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Research Article

Progression along the invasion curve: silver carp growth slows temporally in two Missouri River tributaries

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Abstract

Silver carp (*Hypophthalmichthys molitrix* Valenciennes, 1844) have been invading North American rivers for decades, often altering zooplankton community structure and impacting native fishes. Silver carp invaded eastern South Dakota tributaries of the Missouri River in the early 2000s. Changes in dynamic rate functions can occur as invasive populations move to the latter stages of the invasion curve, but direct temporal assessments of silver carp populations are limited. Our objectives were to compare current growth of silver carp 1) between the Big Sioux and James rivers in South Dakota and 2) with previous growth recorded from the early stages of invasion (2009–2012) in these rivers. We collected silver carp in May and June of 2020–2022 using boat electrofishing and cast netting. We extracted lapilli otoliths for consensus aging from 99 and 82 silver carp from the Big Sioux and James rivers, respectively. We evaluated growth for each population using Bayesian von Bertalanffy models and compared posterior mean length at ages 2–5 to determine the probabilities of differences between rivers and with estimates from the introduction stage. Posterior estimated mean L_∞ values were similar between the Big Sioux (714 mm) and James rivers (709 mm); however, the probability that the posterior mean K estimate was greater for silver carp in the James River (0.271) than the Big Sioux River (0.248) was >99.9%. Estimated mean lengths at age 2 were larger in the Big Sioux and James samples than during the introduction stage, but mean lengths at ages 3–5 were smaller. Changes in growth characteristics indicate that growth has slowed in the current establishment stage of invasion from the earlier introduction stage.

Key words: bigheaded carp, invasion stages, growth, rivers, invasive carp, establishment, von Bertalanffy growth

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Introduction

Invasive species are an ever-increasing problem worldwide and are considered one of the biggest threats to native habitats and biodiversity. Nonnative species move through a progression of stages as they become invasive, but the timing of this progression can vary considerably spatially due to local differences in resources. The invasion curve is the theoretical timeline of progression following a new invasion and consists of four different invasion stages: transport, introduction, establishment, and spread (Blackburn et al. 2011). Following successful introduction to a new location and the introduced individuals starting to reproduce, the introduction stage typically consists of rapid growth in both individual body mass and population size (Williamson and Garvey 2005; Gutowsky and Fox 2011a). Increased growth rates have been documented in several fish species during the early stages immediately after invasion (Gutowsky and Fox 2011b; Feiner et al. 2012; Azour et al. 2015). Upon entering the establishment stage of the invasion curve, the population is expected to become self-sustaining and reach a consistent density subject to natural fluctuations (Azour et al. 2015; Schall et al. 2022). Individual growth rates are expected to decline compared to early invasion stages (Feiner et al. 2012; Azour et al. 2015), although some species, such as flathead catfish (*Pylodictus olivaris*), have demonstrated elevated growth rates for extended periods after reaching the establishment stage (Hilling et al. 2019).

Silver carp (*Hypophthalmichthys molitrix* Valenciennes, 1844) have been widely introduced around the world and have become a prevailing issue in the U.S. since escaping into wild waterways the 1970s (Freeze and Henderson 1982; Williamson and Garvey 2005). Their herbivorous and planktivorous diet made them a cost-effective option to help control algae blooms and clean aquaculture ponds when they were first introduced (Kelly et al. 2011). After escaping into the wild, silver carp spread throughout the Mississippi River basin, and the northwest portion of their range extends into the eastern South Dakota tributaries to the Missouri River (Hayer et al. 2014a). Silver carp threaten native species and habitats by reducing phytoplankton density and outcompeting juvenile fishes and native planktivores (Haupt and Phelps 2015; Pendleton et al. 2017; Shields et al. 2021). As silver carp reach the establishment stage of the invasion curve in these tributaries, we can use a temporal based study to gather information on the changes of silver carp growth.

