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ARTICLE

Freshwater Ecology

Threshold responses of freshwater fish community size spectra to invasive species

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Abstract

Aquatic invasive species (AIS) threaten biodiversity and ecosystem services around the world, but their management has been hampered by the lack of quantifiable control targets. The introduction of Silver Carp (*Hypophthalmichthys molitrix*) throughout the mid-western United States epitomizes both the impacts of AIS and the need for quantitative control targets. Silver Carp are large-bodied planktivores that compete with native planktivores, which can cause cascading effects throughout the food web. Our study tested the threshold of abundance beyond which Silver Carp alter fish assemblage structure. We used a community size spectra (CSS) approach to evaluate fish community size structure across temporal and spatial gradients of Silver Carp abundances. We hypothesized that Silver Carp would flatten the size spectra slope because they are large-bodied and feed at a low trophic position. Electrofishing data were obtained for the La Grange Pool of the Illinois River (1994–2021) and for six pools of the Ohio River (2015–2020). Results supported our hypothesis, showing a 98% probability that the relative biomass of Silver Carp is positively related to the CSS slope (resulting in "flattening"). This pattern was strongest in the Illinois River, where Silver Carp made up >30% of fish assemblage biomass in recent years. The pattern was weakest in the Ohio River (78% probability of a positive relationship) where Silver Carp rarely exceeded 20% of total fish biomass. Subsequent changepoint models indicated that a Silver Carp relative biomass of ~24% represents a threshold below which negative food web impacts should be minimized. Our study demonstrates a clear shift in fish community size structure following invasion by Silver Carp and suggests that pre-invasion CSS slopes may serve as a restoration target. It also illustrates the benefits of CSS to guide Silver Carp and other AIS management.

KEYWORDS

biomass–abundance relationship, fisheries management, food web, individual size distribution, invasive carp, threshold

INTRODUCTION

The ecological and economic impacts of aquatic invasive species (AIS) have been widely documented (Gallardo et al., 2016; Pimentel et al., 2005; Strayer, 2010), yet ecosystem level effects remain under-studied (Thomaz et al., 2015). A central applied question regarding AIS impacts is determining critical density thresholds above which they may have food web and ecosystem-level effects (Thomaz et al., 2015). This question is critical to address as eradication is seldom a realistic goal once AIS are established. It is often more efficient, both ecologically and financially, to prevent their further spread and reduce populations to minimize future impacts (Green & Grosholz, 2021; Johnson et al., 2009). Natural resources managers need tools to more effectively evaluate food web impacts and thresholds of acceptable AIS densities that minimize impacts.

Silver Carp (*Hypophthalmichthys molitrix*) are a species of great concern in North America as they are large bodied, fast growing (potentially reaching 317 mm by Age 1 on average), and feed at a low trophic position, filtering particles as small as 10 μm (Deters et al., 2013; Kolar et al., 2007; Smith, 1989; Vörös et al., 1997; Williamson & Garvey, 2005). Silver Carp are one of the four species of invasive carps which have been introduced into the United States. They were originally studied as a potential biological control for the management of water quality in nutrient-rich spillways, aquaculture ponds, and wastewater treatment facilities (Irons et al., 2007). They escaped due to flooding of the Mississippi River in the 1970s and quickly established populations in the lower Mississippi River basin. Silver Carp have continued to expand their range throughout the Mississippi River and tributary watersheds such as the Illinois River and the Ohio River (Kolar et al., 2007). Like many invasive species, Silver Carp are thought to be nearly impossible to eradicate once established (Chick & Pegg, 2001). There are extensive and on-going commercial fishery harvest efforts targeting invasive carps in the Illinois and Ohio Rivers with the goal to control populations to reduce density-dependent dispersal (i.e., spread) and ecological impacts (Mississippi Interstate Cooperative Resource Association Asian Carp Advisory Committee, 2020).

Management strategies for Silver Carp have focused on traditional species-based approaches to assess impacts and guide actions. For example, there have been observed changes in the growth rate and body condition of native fishes, particularly Gizzard Shad and Bigmouth Buffalo, associated with Silver Carp relative abundance (Chick et al., 2020; Irons et al., 2007; Pendleton et al., 2017; Phelps et al., 2017; Sampson et al., 2009; Shields et al., 2021). Fish and zooplankton community composition have also been shown to change following Silver Carp invasion (Bouska, 2020; DeBoer et al., 2018; Sass et al., 2014; Solomon et al., 2016). However, while studies using taxonomic approaches have had success demonstrating impacts on specific species and prey, developing functional relationships between Silver Carp abundance and impacts have been largely elusive. There are broader ecosystem-level impacts that are less readily quantifiable that may not be reflected in these traditional approaches (Reaser et al., 2007), and community-level approaches remain largely unexplored. What is needed are indicators that quantify impacts of Silver Carp invasion that would allow for the development of data-driven restoration and/or removal targets in impacted systems. Thus, a framework utilizing community or assemblage level indicators is needed for management at a holistic ecosystem level (Love et al., 2018).

In this study, we investigated the use of community size spectra (CSS) as a management tool for assessing impacts, establishing restoration targets, and guiding invasive Silver Carp management actions. CSS is an ataxic representation of an assemblage's size structure (i.e., distribution of body sizes) that quantifies the predictable decrease in fish abundance with increasing body size. It approximates:

$$N \sim cM^{\lambda}, \tag{1}$$

where N is abundance, c is a constant, M is individual body mass, and λ (lambda) is the rate of decline from small to large individuals (or the "CSS slope"; Kerr & Dickie, 2001). The slope of the CSS is an emergent property of community interactions, most notably trophic energy transfer (Mehner et al., 2018). Flatter CSS slopes indicate energy passing more efficiently from small, low-trophic position individuals to larger, high-trophic position individuals (Blanchard et al., 2009; Mehner et al., 2018). However, there are multiple processes that may disrupt this, in particular, deviations in the relationship between body size and trophic position associated with large individuals feeding at low trophic levels (e.g., Broadway et al., 2015). In the past, CSS has been used to address offshore oceanic fishing yields (Blanchard et al., 2014; Kolding et al., 2016; Law et al., 2016; Law & Plank, 2023), changes in ecosystem health relative to climate change (Pomeranz et al., 2021; Queirós et al., 2018), and the effects of oligotrophication, eutrophication, pollution, and invasive species (Arranz et al., 2023; Buba et al., 2017; Murry et al., 2024; Murry & Farrell, 2014; Pomeranz et al., 2019). CSS respond predictably to ecological change, including landscape change (e.g., Benejam et al., 2016; Emmrich et al., 2011) and internal food web changes (e.g., Broadway et al., 2015). Specifically, fishery exploitation tends to steepen the slope (Jennings & Dulvy, 2005), whereas abundance shifts to large-bodied low position fish tends to flatten the slope (Broadway et al., 2015; Murry et al., 2024). CSS provides a more holistic approach than traditional species-based indicators because it accounts for interspecific interactions. Management strategies derived from CSS would be well suited for adaptive management by assessing annual changes of a given system against historical baselines or future desired structure (Dimech et al., 2008).

