3 \cdot H \cdot G)] - [L_\infty + (b_1 \cdot H) \\ & + (b_2 \cdot G) + (b_3 \cdot H \cdot G) - L_0] \cdot e^{[-K + (b_4 \cdot H) + (b_5 \cdot G) + (b_6 \cdot H \cdot G)] \cdot t} \end{aligned} \tag{6}$$

where b_1 tests if L_∞ depends on habitat, b_2 tests if L_∞ depends on gender, and b_3 tests if L_∞ depends on habitat and gender. In a similar manner, the tests conducted by b_4, b_5, and b_6 are analogous to those performed by b_1 - b_3, with the distinction that they are applied to the variable K rather than L_∞ Equations 5–6 were fit with the NLIN (nonlinear) procedure (SAS 2020). Model parameters were considered statistically significant if $P < 0.05$ and results compared to other regional populations studies of silver carp.

Results

Weight-length

A total of 360 silver carp comprised of 209 females and 151 males were collected in the LMR mainstem and lakes from 2011 to 2019. The weight-length regression for all fish combined (equation 1; Table 1) provided a suitable fit with an $R^2 = 0.95$ and suggested an acute allometric growth with a $b_1 = 3.665$. The expanded weight-length procedure (equation 2; Table 1) indicated that the weight-length relations differed between habitat and gender and that there was an interaction between habitat and gender. A plot of these weight-length relations (Fig. 2) with the coefficients for equation 2 (Table 1) indicated that females were heavier in lakes, but that other differences, even if statistically significant, were minor.

Table 1. Relations between $\log_{10}$ weight (g) and $\log_{10}$ total length (mm) for male and female silver carp collected in mainstem and lake habitats in the Lower Mississippi River, 2011-2019. Equation 1 was a regression model fit to the full data set regardless of gender or habitat; equation 2 was an analysis of co-variance that included the effect of gender, habitat, and their interaction on the weight-length relation.

Parameter	Estimate	SE	t-value	P > t
Equation 1 (R^2 = 0.95)				
b_0	-9.88	0.120	-82.1	<0.01
b_1	3.665	0.041	88.6	<0.01
Equation 2 (R^2 = 0.96)				
b_0	-9.596	0.159	-69.3	<0.01
b_1	3.572	0.047	75.8	<0.01
b_2: mainstem	-0.012	0.003	-4.3	<0.01
b_2: lakes	0			
b_3: male	-0.010	0.002	-4.6	<0.01
b_3: female	0			
b_4: mainstem, male	0.013	0.004	3.7	<0.01
b_4: mainstem, female	0			
b_4: lakes, male	0			
b_4: lakes, female	0			

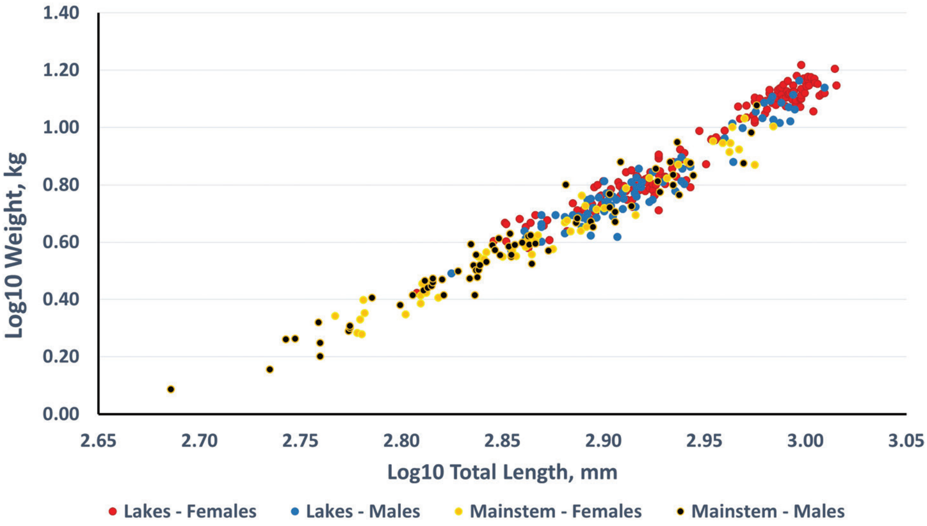

Figure 2. Regression between $\log_{10}$ weight (kg) and $\log_{10}$ total length (mm) for silver carp in the Lower Mississippi River in 2011-2019.

