



# Invasive silver carp is empirically linked to declines of native sport fish in the Upper Mississippi River System

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**Abstract** Empirical assessments of the influence of invasive species on native species are infrequent because the required long-term data are rarely available. The invasion of silver carp in the Upper Mississippi River System (UMRS) provides a unique opportunity to assess the influence of this invasive species on native fishes because a highly standardized, long-term monitoring program has been sampling the fish communities in six reaches of the UMRS for over 20 years. We analyzed fish abundance (catch per unit effort from electrofishing) and water-quality data collected from 1994 to 2013 from three reaches where silver carp populations have been established since

2000, and three reaches where they are not established. Our results provide empirical evidence of a negative effect of invasive silver carp on native sport fish in the UMRS. Although water temperature, suspended solid concentration, and flooding also differed substantially between control and invaded reaches, only silver carp abundance had a direct negative relationship with the abundance of adult sport fish. Our analyses suggest that the mechanism for this decline may be competition for zooplankton between silver carp and larval/juvenile sport fish. In reaches where silver carp is established, recruitment of juvenile sport fish appears to be constrained relative to reaches where silver carp is not established.

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**Keywords** Invasive species · Sport fish · Long-term ecological data · Empirical relationship · Biotic constraints

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## Introduction

Although invasive species are an increasing global threat to ecosystems and the subject of much scientific inquiry, actual empirical assessments of the effects of invasive species on native species are relatively scarce because of the rarity of the long-term data needed to examine these effects while accounting for other drivers and anthropogenic stressors (Capinha et al. 2015; Clavero and Garcia-Berthou 2005; Grarock

et al. 2014; Trexler et al. 2000). Rigorous approaches to detecting the effects of invasive species on native species require standardized data collection on the abundance of native biota before and after the establishment of the invasive species, in multiple invaded areas and multiple control areas where the invasive species is not established (Blossey 1999; Underwood 1992, 1994). Such data are uncommon, but the invasion of silver carp (*Hypophthalmichthys molitrix*) in the Upper Mississippi River System (UMRS; Upper Mississippi River and its navigable tributaries) provides a unique opportunity to empirically examine the effects of this invasive species on native species. The Long Term Resource Monitoring (LTRM) element of the US Army Corps of Engineers (USACE) Upper Mississippi River Restoration Program has been monitoring fish communities and water quality in six reaches of the UMRS for over 20 years including several years before silver carp became established in the system (Irons et al. 2011; Ratcliff et al. 2014).

Silver carp is one of four species of Asian carps that have established reproducing populations in the UMRS (Chick and Pegg 2001; Raibley et al. 1995; Williamson and Garvey 2005). Of the four Asian carps established in the UMRS, the possibility of silver carp and bighead carp (*Hypophthalmichthys nobilis*), hereafter referred to as bigheaded carps, invading the Great Lakes via the Chicago Area Waterway System is a major concern for managers, scientists, and the public (Cudmore et al. 2012; Jerde et al. 2011, 2013; Kolar and Lodge 2002). Assessing the effects of silver carp on the UMRS ecosystem is critical for advancing our understanding of ecological interactions between invasive species and the ecosystems they invade. Silver carp is an omnivorous planktivore that consumes phytoplankton, zooplankton, and detritus (Xu and Xie 2004; Zhou et al. 2009, 2011). There is evidence that silver carp can alter zooplankton communities in the UMRS (Sass et al. 2014) and consume similar zooplankton species as native planktivorous fishes (Sampson et al. 2009), potentially leading to negative effects on native fishes through competition (Irons et al. 2007, 2011; Pendleton et al. 2017). The potential negative effects of silver carp are not limited to native planktivorous fishes because nearly all fish species in freshwater ecosystems begin their lives feeding on zooplankton (Chick and Van Den Avyle 1999). Research to date suggests bigheaded carps may

be having negative effects on native fishes, particularly in the Illinois River (Irons et al. 2007, 2011; Solomon et al. 2016), but the assessments made to date have not compared trends among river reaches invaded by bigheaded carps with reaches where these species have yet to become established. Data from the LTRM element are ideally suited for such an evaluation because this ongoing standardized monitoring program precedes the establishment of silver carp in the UMRS. Furthermore, this monitoring occurs in three reaches that have been invaded by silver carp and three reaches where silver carp is not yet established.