Long-term monitoring of invasive carp populations will allow evaluation of temporal trends as invasive carp become established throughout the U.S. Growth in silver carp is commonly faster close to the leading edge of invasion for expanding populations (Chick et al. 2019; Werner et al. 2022). However, there are limited temporal comparisons of silver carp growth from a single location at the different stages of invasion. Silver carp invaded the three eastern South Dakota tributaries to the Missouri River (Big Sioux, James, and Vermillion rivers) in the early 2000s (Kolar et al. 2005) and were considered in the introduction stage during the early 2010s (Hayer et al. 2014b) when information on their growth was first collected. A current assessment of silver carp growth in these tributaries will allow for a comparison of growth rates as these populations move from the introduction to establishment stage of invasion. Therefore, our study objectives were to compare current growth of silver carp 1) between the Big Sioux and James rivers, South Dakota and 2) against estimates recorded 10 years earlier during the introduction stage of invasion in the eastern South Dakota tributaries to the Missouri River.

Methods

Study site

The Big Sioux and James rivers are two mid-sized rivers and are the largest tributaries to the Missouri River in eastern South Dakota (Morey and Berry 2003). The Big Sioux River basin covers 23,325 square kilometers along the South Dakota, Minnesota, and Iowa borders (Amundson et al. 1985). Sampling on the Big Sioux River occurred at two locations: the first was near Falls Parks and the diversion dam within the city of Sioux Falls and the second was at two downstream boat access sites 192 and 205 river kilometers (rkm) upstream of the confluence with the Missouri River (Figure 1). The James River has one of the lowest gradient slopes from headwaters to confluence of any river in the United States and has a drainage covering approximately 57,000 square kilometers. (Owen et al. 1981; Benson 1983). Sampling on the James River occurred immediately upstream of the confluence (rkm 0 to 9) and near boat access sites at rkm 40 and rkm 105 (Figure 1).