Regional comparisons of weight-length regressions indicated that the slope of LMR fish weight gains were greater than upper basin fish (Table 2). However, predicted weights varied between sizes. For 450 mm fish, LMR predicted weight was less than upper basin fish while predicted weight for 800 mm fish was slightly higher in the LMR or comparable to upper basin fish.

Age

Ages were estimated for 360 silver carp ranging from 2 to 10 years. Of this total, 59% of the pectoral fin rays were read by two readers independently. Percent agreement was 77% for ages 1–2, decreased to 51% for ages 3–5, and 53% for older (ages 6–10) fish. Overall, there was a 56% agreement on the same age, a 95% agreement for ±1 year, and a coefficient of variation of 122% (n=211).

Table 2. Length-weight regression for silver carp based on Hayer et al. (2014). The 95% confidence limits (CL) around the parameter estimates along with predicted fish weights (g) for 450 mm and 800 mm total lengths (mm) are compared among sub-basins of the Mississippi River.

River	L-W Regression Equation	R^2	Intercept 95% CL		Slope 95% CL		450 mm	800 mm	Reference
South Dakota Tributaries, n=469									
James	$\log_{10}$ weight = -5.26+3.11($\log_{10}$ length)	0.96	-5.43	-5.1	3.05	3.17	981	5869	Hayer et al. 2014
Vermillion	$\log_{10}$ weight = -4.82+2.90($\log_{10}$ length)	0.98	-5.16	-4.47	2.82	3.07	748	3971	Hayer et al. 2014
Big Sioux	$\log_{10}$ weight = -5.53+3.21($\log_{10}$ length)	0.98	-5.91	-5.14	3.07	3.36	970	6150	Hayer et al. 2014
Missouri River									
Gavins Point, n=7	$\log_{10}$ weight= -6.92+3.70($\log_{10}$ length)	0.97	0.21		0.59		788	6628	Wanner and Klumb 2009
Interior Highlands, n=68	$\log_{10}$ weight = -5.35+3.13($\log_{10}$ length)	0.93	0.76		0.21		900	5453	Wanner and Klumb 2009
Middle Mississippi River/Illinois River									
Middle, n=145	$\log_{10}$ weight = -5.29+3.11($\log_{10}$ length)	0.81					915	5477	Williamson and Garvey 2005
Illinois River, n=452	$\log_{10}$ weight = -5.29+3.12($\log_{10}$ length)	0.99					972	5856	Irons et al. 2011
Lower Mississippi River, n=360	$\log_{10}$weight= -6.88+3.66($\log_{10}$length)	0.95	-6.647	-7.121	3.58	3.75	691	5695	This Study

A total of 151 males and 209 females were aged with an overall sex ratio between males and females of 1:1.3. However, sex ratio differed between habitats with females constituting 66% of the individuals in lakes compared to 42% females in mainstem. Males and females had similar age distributions (Table 3). Over 80% of the individuals for both sexes were ages 3–7 with 5% or less being older than 7 years. Maximum age was 10 years for males and 8 years for females. The largest male in terms of weight was 13.8 kg with a total length of 1022 mm, and was 7 years old. The largest female weighed 16.0 kg with a total length of 1034 mm TL, and was 7 years old.

The catch curve for all fish combined (equation 3; Table 4) provided an adequate fit with an $R^2 = 0.45$ and a moderate instantaneous annual mortality with a $b_1 = -0.37$. This value translates into an annual interval mortality of 0.311 (i.e., $1-e^{-0.372}$). The expanded catch curve (equation 4) identified an interaction between habitat and gender (Table 4). These results suggest that instantaneous mortality differed across gender, but the difference depended on habitat. The lowest mortality ($-0.454 + 0.067 - 0.055 + 0.256 = -0.186$) was for females in lakes, and the highest ($-0.454 - 0.055 = -0.509$) for females in mainstem. Instantaneous mortalities for males in lakes and mainstem were -0.387 and -0.454, respectively.