In this study, we tested for an empirical relationship between abundance of silver carp and sport fish in the six LTRM study reaches as a natural experiment similar to a before–after–control–impact (BACI) analysis (Underwood 1992, 1994). The initial conception of BACI models relies on a single impact site, a single control site, and multiple temporal samples taken before and after the impact of the stressor at both the control and impacted sites. Analysis of variance is used to test for differences in a response variable in control and impacted sites, before and after the effects of the stressor. The critical test result is the significance of the interaction between time and treatment (control vs impact) in this model. Among other limitations of this approach (Underwood 1992, 1994), the analysis treats the environmental stressor as a categorical variable that either occurs as single point in time event or that begins and continues unchanged from that point on. In contrast, environmental stressors such as invasive species can have effects that vary through time as the abundance and population demographics of the invasive species change. Given the exponential population growth silver carp have exhibited in the UMRS since their introduction (Pendleton et al. 2017), we felt it was critical to analyze their effects as a continuous variable rather than the categorical approach of BACI or Beyond BACI designs. Numerous environmental factors are also subject to anthropogenic changes and can potentially influence the interactions between native biota and invasive species in several ways (Byers 2002; Didham et al. 2007). A continuous data analysis allows the relationship between silver carp and sport fish to be assessed with the addition of environmental covariates that have the potential to influence the abundance of sport fish differentially between control and invaded reaches.

The objectives of this study are to assess the relationships between silver carp with adult and juvenile sport fish in the Upper Mississippi River. We used 20 years (1994–2013) of electrofishing and water-quality data from the LTRM element of the USACE Upper Mississippi River Restoration Program (Ratcliff et al. 2014; Soballe and Fischer 2004) to assess relationships between silver carp and native sport fish. Three environmental variables, flooding, water temperature, and suspended solid concentration, were included as covariates in our analysis because these factors vary longitudinally in the UMRS and may influence sport fish populations.