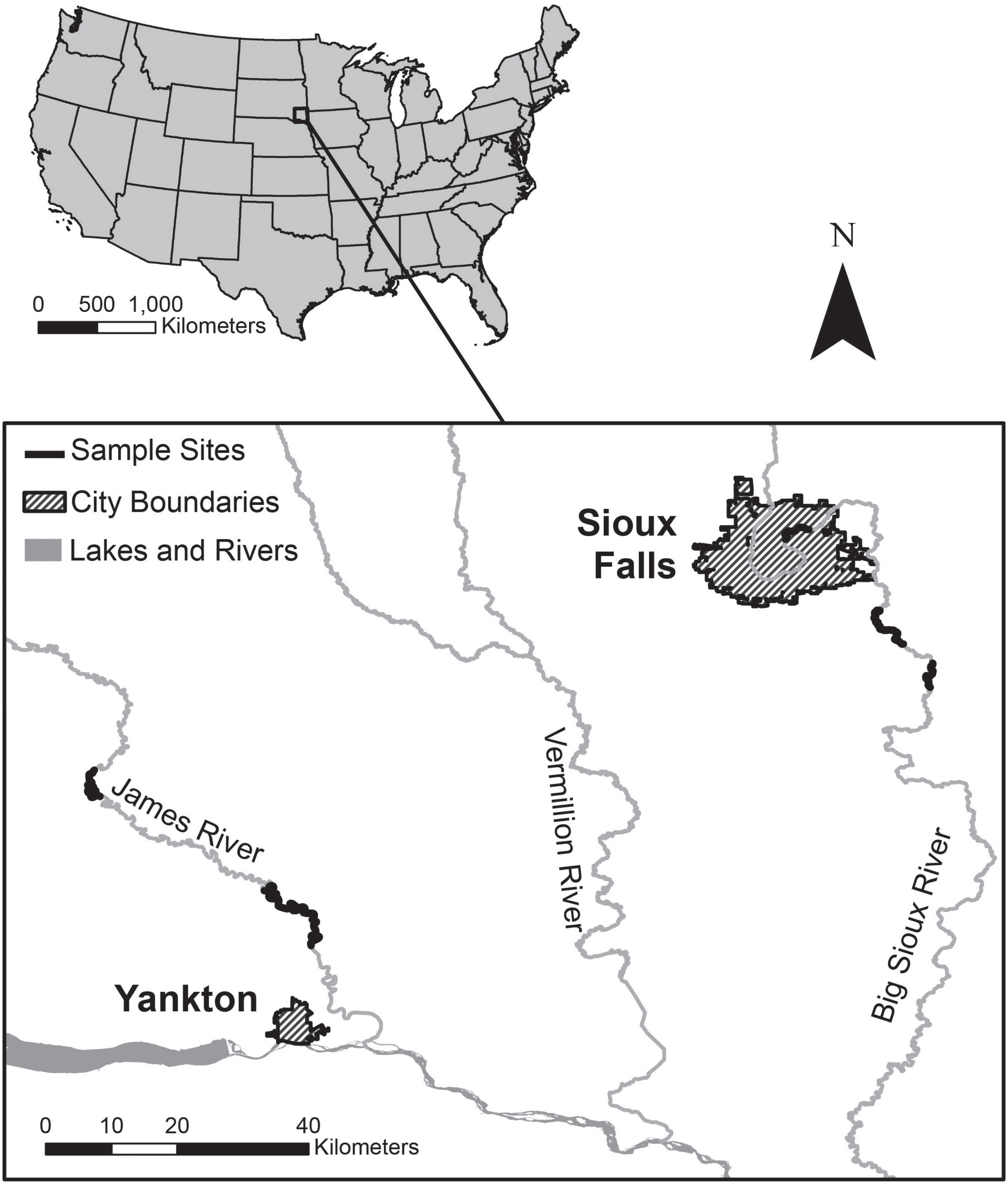

Figure 1. Map of the eastern South Dakota tributaries to the Missouri River showing sample sites on the Big Sioux River (within and southeast of Sioux Falls, South Dakota) and the James River (north and northwest of Yankton, South Dakota).

Fish sampling

Silver carp were primarily collected using daytime boat electrofishing in 2021 and 2022. Electrofishing was performed in a downstream direction with a Smith-Root GPP 7.5 electrofishing boat using pulsed direct current (170 V; 11–14 A; 120 pulses/s). Silver carp were also collected opportunistically as by-catch during electrofishing sampling events for other species. In June of 2020, juvenile silver carp (n = 13) were collected on the Big Sioux River below the falls at Sioux Falls and below the Sioux Falls spillway using a 2.44-m diameter cast net with 6.4-m mesh.

All silver carp were measured for total length (TL; mm). Silver carp were euthanized with either a lethal dose of MS-222 or by pithing, and lapilli otoliths were extracted for age estimation. Lapilli otoliths were used for aging based on the recommendation of Seibert and Phelps (2013). The otoliths were cleaned and placed in polypropylene vials to dry. We mounted the dried otoliths in epoxy and cut an approximately 0.65-mm section from the transverse plane using a Buehler IsoMet Low Speed saw. We polished sections using 1000-grit sandpaper and captured images of each section at 40× magnification using a Canon EOS Rebel T5i camera mounted onto a Nikon Eclipse E400 compound microscope. All otoliths were aged independently by at least two readers, discrepancies in assigned ages were resolved by consensus, and if consensus was not achieved, the otolith was excluded from the analysis.

Data analysis

We modeled silver carp growth using the von Bertalanffy growth equation:

$$L_t = L_\infty \left(1 - e^{-K(t - t_0)}\right)$$

where L_t is the TL at time t, L_∞ is the mean asymptotic TL, K is the Brody growth coefficient, and t_0 is the theoretical time when TL is zero. We ran the model using a Bayesian framework with a Gaussian probability distribution for each waterbody, denoted with a subscript j, as follows:

$$\begin{aligned}
L_t &\sim \text{Normal}(\mu, \sigma)\\
\mu &= L_{\infty j} \left(1 - e^{-K_j(t - t_{0j})}\right)\\
L_{\infty\,[\text{Big Sioux}]} &\sim \text{Normal}(900, 100)\\
L_{\infty\,[\text{difference}]} &\sim \text{Normal}(0, 50)\\
K_{[\text{Big Sioux}]} &\sim \text{Normal}(0.2, 0.1)\\
K_{[\text{difference}]} &\sim \text{Normal}(0, 0.2)\\
t_{0\,[\text{Big Sioux}]} &\sim \text{Normal}(0, 1)\\
t_{0\,[\text{difference}]} &\sim \text{Normal}(0, 1)\\
\sigma &\sim \text{Exponential}(0.25)
\end{aligned}$$