Not only are Silver Carp large-bodied low trophic position fish that compete directly with native planktivores, but they have also been linked to declines in native sport fish (Chick et al., 2020). Sportfish are generally piscivores and when abundant tend to steepen the CSS (Arranz et al., 2019). Thus, there is evidence of two related processes that play out over time as the relative abundance of Silver Carp increases that could promote changes in CSS related to the carp invasion: (1) increased abundance of Silver Carp is expected to flatten the CSS (sensu Broadway et al., 2015; Murry et al., 2024), and simultaneously, (2) their indirect linkage to decreasing or replacing piscivore abundance (sensu Chick et al., 2020) would also tend to reduce the slope (increase efficiency). We used CSS to evaluate how Silver Carp have influenced food web dynamics (specifically size-structure) of the Illinois and Ohio Rivers in the central United States.

There are substantial differences in Silver Carp abundance and previously assessed food web changes among the rivers. The Illinois River zooplankton community was severely degraded evidenced by the loss of large-bodied zooplankton, indicating strong food web effects (DeBoer et al., 2018; Sass et al., 2014), while throughout the Ohio River, the zooplankton community appears unchanged by Silver Carp (Johnston, 2023). With the rapid and intense invasion of Silver Carp in the Illinois River, we hypothesized that the CSS slope would flatten over time throughout the invasion period. We also hypothesized that the fish assemblage species composition and relative abundance would differ among periods in response to Silver Carp. In contrast, given the relatively slow and comparatively lower intensity of Silver Carp invasion across the middle Ohio River, we hypothesized CSS changes (i.e., flattening) only in the lower reaches (or pools) where carp are fully established (Figure 1). We also hypothesized fish assemblages will differ among the lower and upper reach pools in relation to Silver Carp. Ultimately, we hypothesized a threshold in Silver Carp relative abundance above which food web effects will manifest as a flattening of the CSS (slope increase) and demonstrating a clear management goal to minimize density-dependent effects (Figure 2).

METHODS

Study sites

Our study areas consisted of the La Grange Pool of the Illinois River (Figure 1A,B) and six pools in the Ohio River ranging from the upstream R.C. Byrd Pool downstream to the Cannelton Pool (Figure 1A,C). Pools are extended river reaches bounded on either end by a dam and are named by the downstream dam that creates each pool. The La Grange Pool of the Illinois River was selected due to the extensive amount of data collected over a long period of time (1994–2021) including prior to the Silver Carp invasion. The Ohio River pools were selected based on the invasion trends (i.e., the established, invaded, and presence fronts).

Illinois River

The Illinois River is commonly used for shipping, commercial fishing, and recreation (Gibson-Reinemer et al., 2017; Love et al., 2018; Solomon et al., 2019). The Illinois River hydrology is different from many of the other large regional rivers in that there is connectivity to many parts of its floodplain (Raibley et al., 1997). There are also many side channels, backwaters, and tributaries that provide refuge for many fish species. Silver Carp populations have explosively increased in many pools of the Illinois River starting in the

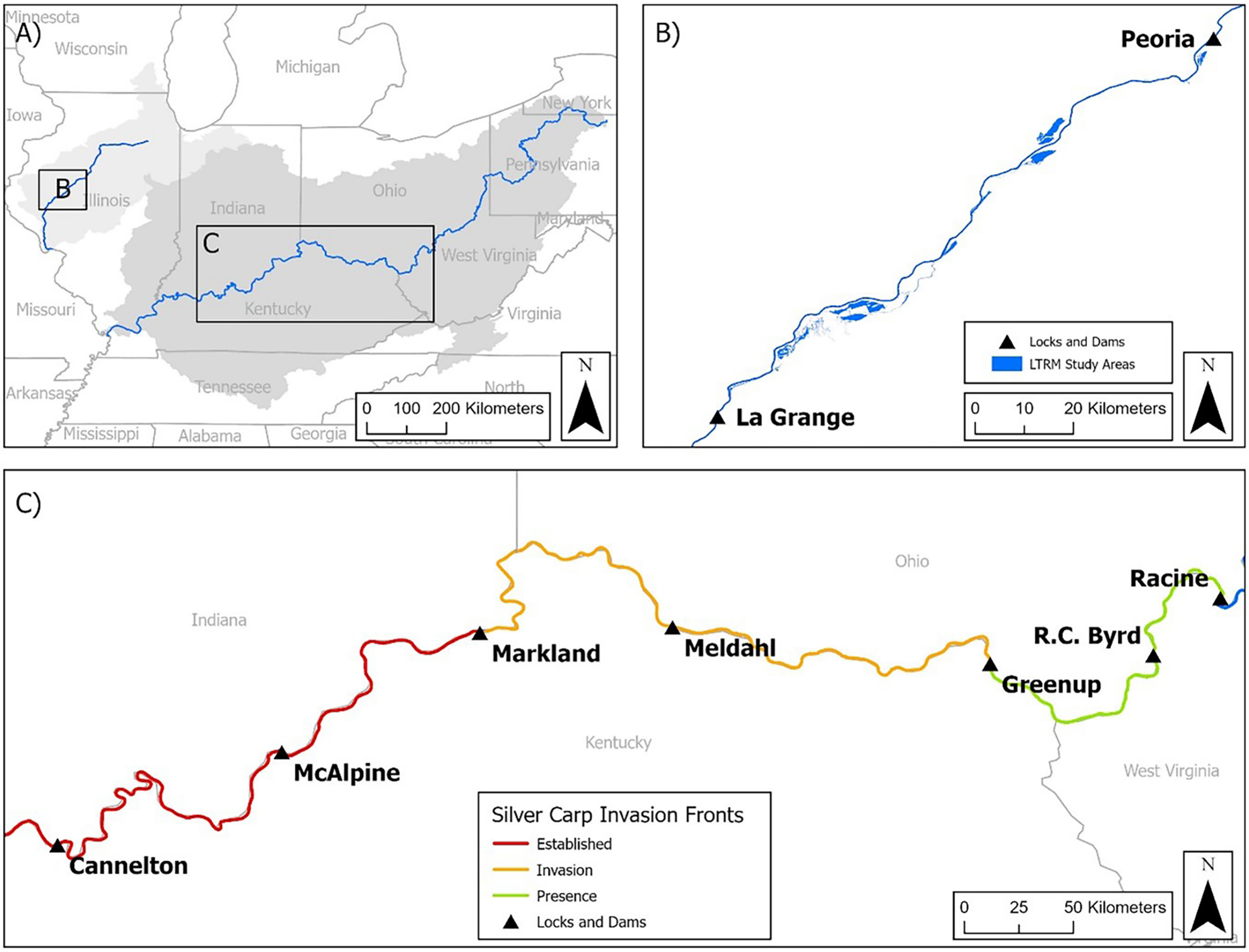

FIGURE 1 Study area maps: (A) the location of both the Illinois and Ohio Rivers in the central United States; (B) a zoomed in view of the La Grange Pool of the Illinois River; (C) the six study pools of the Ohio River. In the Ohio River, the establishment front includes the two downstream reaches depicted in red and is defined by relatively high abundance of adults and periodic recruitment; the two middle pools comprise the invasion front (yellow) defined as relatively low adult Silver Carp abundance and infrequent to rare reproduction with to date no observed recruitment; finally, the upper two pools in green represent the presence front, where there are low densities of adults, but no evidence of reproduction.