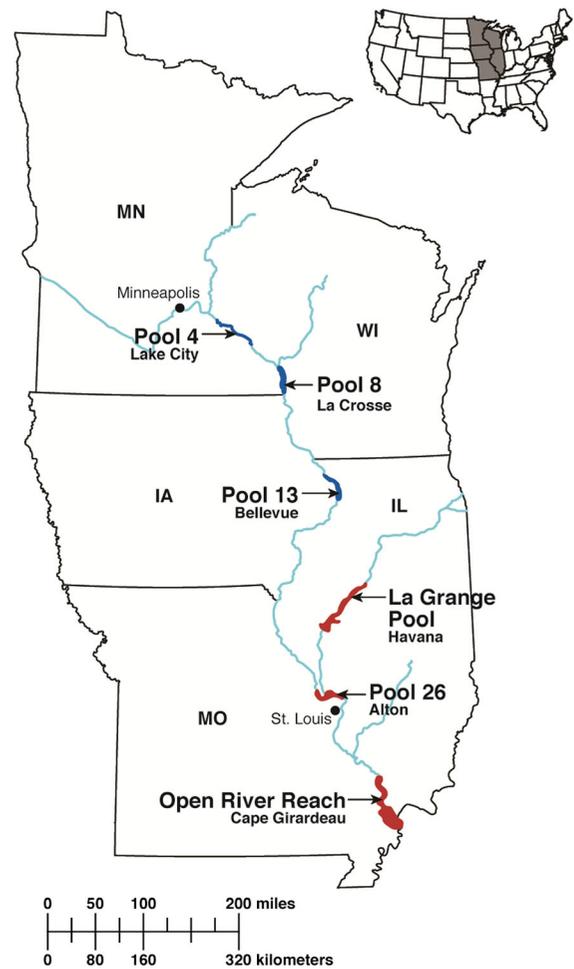
## Methods

### Study system

The LTRM monitoring program samples six study reaches across more than 2000 river km of the UMRS: Mississippi River Pools 4, 8, 13, 26, and an Open River Reach, and the La Grange Reach of the Illinois River (Fig. 1). These reaches include a diversity of aquatic habitats, including the main channel, side channels, backwater lakes, and impounded areas. They vary in length from 52 to 130 km and in total aquatic area (i.e., all contiguous habitats) from 7241 to 11,400 km<sup>2</sup> (Table S1). Silver carp is not yet established in the upper three reaches (Pools 4, 8, and 13, hereafter control reaches) but is established in the lower three reaches (Pool 26, Open River Reach, and La Grange Reach, hereafter referred to as invaded reaches) since 2000 (Fig. 2).

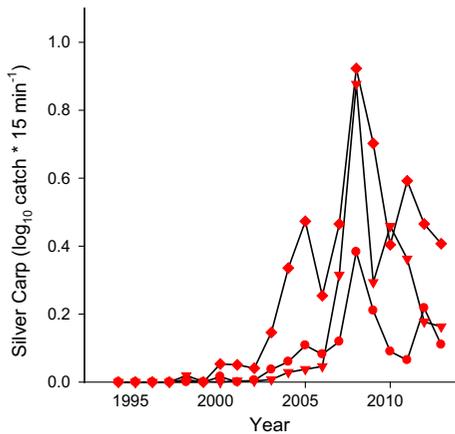
### Statistical analyses

We chose to focus on the effects of silver carp because they are far more abundant in the UMRS than bighead carp and are much better represented in our LTRM data. Sport fish were selected for these analyses because management efforts for these species are relatively consistent among the six LTRM reaches because state and federal agencies are generally focused on maintaining or increasing their abundance throughout the UMRS. Additionally, collection methods and survey designs usually sample sport fish as well as, or better than, other species. To analyze trends of sport fish, we used the combined catch per unit



**Fig. 1** The six reaches of the Upper Mississippi River System sampled by the LTRM. Silver carp is not yet established in three upper pools (Pool 4, Pool 8, Pool 13; control reaches—shaded blue) of the Mississippi River, but have been established in Pool 26 and the Open River Reach of the Mississippi River and the La Grange Reach of the Illinois River (invaded reaches—shaded red) since 2000

effort (CPUE) from electrofishing of 19 fish species native to the Upper Mississippi River System pursued by anglers and considered to be a sport fish in at least one Upper Mississippi River state (Table S2). The fish component of the LTRM uses a stratified random design to sample fishes in several major habitat strata, including the main channel, side channels, contiguous backwater lakes, and impounded areas (Ratcliff et al. 2014). This design allows for the calculation of a pool-wide mean CPUE as an index of abundance, weighting data from each habitat strata by the total area of that habitat in each river reach. Electrofishing is conducted



**Fig. 2** Catch per unit effort ( $\log_{10}$  catch  $\times 15^{-1}$  min electrofishing) of silver carp in the three invaded reaches [Pool 26 (red inverted triangle), Open River (red circle), La Grange (red diamond)] from 1994 to 2013

using pulsed-DC electrofishing boats with each sample consisting of a 15-min electrofishing transect (see Ratcliff et al. 2014 for complete sampling protocols). We considered adult sport fish to be those individuals with total lengths greater than or equal to stock size for each species, a designation used by fish biologists that approximates biological maturity (Table S2, Anderson and Neumann 1996). All LTRM fish data are publicly available online ([http://www.umesc.usgs.gov/data\\_library/fisheries/fish1\\_query.shtml](http://www.umesc.usgs.gov/data_library/fisheries/fish1_query.shtml)). This repository not only includes a user-friendly interface for data downloads, but also has tools for graphically exploring LTRM data online.