The growth model estimated that silver carp in the LMR attained an L_∞ of 911 mm TL, with 95% confidence limits stretching 891–930 (equation 5, Table 5). The growth coefficient K was estimated at 0.548 with 95% confidence limits stretching 0.5–0.6. The expanded model (equation 6, Table 5) indicated a habitat effect with fish in lakes attaining a larger L_∞ ($776 + 137 = 913$) and a lower K ($0.925 - 0.425 = 0.5$). There was no significant gender effect or habitat by gender interaction as suggested by confidence limits overlapping zero.

The model predicted that silver carp in the LMR reached total lengths of 600 mm or greater by age 2, and almost 900 mm total length by age 5 (Fig. 3). Growth rates for the Tennessee River and LMR silver carp were similar up to age 3, but LMR silver carp subsequently grew faster at older ages. Silver carp growth rates declined at higher latitudes and were slowest in Illinois, Wabash, and Missouri rivers (Fig. 3). The Middle Mississippi River had intermediate growth rates between higher and lower latitudes.

Table 3. Age (years) frequency of silver carp in the Lower Mississippi River, 2011-2019.

Age	Females (N = 209)				Males (N = 151)			
	Frequency	Percent	Cumulative Frequency	Cumulative Percent	Frequency	Percent	Cumulative Frequency	Cumulative Percent
2	10	4.8	10	4.8	17	11.3	17	11.3
3	27	12.9	37	17.7	19	12.6	36	23.8
4	37	17.7	74	35.4	35	23.2	71	47.0
5	45	21.5	119	56.9	31	20.5	102	67.6
6	30	14.4	149	71.3	24	15.9	126	83.4
7	49	23.4	198	94.7	20	13.3	146	96.7
8	11	5.3	209	100.0	3	2.0	149	98.7
9	0				0			
10	0				2	1.3	151	100.0

Table 4. Relation between $\log_e$ number of fish and age (years) for male and female silver carp collected in mainstem and lake habitats in the Lower Mississippi River, 2011-2019. Equation 3 was a regression model fit to the full data set regardless of gender or habitat; equation 4 was an analysis of covariance that included the effect of gender, habitat, and their interaction on the relation between number and age.

Parameter	Estimate	SE	t-value	P > t
Equation 3 (R^2 = 0.45)				
b_0	4.317	0.37	-7.9	<0.01
b_1	-0.372	0.088	-4.2	<0.01
Equation 4 (R^2 = 0.80)				
b_0	4.411	0.159	11.9	<0.01
b_1	-0.454	0.064	-7.1	<0.01
b_2: mainstem	0			
b_2: lakes	0.067	0.048	1.4	0.18
b_3: male	0			
b_3: female	-0.055	0.061	-0.9	0.38
b_4: mainstem, male	0			
b_4: mainstem, female	0			
b_4: lakes, male	0			
b_4: lakes, female	0.256	0.080	3.2	<0.01

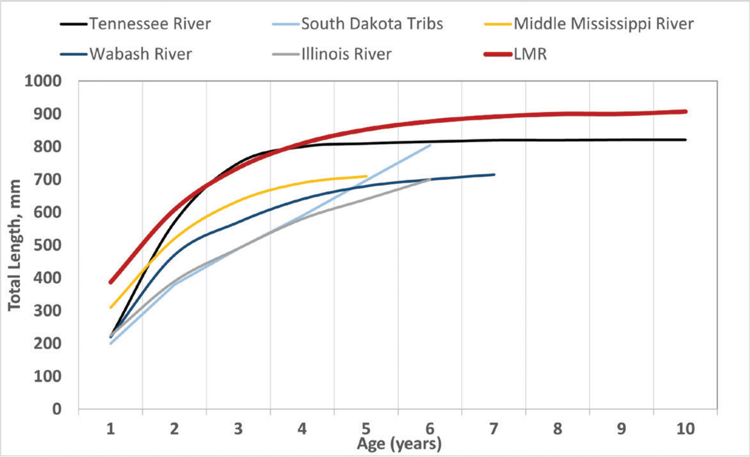

Figure 3. Von Bertalanffy growth curves for silver carp (combined sexes) in LMR mainstem and lakes compared to the Tennessee River (Ridgway and Betolli 2017), Middle Mississippi River (Williamson and Garvey 2005), South Dakota tributaries of the Missouri River (Hayer et al. 2014), Wabash River, IL and the Illinois River (Stuck et al. 2015). Latitudes ranged from 30° - 37°N in the LMR and Tennessee Rivers to 42°N in the South Dakota tributaries.