Bayesian modelling allows for the incorporation of prior knowledge in the form of a prior probability distribution and can improve the estimates of von Bertalanffy growth parameters when year classes are missing or older ages are underrepresented in the sample, making the results more biologically realistic (Doll and Jacquemin 2018; Smart and Grammer 2021). We selected prior distribution values for the Big Sioux River L_∞ and K parameters following prior predictive simulation (Wesner and Pomeranz 2021) that were lower than the estimates given by Hayer et al. (2014b) because we hypothesized that growth was slower than during the earlier invasion stage. We assumed no difference in L_∞, K, or t_0 expected values between the Big Sioux and James rivers and set the mean for all difference priors (denoted with the [*difference*] subscript) to zero. We fit the model using rstan (Stan Development Team 2022) with the brms package (Bürkner 2017) in program R (R Core Team 2022). We estimated model parameters using Hamiltonian Monte Carlo with a no-U-turn sampler (Hoffman and Gelman 2014; Monnahan et al. 2017). The model was fit using 4 Markov chains, 2,000 iterations per chain, and a 1,000 iteration warm-up phase. We assessed model convergence by examining traceplots, a posterior predictive check plot (Gabry et al. 2017), and the Gelman-Rubin statistic ($\hat{R}$) for each parameter, with $\hat{R}$ values near 1.00 indicating model convergence (Gelman and Rubin 1992).

We sampled from the posterior from ages 2 to the maximum observed age for both rivers to evaluate parameter trends. We compared posterior parameter estimates for L_∞ and K between the Big Sioux River and James River population samples. We determined the probabilities that the L_∞ and K values were greater for the Big Sioux River population than for the James River population. We calculated 90% prediction intervals (PI) for TL at ages 2–5 and calculated the probabilities that posterior estimated PI TL values were larger for silver carp in the Big Sioux River than the James River. We estimated mean length at ages 2–5 for silver carp in the introduction stage using the von Bertalanffy equation provided by Hayer et al. (2014b) and compared against posterior estimated mean TL at ages from the Big Sioux and James River samples. We then estimated the probability that our Bayesian posterior estimated mean TLs at ages 2–5 were less than the estimated mean TLs at ages 2–5 from the introduction stage von Bertalanffy growth model (Hayer et al. 2014b). We determined the age at which the probability that the estimated TL at age from the early invasion curve was greater than 95% of PI estimates from the posterior distribution. Probabilities were calculated as the number of iterations where the specified condition was met divided by the total number of posterior iterations (4,000) and multiplied by 100.

We performed a sensitivity analysis to ensure that our prior distribution values did not negatively impact model fit. The sensitivity analysis utilized the same data and model specifications as the original model, except all prior standard deviation sizes were doubled for L_∞, K, and t_0 parameters, and the σ prior value was halved. We assessed model fit using the same methods as for our original model and compared the difference in posterior parameter estimates between the sensitivity and original models.

Results

We collected and aged 99 silver carp from the Big Sioux River and 82 silver carp from the James River. Silver carp age estimates ranged from 2–14 years for the Big Sioux River and 2–11 years for the James River. The posterior mean (95% credible interval) von Bertalanffy growth parameter estimates were L_∞ = 714 mm (683–753 mm), K = 0.248 (0.190–0.314), and t_0 = -1.299 (-2.149 – -0.610) for the Big Sioux River population and L_∞ = 709 mm (646–774 mm), K = 0.271 (0.191–0.393), and t_0 = -1.314 (-2.702–0.067) for the James River population (Figure 2). There was a 61.6% probability that the L_∞ value was larger in the Big Sioux River population than the James River and a >99.9% probability that the posterior K was lower. The probabilities that the posterior estimated PI TL values at ages 2–5 were larger for silver carp in the Big Sioux River than in James River were 37.4%, 38.7%, 40.1%, and 40.8%, respectively, and the differences in posterior estimated mean TL at age decreased with age and were ≤22 mm at each age (Table 1).