Our data included 6 years prior to the establishment of silver carp and 14 years post-establishment (Fig. 2), allowing this invasion to be analyzed as a natural experiment. We used a repeated-measures mixed model to test whether trends in the CPUE of adult sport fish in the three invaded reaches differed from those in the three control reaches and whether any differences were associated with silver carp CPUE. As is the case with most BACI designs, control reaches are not perfect controls. Several environmental variables are known to vary among the LTRM study reaches (Johnson and Hagerty 2008). Therefore, we included data for the number of days the river was in flood stage, water temperature during the growing season (April–October), and total suspended solids as covariates in the model. All three of these covariates can influence the abundance of adult and juvenile sport

fish independently from silver carp. When independent variables were significant, we assessed the effect size using Cohen's  $f^2$  (Selya et al. 2012).

Data for water temperature and suspended sediments are from publicly available LTRM water-quality component (Soballe and Fischer 2004; [https://www.umesc.usgs.gov/data\\_library/water\\_quality/water\\_quality\\_page.html](https://www.umesc.usgs.gov/data_library/water_quality/water_quality_page.html)), whereas data on river stage (gage height) were taken from gages maintained by either the USACE or the US Geological Survey (USGS, Table S3). The frequency and duration of flooding is a critical environmental variable affecting all aspects of river-floodplain ecosystems (Junk et al. 1989; Sparks 1995). We quantified the number of days the river met or exceeded the specified flood stage each year (flood days) as an index of flooding. All river stage data are available online for both the USACE (<https://www.rivergages.com>) and USGS (<http://waterdata.usgs.gov/nwis/sw>) gages.

Water temperature is a critical factor for fishes known to affect the growth and survival of larvae and juveniles (Houde 1987; Wuellner et al. 2008). We used data from LTRM water-quality fixed sites located in the main channel of the Mississippi and Illinois rivers to quantify water temperature (Table S4). Because the frequency of sample collection changed over the 20-year period we were analyzing ([http://www.umesc.usgs.gov/reports\\_publications/ltrmp/water/fixes/fs\\_methods.html](http://www.umesc.usgs.gov/reports_publications/ltrmp/water/fixes/fs_methods.html)), we analyzed annual mean temperature for each LTRM reach based on monthly averages from April through October so that differences in the number of observations per month would be less likely to influence the overall temperature trends among years. Monthly data from November–March were not included in these analyses because river access during winter can be challenging, causing sample collection to be less consistent from year to year in these months. Additionally, April–October corresponds roughly with the growing season for most fishes.

The concentration of suspended solids directly influences water turbidity and is greatly influenced by sediment loading associated with agriculture and other anthropogenic ecosystem alterations (Houser et al. 2010; Houser 2016). We calculated annual mean suspended sediment concentrations ( $\text{mg L}^{-1}$ ) from LTRM stratified water-quality sampling during the summer. These data were collected from multiple random sites in the main channel, side channels,

backwater lakes, and impounded habitat strata at each LTRM river reach during the last week of July and the first week of August each year. Suspended sediment data were log transformed prior to analysis to reduce heteroscedasticity and linearize the trends. Soballe and Fischer (2004) provided further details on LTRM fixed-site and stratified random water-quality methods and sampling design.

Because silver carp is not piscivorous, their effects on adult sport fish would likely be indirect, resulting from competition for zooplankton between silver carp and both forage fish, and juvenile sport fish. Therefore, we conducted additional repeated-measures analyses for a multi-species index of forage fish and the juvenile sport fish. Our forage fish index was the combined CPUE of emerald shiner (*Notropis atherinoides*) (all sizes) and all native fishes  $\leq 80$  mm total length, a modification of the forage fish indicator used in Johnson and Hagerty (2008). Three species comprised the majority of forage fish in the six reaches: gizzard shad (*Dorosoma cepedianum*), emerald shiners, and bluegill (*Lepomis macrochirus*) (Table S5). Our multi-species index of juvenile sport fish was the combined abundance of 19 sport fish  $<$  the species stock size (Table S2, Anderson and Neumann 1996). Identification of adult and juvenile silver carp was made in the field for the vast majority of individuals, although smaller juveniles were occasionally brought back to the laboratory for identification. Because silver and bighead carp hybridize in the UMRS (Lamer et al. 2010), it is possible that some of the individuals identified as silver carp were silver carp  $\times$  bighead carp hybrids or backcrosses.