2000s. In recent years on the La Grange Pool, Silver and Bighead carp biomass has surpassed the combined biomass of all native fish species (Ickes et al., 2022). Due to the high abundance and demonstrated impacts of Silver Carp on the zooplankton community and many species of fish in the Illinois River (DeBoer et al., 2018; Pyron et al., 2017; Solomon et al., 2016), the Illinois River is an excellent model system to test the sensitivity of CSS to changes in Silver Carp relative abundance.

We used the Upper Mississippi River Restoration Program Long-Term Resource Monitoring (LTRM) element's fish community electrofishing dataset collected by the Illinois Natural History Survey as described in Ratcliff et al. (2014). The fish sampling was completed using pulsed-DC boat-electrofishing surveys from a randomized stratified design. The data spanned the time 1994–2021, omitting 1993 due to a large sustained flooding event (Solomon et al., 2019). The total length (in millimeters) was measured for all captured fish, and a subsample was weighed. When sufficient fish were weighed, we developed Illinois River-specific length: mass regressions to calculate individual fish masses (in grams) and used standard equations from Fishbase.org as necessary. Silver Carp abundance increased in 2000, and adult fish fully recruited to gear (i.e., were reliably collected) by about 2003. Therefore, we consider the period prior to 2003 as our pre-invasion period, with post-invasion after 2003 (Irons et al., 2011).

Ohio River

The Ohio River is commonly used for shipping traffic, commercial fishing, and recreation. The Ohio River has been

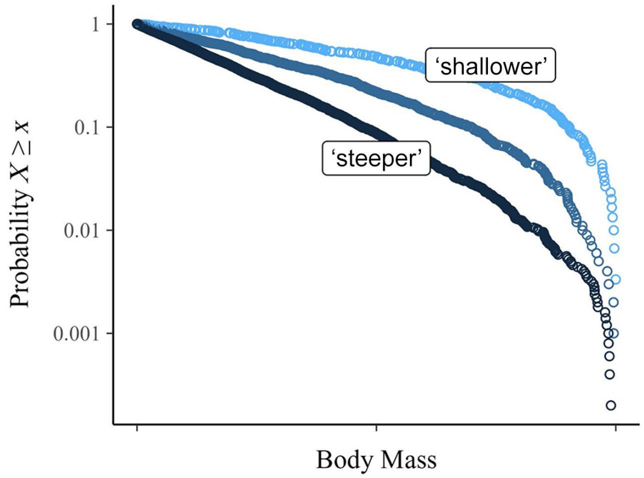

FIGURE 2 Community size spectra showing hypothetical change from the normal state (middle) to a "shallower" slope or "steeper" of the slope. Overfishing results in a steepening of the community size spectra (CSS) (Kolding et al., 2016; Sweeting et al., 2009; Wilson et al., 2010), while dominance of large-bodied, low trophic position fish will tend to flatten the line (Broadway et al., 2015; Murry et al., 2024). The data points are individual body sizes of fish with truncation at the smallest and largest fish. The y-axis is the probability of a body size being greater than or equal to a given body size. The shape of these curves is governed by the parameter λ in individual size distributions (ISD; see *CSS methodology* section below for details).

diked and channelized affecting the hydrology and fragmenting lateral connectivity with the floodplain (Taylor et al., 2013). Portions of the Ohio River have seen an increase of Silver Carp since their introduction; however, the relative abundance of Silver Carp is lower than that found in the Illinois River (Mississippi Interstate Cooperative Resource Association Asian Carp Advisory Committee, 2020; Sass et al., 2010). The spread of Silver Carp in the Ohio River has been slower than many other tributary rivers in the Mississippi River basin. Ohio River fishery managers recognize four zones, or "fronts": (1) the establishment front, where adult density is high and there is evidence of both reproduction and recruitment; (2) the invasion front, where adult density is moderate and there has been sporadic reproduction, but to date no evidence of successful recruitment; (3) the presence front where adult abundance is low and there is no evidence of reproduction; and (4) the uninvaded front. The leading edge of Silver Carp invasion (i.e., invasion front) on this river is currently located in the middle pools between Cannelton and R.C. Byrd Pools (Figure 1C). Silver Carp abundance increases as you move down the Ohio River.

Fish community data for the Ohio River were collected by the Kentucky Department of Fish and Wildlife, Indiana Department of Natural Resources, and the West Virginia Division of Natural Resources from 2015 to 2020 from the R.C. Byrd to Cannelton Pools of the Ohio River (Figure 1). Fish were collected using pulsed-DC boat electrofishing for approximately 200 m downstream with one dip netter for a duration of 900 s (Mississippi Interstate Cooperative Resource Association Asian Carp Advisory Committee, 2020). A target power goal with a minimum 3000 watts was set to target fish with no more than 20% change in power goal due to the effect of electricity on fish (Burkhardt & Gutreuter, 1995). The number of transects sampled ranged from 6 to 24 transects for each pool each year sampled. Similar to the sampling in the Illinois River, the total length (in millimeters) was measured for all fish and a subsample was weighed. Where possible, we used Ohio River-specific length:mass regressions to calculate individual masses and used standard equations from Fishbase.org as necessary.

CSS methodology

To estimate how Silver Carp invasion has impacted the CSS, we fit a generalized linear mixed model with a truncated pareto likelihood (Wesner et al., 2024). The response variable was individual body size (mass [in grams], $n = 106{,}612$ individuals); the predictor variables were the proportion of Silver Carp biomass in each sample, river (Ohio or Illinois), and the interactive effect of Silver Carp biomass and river. Individual sample events (i.e., collections of fish in a given year and pool) were included as varying intercepts. Priors were set as Normal(−1.2, 0.2) for the intercept, Normal(0, 0.2) for all fixed effects and interactions, and Exponential(5) for the SD of the hyperparameters. The prior for the intercept was chosen to reflect a range of typical values for lambda, λ (a parameter estimate to the CSS slope that describes the truncated pareto distribution) in freshwater streams. All other priors were chosen using prior predictive simulation (Wesner & Pomeranz, 2021), ensuring a wide range of values with most of the prior densities contained between ~−2 and −1 (Appendix S1: Figure S1).