Table 5. Von Bertalanffy growth coefficients of silver carp collected in the Lower Mississippi River from 2011-2019 using a nonlinear model where L∞ is the mean asymptotic length and K is a growth coefficient (Equation 5). Equation 5 was expanded to test for potential differences in growth characteristics between habitats and between fish gender (Equation 6).

Parameter	Estimate	Approximate SE	Lower 95% CL	Upper 95% CL
Equation 5				
L_∞	911	9.789	891	930
K	0.548	0.025	0.498	0.598
Equation 6				
L_∞	776	15.573	745	806
K	0.925	0.102	0.726	1.125
b_1: lake	137	29	**80**	**194**
b_1: mainstem	0			
b_2: female	48	27	-5	102
b_2: male	0			
b_3: lake, female	29	41	-52	111
b_3: lake, male	0			
b_3: mainstem, female	0			
b_3: mainstem, male	0			
b_4: lake	-0.425	0.118	**-0.657**	**-0.194**
b_4: mainstem	0			
b_5: female	-0.119	0.145	-0.404	0.165
b_5: male	0			
b_6: lake, female	0.037	0.159	-0.276	0.350
b_6: lake, male	0			
b_6: mainstem, female	0			
b_6: mainstem, male	0			

Discussion

Since silver carp were introduced into the USA over 50 years ago, they have become widespread in the LMR potentially providing source populations for range expansion and establishment. Hayer et al. (2014) points out that other invasive populations including bigheaded carps seem to peak in abundance after a rapid and/or exponential increase in density or biomass, which is followed by a leveling off corresponding to some carrying capacity. Although the absolute population density of silver carp in the LMR is not known, the carrying capacity of the LMR may not have been reached particularly when repeated flooding events expand open-river spawning habitat and longer temporal connections to extensive backwater lakes used as rearing and foraging habitat.

Silver carp gained weight with increasing length at larger sizes similarly throughout the lower and upper basin, whereas annual growth rates were faster in the lower basin including the Tennessee River (Ridgway and Bettoli 2017). Growth rates in the LMR were also higher than reported in their native river systems in Asia (Tandon et al. 1993, cited in Williamson and Garvey 2005). Weight-length relations indicate that silver carp will achieve their largest sizes as females in oxbow lakes and likely other floodplain waterbodies such as abandoned channels, borrow areas, and meander scarps, which comprise over 60,000 hectares of the LMR floodplain (Baker et al. 1991). These backwater habitats provide ideal conditions for successful nursery, foraging, and overwinter habitats that likely contribute to an L_∞ of 911 mm, which is higher than the Upper Mississippi River System above the confluence of the Missouri River ($L_\infty < 775$ mm, Sullivan et al. 2021), Middle Mississippi River between the mouths of the Missouri and Ohio River ($L_\infty = 778$ mm, Williamson and Garvey 2005), the Ohio River ($L_\infty < 900$ mm, Supplement 2, Erickson et al. 2021), and Tennessee River ($L\infty = 881$ mm, Ridgway and Bettoli 2017). Based on the leaping characteristics of silver carp, larger individuals were also noted in lower latitudes compared to the Illinois and Missouri rivers (Stell et al. 2020). An exception in the Upper Mississippi River was higher growth rates and $L_\infty > 963$ mm of silver carp upstream of Lock and Dam 19 than downstream suggesting that increased lacustrine habitat (backwaters, impounded habitats, and tributary mouths) and lower population densities in reaches above Pool 19 were contributing factors (Broaddus and Lamer 2022). Irons et al. (2011) citing MacArthur and Wilson (1967) indicated that bigheaded carps most closely resemble r-strategists, capable of phenomenal reproductive potential and growth. This strategy is evident in the LMR.