Two important considerations for our repeated-measures mixed model are the possibility that autocorrelation may violate the assumption of independent variables and whether the Y-intercept should be fixed across subjects (river reaches) or random. We explored the variance structure of our data for signs of autocorrelation by calculating the mean correlation (averaged across the six river reaches) of adult sport fish abundance among time steps from 1 to 19 years apart (Table S6). Although the correlation between time steps decreased as time step increased, indicating autocorrelation was present, the mean correlation decreased only slightly with time step relative to the standard autoregressive AR(1) model (Table S6). Additionally, we felt a single fixed Y-intercept across the six river reaches was an unrealistic assumption

given the size and complexity of the UMRS. Therefore, we modeled the Y-intercept as a random variable with river reach as the subject and used an unstructured covariance structure. We used identical repeated-measures models for analyzing adult sport fish, forage fish, and juvenile sport fish. Additionally, we used a simplified model to analyze trends of juvenile sport fish that included only silver carp abundance, temperature, and the interaction of these factors as a follow-up to the main repeated-measures analysis.

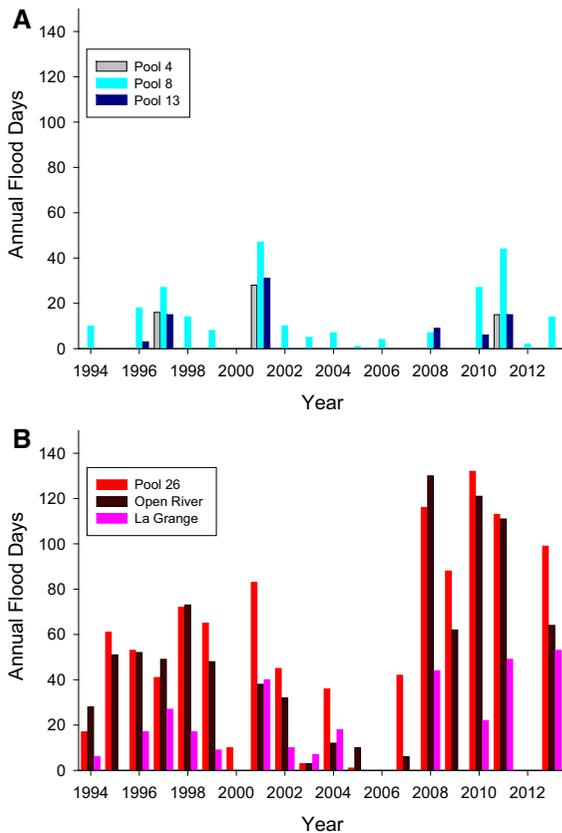
## Results

### Covariate trends

Both the frequency and duration of flooding show a clear dichotomy between the control and invaded reaches. The number of days the river was in flood stage never exceeded 50 days in the control reaches (Fig. 3a), whereas floods extending  $\geq 50$  days were common in the invaded reaches (Fig. 3b). In Pool 26 and the Open River Reach, flooding exceeded 100 days in 2008, 2010, and 2011 (Fig. 3b). As with flood duration, water temperature in the main channel also varied substantially between control and invaded reaches (Fig. 4a). Additionally, positive linear trends were evident at all six reaches and all reaches were warming at a similar rate. Greater concentrations of suspended solids are found in the invaded reaches than in the control reaches (Fig. 4b). Negative linear trends were evident in Pools 4 and 8, but no trends through time were evident in the other four reaches (Fig. 4b).