We specified the models above in R (version 4.3.2; R Core Team, 2023) using the *rstan* (Stan Development Team, 2023), *brms* (Bürkner, 2017), and *isdbayes* (Wesner & Pomeranz, 2024) packages. Models had four chains with 2000 iterations each. The first 1000 iterations were discarded during warm-up. We checked convergence by confirming that all R-hats were <1.1. We also examined model fit using posterior predictive checks (Gabry et al., 2019; Appendix S1: Figures S2 and S3).

One outcome of the model above was a clear change in λ following invasion by Silver Carp in the Illinois River. To determine how Silver Carp impacted this change, we re-ran a similar model, but only for the

Illinois River and with "year" included as the only predictor. Silver Carp body sizes were excluded from this model. This allowed us to compare how much of the dynamics of λ in the full model were caused by Silver Carp directly versus changes in the size distribution of the other fish in the community. In addition, plots of λ from the full model also indicated a possible threshold in which λ appeared to increase with silver carp invasion only at higher levels of carp invasion. To test this exploratory hypothesis, we fit a segmented regression (Muggeo, 2008). For this model, the response variable was the mean of the posterior λ obtained from the full model above, the predictor variable was the proportion of Silver Carp biomass, and the likelihood was Gaussian. The model has a changepoint parameter that estimates how the relationship between x and y changes before and after a threshold value of x.

Redundancy analyses (RDAs) were performed to assess potential changes in fish assemblage species composition associated with the invasion in the Illinois and the Ohio Rivers. We removed species that represented less than 1% of the total fish catch from both rivers (McCune et al., 2002). Excluding Silver Carp, there were 16 fish species in the Illinois River and 17 species in the Ohio River (>1% relative abundance). Fish data were transformed using Hellinger transformation. The annual abundance of all captured species (>1% and excluding Silver Carp) were the response variables. Silver Carp catch per unit effort ("CPUE"), "pool," and "year" were included as predictor variables for the Ohio River, while for the Illinois River, explanatory variables included only Silver Carp CPUE and year. We tested for significance using a Monte Carlo permutation test with 999 random permutations under the null model of no effect of the explanatory variables on the assemblages. R package *vegan* was used to perform the RDA (Oksanen, 2011).

RESULTS

Across the 53 fish collections, the proportion of Silver Carp biomass ranged from 0% to 46%. The median percentage of Silver Carp biomass was nearly twice as high

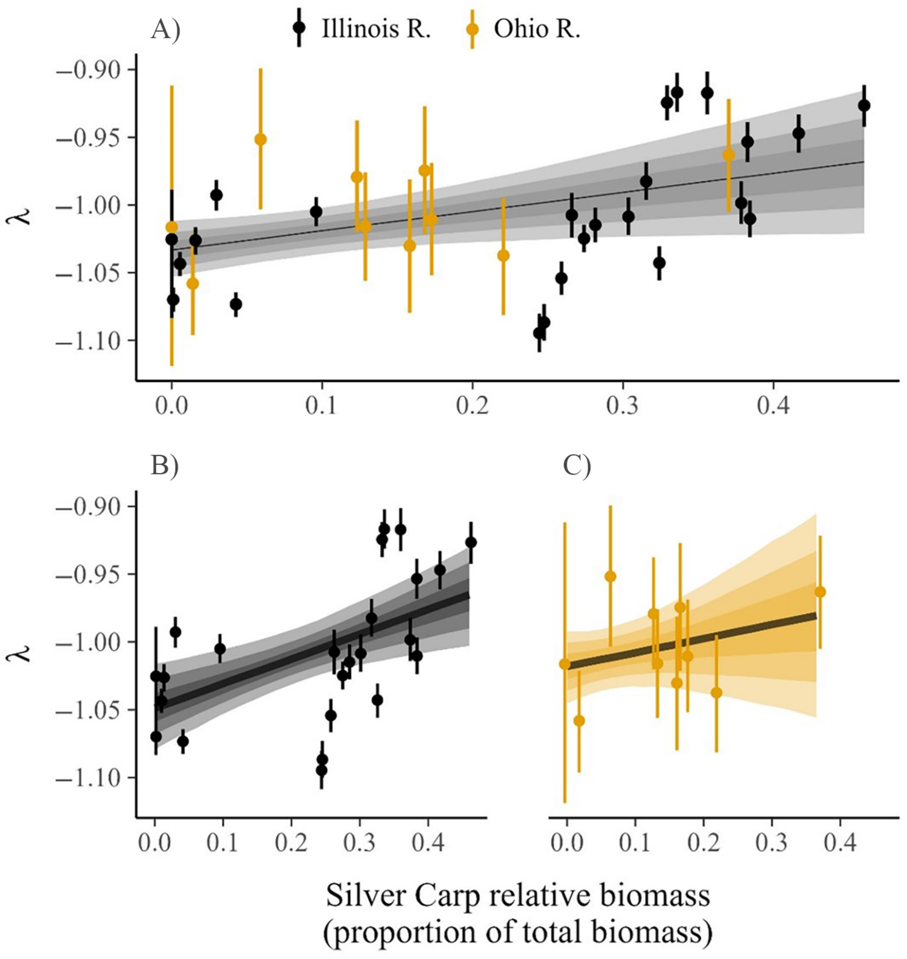

FIGURE 3 Relationship between community size spectra (λ) and Silver Carp invasion. (A) The model outcome averaged over both rivers; (B, C) the conditional model outcomes for each river separately. Regression lines show the median (black) regression. Shading shows the 50%, 80%, and 95% credible intervals (CrIs). Data points are the varying intercept estimates for each sample (±95% CrI).