Mean posterior estimated TL values in the Big Sioux River and the James River were lower than the introduction stage estimates after age 2 (Table 1). The probabilities that mean posterior estimated TLs were lower than the estimated values

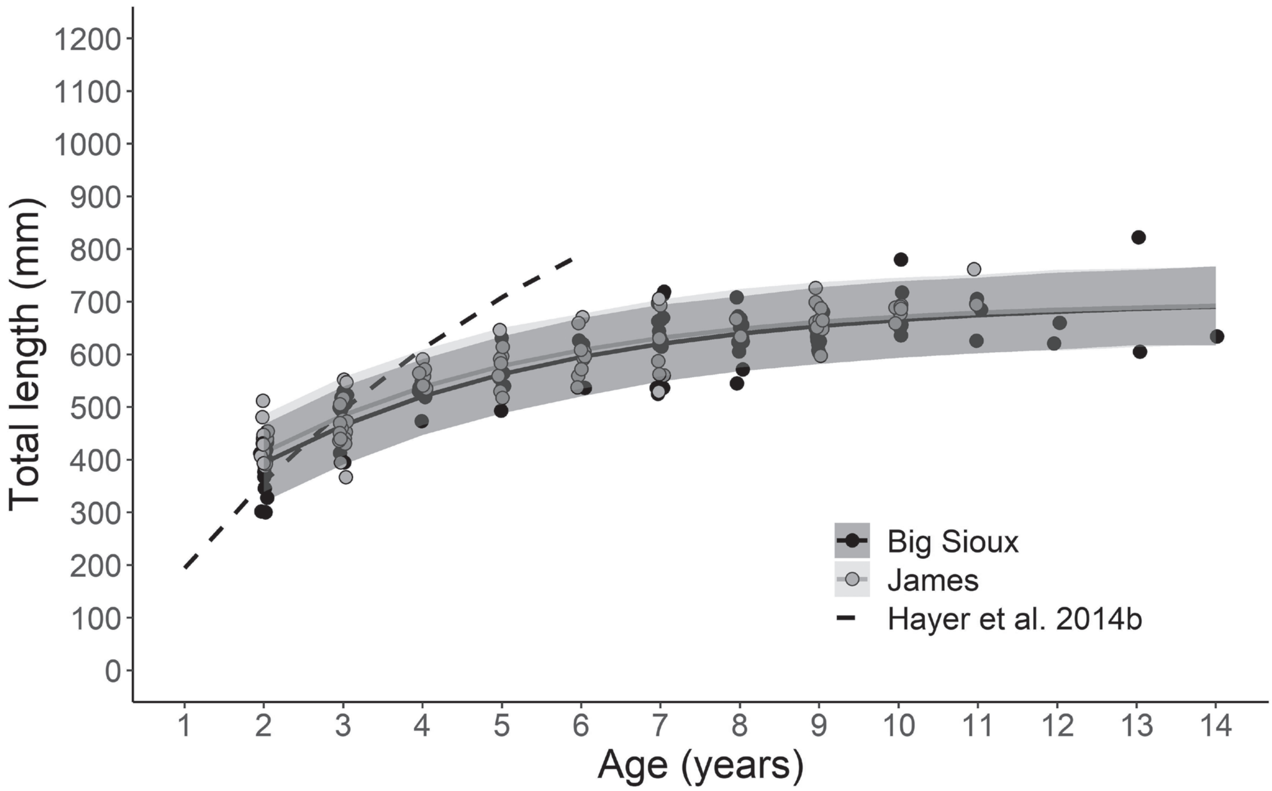

Figure 2. Von Bertalanffy growth curves and 90% prediction intervals (shaded) for Silver Carp collected in the Big Sioux and James rivers, South Dakota from 2020–2022. Circles represent individual length-at-age estimates and are randomly offset to reduce overlap, and the dashed line represents the combined von Bertalanffy growth curve across the observed ages from the early stages of invasion (2009–2012) in the eastern South Dakota tributaries to the Missouri River (Hayer et al. 2014b).