### Repeated-measures mixed model results

We found a negative empirical relationship between silver carp and adult sport fish abundance that varied with year. Convergence criteria were met for the repeated-measures mixed model for adult sport fish abundance and the null model likelihood ratio test was significant ( $df = 1$ ,  $\chi^2 = 28.40$ ,  $p < 0.001$ ), indicating that the unstructured covariance matrix is preferable to the null model matrix (ordinary least squares). Year ( $F_{1,105} = 8.95$ ,  $p = 0.003$ ), silver carp ( $F_{1,105} = 5.14$ ,  $p = 0.025$ ) and the interaction between year and silver carp ( $F_{1,105} = 5.17$ ,  $p = 0.025$ ) were all significant (Fig. 5a). Effect size was greatest for silver carp



**Fig. 3** Trends for the number of days above flood stage for **a** the three control reaches (Pool 4, 8, and 13) and **b** the three invaded reaches (Pool 26, Open River Reach, La Grange Reach), sampled by the Long Term Resource Monitoring element of the USACE Upper Mississippi River Restoration Program from 1994 to 2013

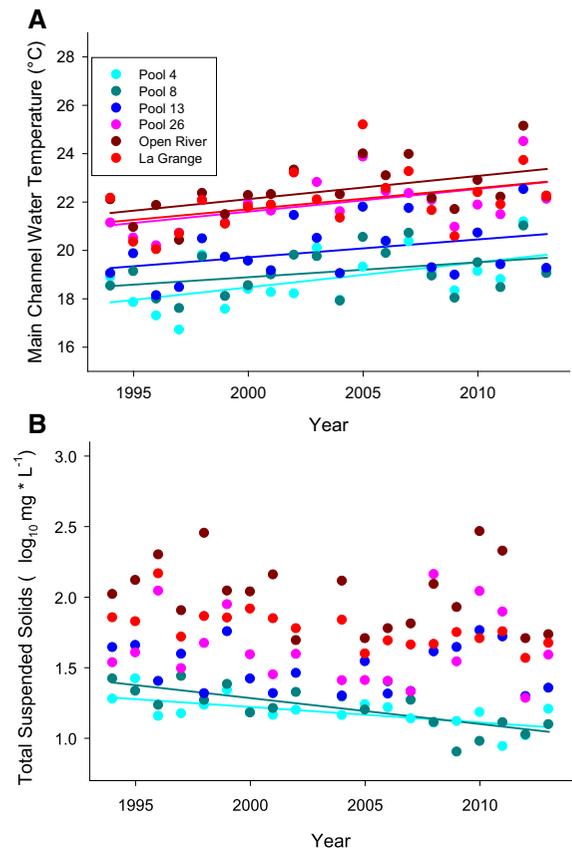
(Cohen's  $f^2 = 0.134$ ), followed by the interaction of year and silver carp (Cohen's  $f^2 = 0.131$ ) and year (Cohen's  $f^2 = 0.07$ ). None of the three covariates were significant ( $F_{1,105} \leq 0.34$ ,  $p \geq 0.559$ ).

Our repeated-measures mixed model provides an estimate of when silver carp began adversely affecting adult sport fish. The model and coefficients derived from the analysis are:

$$ASF = (0.0095)Year + (178.3800)SC + (-0.0890)Year * SC + (0.1313)LogSS + (0.0004)FD + (-0.0135)T$$

where ASF = Adult sport fish abundance, SC = Silver carp abundance, SS = Suspended solids, T = Water temperature.

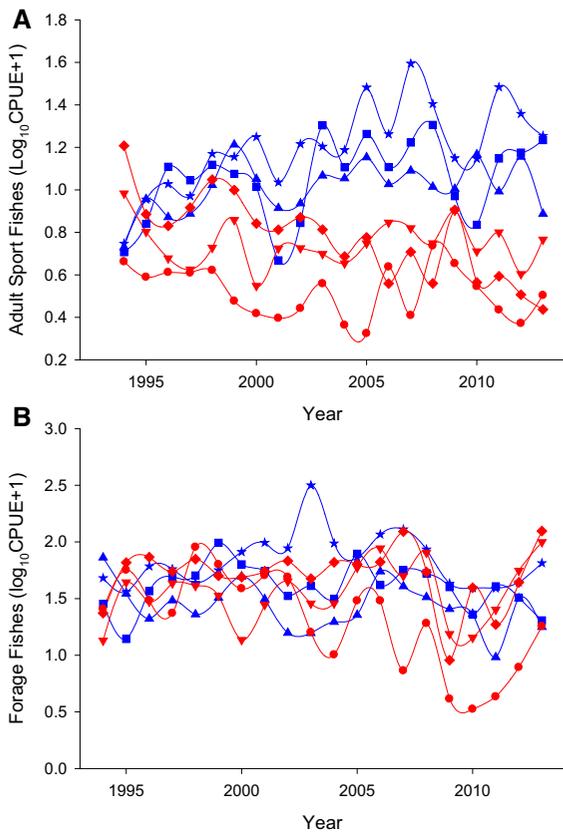
Dividing the coefficient for silver carp (178.3800) by the coefficient for the interaction of year and silver