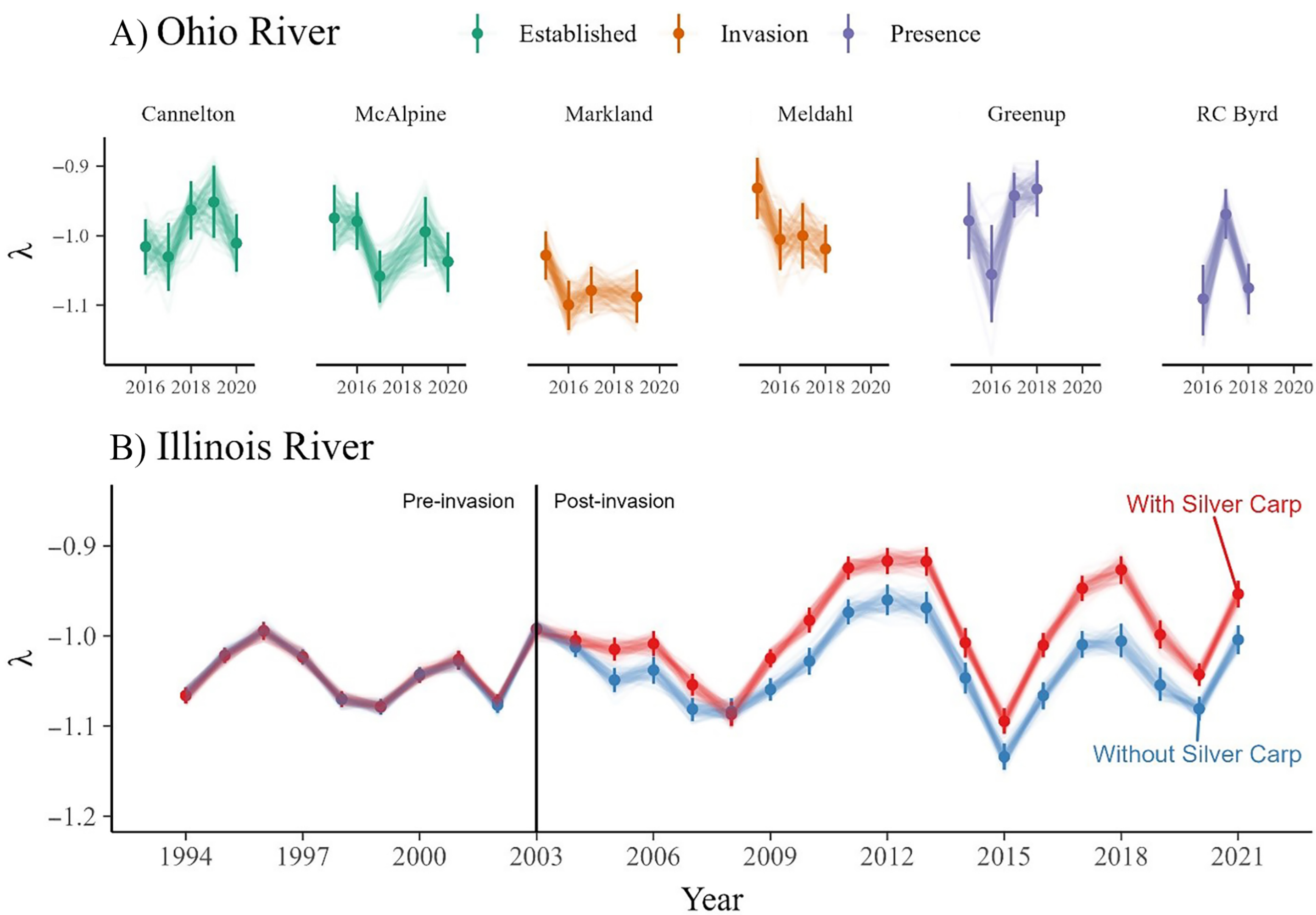

FIGURE 4 Time series of λ in (A) six pools of the Ohio River and (B) the Illinois River. Data points show the median and 95% CrI based on varying intercepts from the generalized linear mixed model. An exception are the data points and lines in (B) "Without Silver Carp." These come from a separate model with year as a fixed effect and Silver Carp excluded from the body size data. Lines connecting the data points show 100 draws from the posterior distribution to aid in visual interpretation.

in the Illinois River (28%) compared to the Ohio River (14%). Overall, there was a 98% probability that the proportion of Silver Carp biomass was associated with an increase in λ (slope = 0.14, 0.01–0.27, mean, 95% credible interval (CrI); Figure 3A). There was also an interaction of Silver Carp proportion and river; the slope was reliably positive in the Illinois River (Figure 3B; slope = 0.18, 0.05–30), but not in the Ohio River (Figure 3C; slope = 0.1, −0.13 to 0.3). However, there was only a 73% probability that the Illinois slope was greater than the Ohio slope, indicating high uncertainty in the difference between rivers.

In the Illinois River, Silver Carp relative abundances increased substantially following the 2003 invasion with individuals present along the size continuum, from the largest fish in some years to multiple samples of fish <100 g. Following invasion, the mean λ increased by 0.04 (0.03–0.05) units compared to pre-invasion λ, with much higher variation in amplitude (i.e., distance between highest and lowest λ over time; Figure 4B). When the data were re-analyzed without Silver Carp, the difference was smaller (0.003, −0.002 to 0.008) with only an 88% probability of an increased λ (compare to >99% for the model with Silver Carp). In other words, the increase in λ can be attributed to the addition of Silver Carp to the fish community, rather than to a change in the size distribution of other fish species (Appendix S1: Figure S4).

In contrast, the Ohio River, sites categorized as having "established" populations of Silver Carp, showed variable λ among years but did not differ appreciably from other sites without established Silver Carp populations (Figure 4A). For example, credible intervals of the differences in λ among the site categories ranged above and below zero, indicating weak evidence of a clear difference.

The changepoint analysis indicated a threshold at 24% Silver Carp biomass (95% CI: 14%–35%), indicating that the rate of change in λ may vary around a threshold invasion level. Below this point, there was no change in λ with increasing carp abundance, but above this point, the

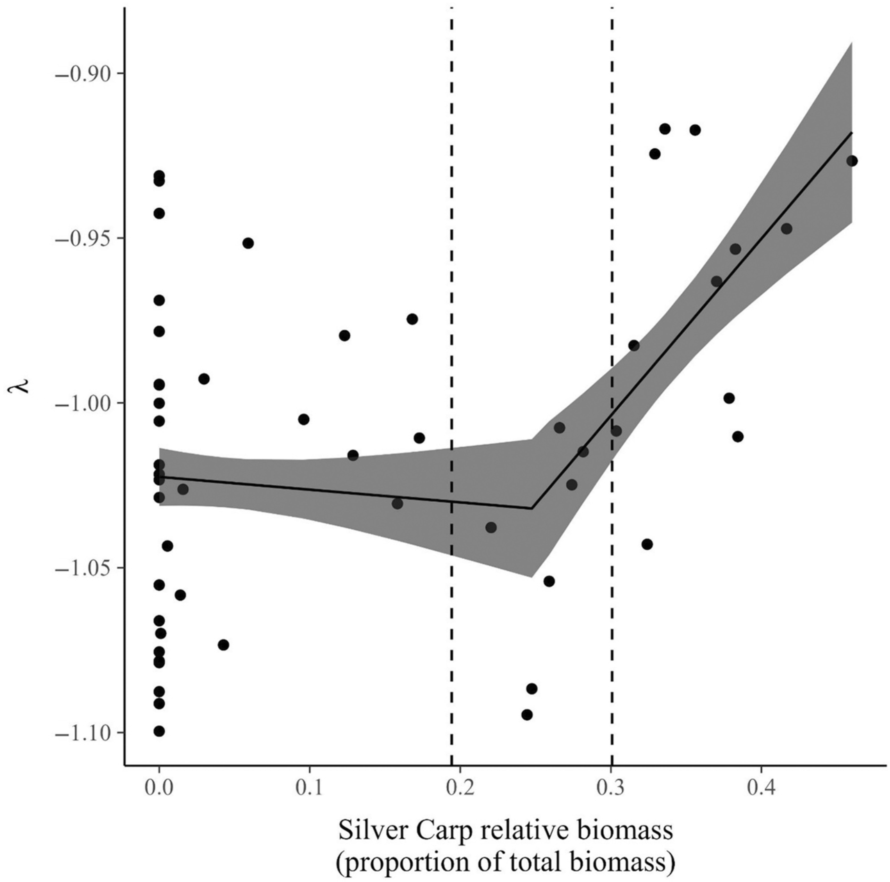

FIGURE 5 Results of a segmented regression between lambda and silver carp relative biomass. The data points are the posterior mean lambdas, obtained from the varying intercepts of the full truncated Pareto model. The regression line and shaded area show the fitted relationship between lambda and silver carp relative biomass below and above the threshold. The dashed lines indicate one SD below and above the mean threshold estimate of 0.24.

slope steepened with a mean of 0.57 (95% CI: 0.12–1.02) (Figure 5).