Spatial variation in growth, weight, lifespan and mortality of silver carp have been noted in several studies. In addition to this study, a latitudinal decrease in silver carp growth rates have been reported (Hayer et al. 2014; Ridgway and Bettoli 2017), possibly due to habitat availability and colder temperatures. River discharge was correlated to spatial differences in silver carp year class strength in the Middle and Upper Mississippi River Basin (Sullivan et al. 2018). Demographic rates varied within and among the Illinois, Ohio, and Mississippi rivers due to different flow conditions and habitats of these pools (Erickson et al. 2021). For example, estimated total annual mortality of silver carp in the LMR was less than 30% compared to 50% or greater in a study in the Illinois River (Stuck et al. 2015) and its native range in China where extensive commercial fishing exists (Zhu et al. 2021). Silver carp in the LMR may have almost infinite resources in a temperate environment contributing to rapid growth rates, whereas carp moving upstream into the Middle Mississippi and Missouri rivers face a reduced floodplain and colder temperatures that potentially impact growth rates. Lakes in the LMR floodplain support larger, older, and heavier females than mainstem habitat by providing a low/no-velocity environment reducing energy expenditures during swimming and by providing abundant preferred plankton (Ochs et al. 2019). Mortality is lower in lakes possibly due to expanded preferred habitat in larger waterbodies, although unknown predation and fishing pressure may influence multiple demographic functions.

Lock and dams on the Upper Mississippi, Illinois, and Ohio rivers affect passage (Lohmeyer and Garvey 2009; Coulter et al. 2018; Whitledge et al. 2019). Dams also reduce free-flowing river reaches that form the "vortex water" necessary to illicit silver carp spawning behavior in the Yangtze River (Fang et al. 2022) and also observed in a sinuous reach of a LMR tributary (Killgore and George 2021). High population densities are encountered in the navigation pools of the Illinois River (Sass et al. 2010), which may eventually limit available food and reduce growth rates and survival. However, fish immigrating from the LMR, which is free flowing with a largely well-connected floodplain, may provide a steady supply of reproductive adults.

Norman and Whitledge (2015) suggest that substantial immigration from the Mississippi River could reduce sustainability and efficiency of control efforts currently being taken in northern latitudes including the Illinois River and Chicago Sanitary and Ship Canal where electric barriers are preventing passage into the Great Lakes (Holliman et al. 2015). Control and management strategies depend on knowledge of demographic rates and recruitment dynamics of bigheaded carp (*Hypophthalmichthys* spp.) sub-populations throughout the range (Norman and Whitledge 2015; Erickson et al. 2021; Kallis et al. 2023). Since silver carp were first introduced into Arkansas in the early 1970's, they established reproductive populations and moved throughout much of the Mississippi River Basin.

Fifty years later, this study indicates that relatively low mortality and rapid growth rates in the LMR with limited commercial fishing, extensive river-floodplain connectivity, and vast amounts of spawning areas ensures that silver carp will continue to exert competitive pressure on biotic assemblages and provide source populations to river reaches throughout the Mississippi River Basin. Kallis et al. (2023) emphasizes the benefits of adopting a multipronged approach for invasive species management, combining suppression of source populations, such as the LMR, with disrupting movement between source and sink populations thereby producing compounding benefits for control. However, Schoolmaster et al. (2022) points out that aquatic invasive species often have high rates of dispersion and migration among heterogeneous locations, which complicates traditional metapopulation models and may require very different management actions.

Our study contributes to a better understanding of key demographic rates of silver carp in the LMR needed for three distinct goals: i.) evaluating the probability of local establishment based on an age-structured population model, predicting the risk of establishing a population, and identifying the most vulnerable stage to control (Currie et al. 2012); ii) estimating impacts to local native fish populations by pairing bioenergetics and population models to assess risk (Kinlock et al. 2020); and iii) evaluating efficacy of management techniques with simulation models to compare the performance of alternative removal strategies (Tsehaye et al. 2013). In addition, rapid growth rates of silver carp in the LMR, particularly in oxbow lakes, indicate that management can include removal for human consumption and other uses in a highly prolific population (Varble and Secchi 2013). The likelihood of achieving these goals, at local, regional, or national levels, will require a metapopulation approach similar to Kallis et al. (2023) due to disparate demographic rates now demonstrated for populations in the Mississippi Basin.

Authors' Contribution

KJK, JJH, WTS, JPK, LEM contributed to research conceptualization, sampling, and data analysis, and BRL and SGG led field and laboratory data collection activities

Ethics and Permits

All research was performed in accordance with the Guidelines for the Use of Fishes in Research by the American Fisheries Society, and under the Institute of Animal Care Committee at the Engineer Research and Development Center, and accredited by the Care and Use of Laboratory Animals in DOD Programs.

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