Table 1. Mean total length (mm) for ages 2–5 silver carp estimated from von Bertalanffy growth models for fish collected in 2020–2022 in the Big Sioux and James rivers, South Dakota (this study) and for fish collected in 2009–2012 in the Big Sioux, Vermillion, and James rivers, South Dakota (Hayer et al. 2014b). Estimates for the Big Sioux and James rivers were derived from the posterior distribution of a Bayesian model and include 90% prediction intervals in parentheses.

Study	Age 2	Age 3	Age 4	Age 5
Big Sioux	394 (321–467)	465 (391–539)	519 (447–591)	561 (489–635)
James	416 (339–486)	484 (407–557)	536 (466–609)	577 (506–650)
Hayer et al. 2014b	358	495	611	708

from the introduction stage von Bertalanffy growth model (Hayer et al. 2014b) were <0.1% at age 2 and >99.9% at ages 3–5 for the Big Sioux River and <0.1% at age 2, 95.4% at age 3, and >99.9% at ages 4 and 5 in the James River. More than 95% of the posterior PI samples were lower than the estimated mean TL at age from the introduction stage growth model (Hayer et al. 2014b) at ages 4 in both the Big Sioux and James rivers. Mean TL at age 4 in the introduction stage was estimated to be 611 mm, while the upper bound of the 90% prediction interval for age-4 silver carp in the Big Sioux and James rivers were 591 mm and 609 mm (Table 1).

Our model successfully converged, with $\hat{R}$ values being <1.01 for all parameter estimates. Traceplots exhibited full mixing of the Markov chains, and posterior predictive check plots showed that the posterior estimates for the model closely matched the observed values. Additionally, all parameter estimates in the sensitivity analysis were within 5% of the original model parameter estimates, indicating low sensitivity to prior value selection.

Discussion

Our study demonstrates that growth has slowed after a 10-year period as silver carp became established in two eastern South Dakota tributaries to the Missouri River. The substantial reduction in growth potential suggests that silver carp in the Big Sioux and James rivers have transitioned to the establishment stage of the invasion curve. Comparisons of length at age estimates indicated that mean TL at ages 2–5 were lower than mean estimates during the introduction stage (Hayer et al. 2014b) and that mean posterior estimated TL at age 4 declined >12% from the introduction stage. We also determined that the introduction stage mean length was greater than 95% of the prediction interval TL estimates beginning at age 4, which indicates a high likelihood of differentiation in growth at least by age 4. While much of the literature examining silver carp growth trends has focused on differences across spatial scales (Erickson et al. 2021; Broaddus and Lamer 2022; Werner et al. 2022), limited information was provided about the timing of invasion for each sub-population. Gibson-Reinemer et al. (2022) documented declining length at age-0 and overall population size structure of silver carp in the Illinois River, but length-at-age data for age-1 and older fish were not compared across time. Individual growth rates are expected to decline as fish populations move from the early invasion stages to establishment (Feiner et al. 2012; Azour et al. 2015), and the decline in estimated length at age for silver carp in this study follows this expected trend. Our results provide novel information from two invaded mid-sized rivers that substantial reduction in growth can occur within 10 years of silver carp reaching the introduction stage of the invasion curve.

The Big Sioux and James rivers exhibited similar silver carp growth characteristics. The probabilities that silver carp in Big Sioux River had larger posterior estimated L_∞ (61.6%) and TL at ages (all approximately 40%) than in the James River demonstrated substantial overlap in estimated values. The similarity among populations may be a result of population mixing between the Big Sioux, James, and Missouri rivers, as silver carp are known to make large-scale movements in other free-flowing (Coulter et al. 2016) and large impounded systems (DeGrandchamp et al. 2008; Coulter et al. 2018a). The extent to which silver carp move among the Missouri River and its tributaries in eastern South Dakota is not well-understood and requires additional study to better understand the impact on population dynamic rates, including recruitment.

Due to low water conditions, we were unable to sample the Vermillion River in areas upstream of the confluence, so we were not able to include the Vermillion River population in our comparison of growth. Hayer et al. (2014b) sampled from all three eastern South Dakota rivers, and the combined growth curve presented in that study included Vermillion River silver carp. However, the Vermillion River is smaller than either the Big Sioux River or James River, and the potential for more frequent low water levels and fish kills would have been unlikely to result in substantially faster growth that impacted the combined growth curve from the introduction stage presented in Hayer et al. (2014b).