In addition to changes in body-size distributions, we also observed changes in the species composition and relative abundance of fish assemblages associated with Silver Carp abundance in the Illinois River, but not the Ohio River. In the Illinois River, we observed a significant change in the fish assemblage species composition starting a year after the first major increase in Silver Carp CPUE (i.e., after they initially recruited to gear; Figure 6). The RDA full model (16 fish species matrix = Silver Carp CPUE + Year) was significant ($F_{2,25} = 4.52$, $p = 0.001$, adjusted $R^2 = 0.21$) and both predictors were significant (Silver Carp CPUE $F_{1,25} = 3.89$, $p = 0.001$, Year $F_{1,25} = 5.15$, $p = 0.001$). The first RDA was the only significant axis but explained 81.4% of the variance within the fish assemblage. The pre-invasion period (1994–2004) was dominated by Smallmouth Buffalo and Bigmouth Buffalo, Largemouth Bass, and White Crappie. After Silver Carp became established in large numbers (2003–2020), the fish assemblage was dominated by Gizzard Shad, Grass Carp, Freshwater Drum, and Shortnose Gar. Interestingly, the CPUE of both Gizzard Shad and Freshwater Drum dropped substantially from the pre- to post-invasion period (Gizzard Shad CPUE from 36.8 to 17.4 and Freshwater Drum from 7.5 to 5.8), but in both cases, their abundance remained high relative to other species (Table 1). In addition to the decrease in Gizzard Shad CPUE, we observed roughly a 66% decrease in Smallmouth Buffalo and Bigmouth Buffalo CPUE as well (Table 1).

In contrast, in the Ohio River where invasive carp abundance is lower, the RDA full model was significant (17 fish species matrix = Silver Carp CPUE + Pool + Year; $F_{7,17} = 1.92$, $p = 0.002$, adjusted $R^2 = 0.21$) and highlighted a longitudinal change in fish species composition and patterns of relative abundance across pools ($F_{5,17} = 2.27$, $p = 0.001$), but neither Silver Carp CPUE nor year contributed to the variation ($F_{1,17} = 1.26$, $p = 0.25$ and $F_{1,17} = 0.82$, $p = 0.57$, respectively). Only the first RDA axis was significant ($F = 4.48$, $p = 0.031$) and described 33.3% of the variation in the fish assemblage across pools and years. The lowest two pools (Cannelton and McAlpine), the middle two pools (Meldahl and Markland), and the upper two pools

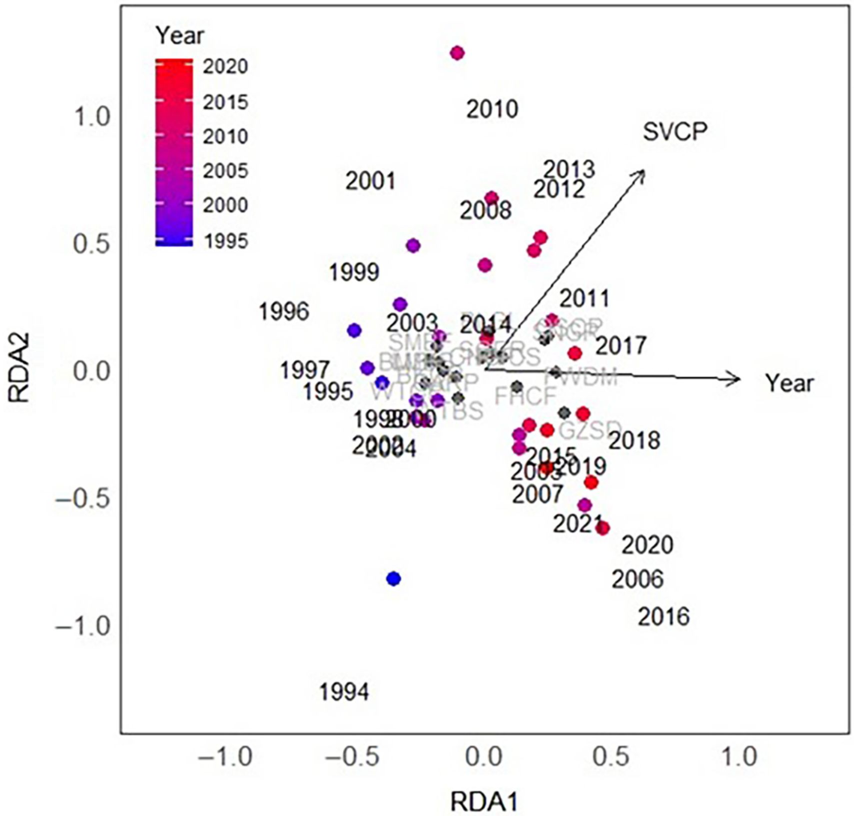

FIGURE 6 Redundancy analysis (RDA) results for the Illinois River. Silver Carp catch per unit effort (CPUE) (SVCP) and year were the predictor variables to describe variation in the 16 fish species CPUE matrix. There is temporal separation on the left 2004 and earlier and on the right 2005 and beyond, a year after invasive carp recruited to sampling gear in high numbers. In the earlier period (1995–2004), dominant fish included Smallmouth and Bigmouth Buffalo, Largemouth Bass, and White and Black Crappie. The post-invasion time period (2005–2020) species dominance shifted to Gizzard Shad, Freshwater Drum, Grass Carp, and Shortnose Gar. While the CPUE of Gizzard dropped (Table 1), their relative abundance increased slightly.

(Greenup and RC Byrd) formed separate groups (Figure 7), but again, were not related to Silver Carp CPUE. The prominent fish species within each group consisted of Channel Catfish, Longnose Gar, Golden Redhorse, and Spotted Bass in the lower pools (establishment front); White Crappie and Largemouth Bass in the middle pools (invasion front); and Freshwater Drum and hybrid White Bass-Striped Bass in the upper pools (presence front).