Growth of silver carp in the Big Sioux and James rivers was slower than in low-density, leading-edge populations in the Wabash, Mississippi, and Ohio rivers (Stuck et al. 2015; Erickson et al. 2021; Broaddus and Lamer 2022), but mean maximum estimated lengths were consistent with those for long-established populations in portions of the Mississippi and Illinois rivers (Erickson et al. 2021; Broaddus and Lamer 2022) and within their native range (Nikolskii 1961). Silver carp growth and condition have been shown to be density dependent and can increase following large-scale commercial harvest and subsequent declines in population densities (MacNamara et al. 2016; Coulter et al. 2018b), but we do not have current density or relative abundance information on the Big Sioux and James river populations for comparison. Density-independent factors such as water quality and flow regimes may vary among the different river systems, which could impact silver carp bioenergetic requirements and subsequent growth. An understanding of the limiting factors of a river to support invasive carp may not only shed light on the population dynamics of these invaders but also on the potential that these invasive populations will have on native fish communities (Sampson et al. 2009).

The larger length at age 2 during this study can likely be attributed to the reduction in the mean asymptotic length and the lack of age-1 silver carp among our aged individuals. The Brody growth coefficient (*K*) is a measure of how quickly fish will achieve their asymptotic length, so *K* and L_∞ values tend to be negatively correlated (Gallucci and Quinn 1979). Additionally, the lack of age-1 silver carp in our sample may have limited the von Bertalanffy model from pulling the growth curve down at early ages. Therefore, the combination of lower L_∞ values in this study and the lack of age-1 fish may have led to an overestimation of length at age 2. Boat electrofishing does not effectively target smaller-sized silver carp, and dip netters can be biased toward selecting larger individuals (Hammen et al. 2019). The use of alternative gears, such as trap and cast nets or an electrified dozer trawl, may have more efficiently captured age-1 fish than conventional boat electrofishing (Collins et al. 2017; Hammen et al. 2019), so a multi-gear approach may prevent gear bias and over estimation of length at ages 1 and 2. We included 13 silver carp in our analysis that were collected in the Big Sioux River with our limited cast net sampling, but additional effort or use of other gears may have allowed for the capture of additional juveniles. Finally, differences in *K* values between the Big Sioux and James rivers did not appear to be biologically significant, as length-at-age estimates were consistent (within 20 mm) between waters.

The transition of silver carp from introduction to establishment stages on the invasion curve has likely caused ecosystem shifts in the eastern South Dakota tributaries to the Missouri River. Changes in silver carp growth have been linked to shifts in the zooplankton community (Fukushima et al. 2001; Irons et al. 2007; Sass et al. 2014). There has been documentation of declining relative abundance and condition of planktivorous species due to the altering of zooplankton communities following invasive carp establishment (Pendleton et al. 2017). Impact of silver carp on native species within these rivers may have resulted in a trophic level change (Sampson et al. 2009). Established populations of silver carp have also been known to impact the native fish community (DeBoer et al. 2018; Shields et al. 2021). Native species such as bigmouth buffalo (*Ictiobus cyprinellus* Valenciennes in Cuvier and Valenciennes 1844) and gizzard shad (*Dorosoma cepedianum* Lesueur, 1818) have decreased in both biomass and CPUE in areas that have been invaded by silver carp (Pendleton et al. 2017). However, limited research has been done comparing the change in fish communities in the eastern South Dakota tributaries into the Missouri River before and after the invasion of silver carp (Hayer et al. 2014b; Schall and Lucchesi 2021). Evaluation of changes to zooplankton and the fish community response in the eastern South Dakota tributaries to the Missouri River is warranted.

Authors' Contribution

JDH, KRJ, JMS, and BJS contributed to research conceptualization, sampling, and data analysis, and all authors contributed to writing and revision of this manuscript.

Ethics and Permits

All research was performed in accordance with the Guidelines for the Use of Fishes in Research by the American Fisheries Society.

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