DISCUSSION

Our study demonstrates a shift in fish CSS following invasion by Silver Carp. Importantly, this shift was associated with a threshold where the fish community size structure remained relatively unchanged when Silver Carp made up less than 24% of total fish community biomass. In contrast, when Silver Carp biomass exceeded 24% of the total fish biomass, the CSS flattened. The CSS of the Illinois River responded quickly to increasing Silver Carp abundance. We observed both a flattening of CSS slope as well as increased interannual oscillation, both responses coinciding with the invasion of Silver Carp in the Illinois River in 2003. These results demonstrate a strong sensitivity of the fish assemblage with limited to no lag response to the invasion. Our hypothesis was based on the findings of Broadway et al. (2015) who found a flattening of the CSS slope (increase in ecological efficiency) that coincided with a shift of functional feeding groups from a planktivore-omnivore-piscivore, or a large bodied high trophic level dominated system to a benthic invertivore, large-bodied low trophic level dominated system. In the Illinois River, zooplankton, along with native planktivores and piscivores, decreased in abundance, body condition, and exhibited changes in feeding strategies during the Silver Carp invasion (Chick et al., 2020; DeBoer et al., 2018; Irons et al., 2007; Sass et al., 2014; Solomon et al., 2016). The changes in CSS slope also correspond to directions of change for other indicators of Silver Carp impacts such as the zooplankton community where Sass et al. (2014) and DeBoer et al. (2018) found Cladocera and Copepoda grazed to very low densities.

TABLE 1 Catch per unit effort (CPUE) and relative abundance (% total = proportion each species represents of the total fish catch) for the 10 most abundant species during the (A) pre- and (B) post-Silver Carp invasion periods (1994–2003 and 2004–2020, respectively) in the Illinois River.

Species	CPUE	% total
(A) Pre-invasion		
Common Carp	55.31	26.2012
Gizzard Shad	36.76	17.4156
White Bass	19.11	9.0523
Smallmouth Buffalo	17.65	8.3593
Bigmouth Buffalo	15.44	7.3157
Bluegill	11.80	5.59
Largemouth Bass	10.07	4.7711
Black Crappie	8.34	3.9495
White Crappie	7.75	3.6721
Freshwater Drum	7.45	3.5286
(B) Post-invasion		
Gizzard Shad	17.41	18.18
Common Carp	15.45	16.14
Silver Carp	15.00	15.67
Smallmouth Buffalo	6.07	6.34
Freshwater Drum	5.57	5.81
White Bass	5.03	5.25
Bluegill	4.45	4.65
Bigmouth Buffalo	4.39	4.59
Largemouth Bass	3.92	4.10
Channel Catfish	3.12	3.26

In contrast to the Illinois River where Silver Carp relative abundance frequently exceeded 24% of the total fish biomass and elicited a strong response in the CSS, Silver Carp in the Ohio River only exceeded 24% total fish assemblage biomass once (a single pool and year) and had limited influence on the Ohio River fish CSS. In accordance with the limited food web impacts, Johnston (2023) observed negligible to no effects of Silver Carp on the Ohio River zooplankton assemblage during 2021–2022 within the same Ohio River pools studied here. Collectively, we observed a strong congruence between the Illinois and Ohio Rivers that point to a critical threshold of Silver Carp biomass around 25% of the total fish assemblage biomass. When Silver Carp biomass is below 25% of the total fish assemblage biomass, the CSS appears to remain unchanged and the zooplankton community remains diverse across size and taxonomic units, but when they exceed this threshold, we see increased interannual fluctuation and flattening of the fish CSS along with dramatic changes to the zooplankton assemblage (DeBoer et al., 2018; Sass et al., 2014). This strongly suggests a working management target to depress Silver Carp densities below ~25% of total fish biomass sampled.

There is on-going commercial and contract fishery harvest of Silver Carp in high density areas of the Ohio River (i.e., the establishment front in the Cannelton Pool) (Mississippi Interstate Cooperative Resource Association Asian Carp Advisory Committee, 2020). Targeted removal efforts may be helping to maintain lower relative abundance of Silver Carp and slowing their density-dependent spread into upstream reaches. Commercial harvest has increased over the last several years (KDFR unpublished data), but unfortunately, fish community surveys stopped in 2020, so we cannot estimate more recent food web changes. Assessment of the harvest is the next logical research step, and CSS provides an excellent tool for such an endeavor.

CSS applications have broadened in the last two decades from focusing largely on marine ecosystems (Law et al., 2016; Law & Plank, 2023), top–down versus bottom–up control (Braun et al., 2021), and coupled food webs (Blanchard et al., 2011) to include a variety of freshwater applications. CSS has been used to investigate impacts of acid mine drainage (Pomeranz et al., 2019), climate change (Pomeranz et al., 2021), regime shifts (Broadway et al., 2015), along with invasive species and eutrophication (Arranz et al., 2023; Murry et al., 2024; Murry & Farrell, 2014). There have been very limited applications of CSS to invasive species problems even though invasive species are widely considered one of the greatest threats to freshwater ecosystems (Havel et al., 2015). Our study thus demonstrated that a CSS-based framework is useful to assess food web level impacts of AIS and to develop quantitative control targets.

AIS impacts are notoriously difficult to quantify but commonly consist of population-level indicators such as changes in species abundance or body condition (DeBoer et al., 2018; Pendleton et al., 2017; Phelps et al., 2017; Solomon et al., 2016). Few effective food-web level indicators currently exist (but see Harris et al., 2022; Love et al., 2018). The CSS approach has been used as a food-web level indicator of over-fishing (Jennings & Dulvy, 2005), and it appears to be an effective indicator of food-web level impacts of invasive species. For the Illinois River, the pre-invasion mean slope was steeper with small interannual variation suggesting a state of relative equilibrium. The post-invasion CSS was flatter (higher efficiency) but also showed greater interannual variation likely due to the system trying to adjust and react to the invasion of Silver Carp (sensu Blanchard et al., 2011).

Pre-invasion data are useful to identify restoration goals. Historic or pre-invasion mean CSS slope and the annual variance serve as an obvious restoration goal.

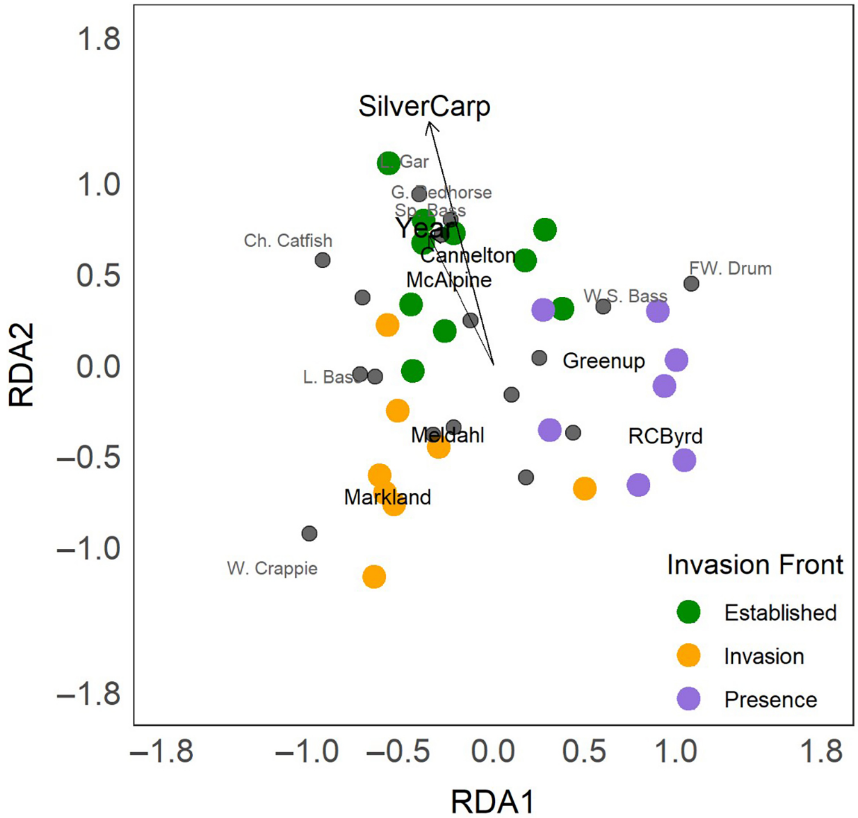

FIGURE 7 Redundancy analysis (RDA) results for the Ohio River. Silver Carp catch per unit effort (CPUE), Pool (from downstream to upstream: Cannelton, McAlpine, Markland, Meldahl, Greenup, RC Byrd), and Year were the main effects. Silver Carp CPUE and Year were not significant, but differences in fish assemblage were related to pool. The gray circles depict individual species.

The Illinois River had a mean CSS slope (λ) of −1.04 ± 0.03 (posterior mean ± SD) during the pre-invasion years. It ranged from a minimum of −1.08 in 1999 to a maximum of −0.99 in 2003. While these changes might appear small (i.e., −1.08 to −1.04 is just 0.04 units of λ), they represent potentially large changes to the food web. For example, metabolic theory predicts that the CSS slope (λ) is determined by trophic efficiency (α), the predator prey mass ratio (PPMR, β), and metabolic scaling (γ), such that (from Reuman et al., 2008):

$$\lambda + 1 = \frac{\log_{10}\alpha}{\log_{10}\beta} + \gamma. \tag{2}$$

Solving this equation for different values of trophic efficiency indicate that a λ increase of 0.04 could represent a near doubling of trophic transfer efficiency (e.g., from $\alpha = 0.1$ to 0.18). Alternatively, it could represent an order of magnitude increase in the PPMR (e.g., from $\beta = 10^4$ to 10^5). Because λ is explained by multiplied parameters, it is not clear which of these changes in the food web have occurred, but the main point is that a seemingly small change in λ reflects a potentially large change in ecosystem function. Yearly sampling and CSS assessment within an adaptive management framework should facilitate development of annual Silver Carp removal targets to maintain the historic community size structure, or work toward restoring a system to a pre-invasion baseline. When pre-impact data are not available, rivers with similar hydrology, geology, and species composition can be used to create a generalized restoration target (Stranko et al., 2012).

Concurrent with changes in CSS slope in the Illinois River, we observed significant changes in the species composition and relative abundance. Some predators (e.g., gars) are known to eat Silver Carp and were associated with post-invasion period. These species might serve as a biological control if stocked in greater numbers (Anderson et al., 2023), but Lampo et al. (2023) suggest that such biological control is unlikely even with piscivore population enhancement. In our study, the CPUE of three species of gar (Shortnose *Lepisosteus platostomus*, Longnose *Lepisosteus osseus*, and Spotted *Lepisosteus oculatus*), all predators capable of consuming young Silver Carp, remained constant or slightly increased after the Silver Carp invasion. Other piscivorous species decreased in sampled abundance, including

Flathead Catfish (*Pylodictis olivaris*), Freshwater Drum (*Aplodinotus grunniens*), White Bass (*Morone chrysops*), White Crappie (*Pomoxis annularis*), Black Crappie (*P. nigromaculatus*), Channel Catfish (*Ictalurus punctatus*), and Largemouth Bass (*Micropterus salmoides*). It is worth noting that these piscivorous species have not declined as much as many of the other species (e.g., Sauger, *Sander canadensis*; Anderson et al., 2023; Chick et al., 2020; Solomon et al., 2016). In contrast, Bigmouth Buffalo, Smallmouth Buffalo, and Gizzard Shad were some of the most negatively impacted species (in terms of reduction in CPUE). However, gizzard shad CPUE and relative weight have increased where intensive bigheaded carp harvest occurs in the upper Illinois River (Love et al., 2018), indicating that a certain level of bigheaded carp management ("functional eradication"; sensu Green & Grosholz, 2021) may be possible. Paddlefish is another notable native planktivore that is also the focus of extensive restoration activity (Bettoli et al., 2009). Unfortunately, we were unable to evaluate how they may or may not have been impacted because there were only five individuals captured from 1994 to 2021. In contrast, we did not observe changes in the fish assemblage in the Ohio River associated with Silver Carp, likely reflecting the lower relative abundance of Silver Carp below the tentative 25% biomass threshold.

CONCLUSIONS

Our findings provide a foundation to develop a CSS-based framework to guide invasive species management. The CSS framework can serve invasive species management by providing (1) quantification of food web-level impacts on local communities, (2) food web-level restoration targets (i.e., pre-invasion condition, including historic mean and range of interannual variation in CSS slopes), and (3) identifying critical thresholds of ecosystem impacts that can serve as reduction or control targets. Specifically, for Silver Carp, we identified a relative abundance threshold (~25% of total fish biomass) beyond which food web effects were observed (conversely, below which the food web appeared unaffected). Quantifying impacts is a critical step toward more effective and efficient AIS management. Additionally, particularly in the Illinois River, once Silver Carp relative biomass exceeded the 25% threshold of total biomass, we observed a rapid response demonstrating the sensitivity of CSS to food web changes. Sensitivity is clearly an important feature for ecological indicators. The threshold in this case would serve as a removal target, that is, remove enough Silver Carp to reduce their biomass to less than a quarter of the total fish biomass. While there has been an increase of Silver Carp in the Ohio River because states began sampling in 2015, management and commercial removal may have kept them below the 25% total fish biomass threshold where we predict they would impact the CSS. That may have changed because the last fish assemblage survey on the Ohio River was completed in 2020. Fish community surveys should be completed annually in all areas invaded by Silver Carp or anticipated to have the potential for invasion to create robust datasets that can be used to develop targets for population suppression and maintaining food web functionality. Removal targets using CSS can be established using the annual CSS slope as an indicator of change, as annual removal targets, and as longer-term restoration goals. CSS can be a useful tool for the management of Silver Carp and potentially other AIS.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data, models, and code (Wesner, 2024) are available from Zenodo: https://zenodo.org/records/14160857.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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