**Fig. 4** Trends for **a** water temperature, and **b** suspended solids in the three control reaches (Pool 4, 8, and 13), and three invaded reaches (Pool 26, Open River Reach, La Grange Reach) sampled by the Long Term Resource Monitoring element of the USACE Upper Mississippi River Restoration Program from 1994 to 2013. Lines indicate significant ( $p \leq 0.05$ ) linear regressions of water temperature or suspended solids with year

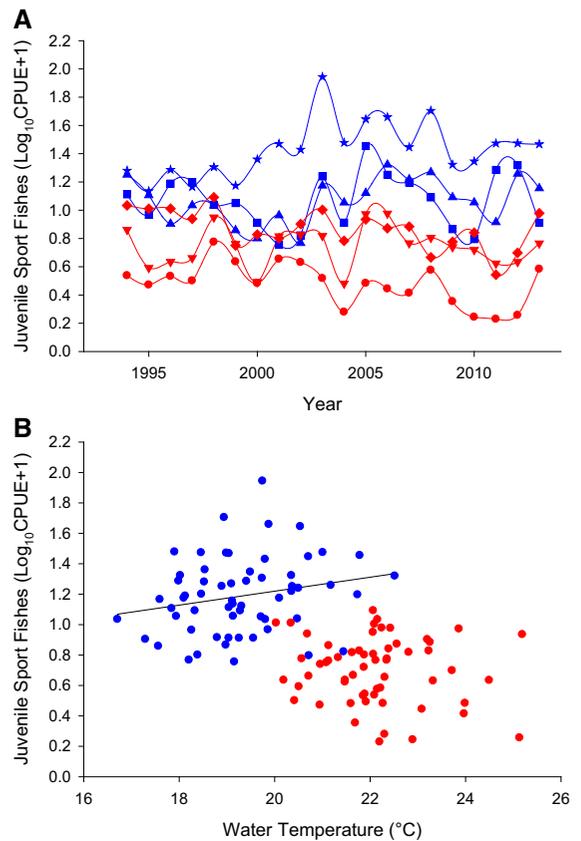
carp ( $-0.0890$ ) yields  $-2004.26$  suggesting that silver carp began to cause reductions in the CPUE of adult sport fish shortly after 2004.

We found no relationship between abundances of silver carp and forage fish, and an interactive effect of water temperature and silver carp on juvenile sport fish. Convergence criteria was met for the repeated-measures mixed model for forage fish and the null model likelihood ratio test was significant ( $df = 1$ ,  $\chi^2 = 56.95$ ,  $p < 0.001$ ), but none of the effects in the model were significant ( $F_{1,105} \leq 3.60$ ,  $p \geq 0.061$ ) (Fig. 5b). Convergence criteria were met and the null model likelihood ratio test was significant for the repeated-measures mixed model for juvenile sport fish ( $df = 1$ ,  $\chi^2 = 56.95$ ,  $p < 0.001$ ), with temperature the



**Fig. 5** Trends in abundance of **a** adult sport fish, and **b** forage fish, for the three control reaches [Pool 4 (blue triangle), Pool 8 (blue star), Pool 13 (blue square)], and three invaded reaches [Pool 26 (red inverted triangle), Open River (red circle), La Grange (red diamond)] sampled by the Long Term Resource Monitoring element of the USACE Upper Mississippi River Restoration Program from 1994 to 2013

only significant effect ( $F_{1,105} = 6.58, p = 0.012$ ) (Fig. 6a). Using the simplified model with only silver carp, temperature, and their interaction, convergence criteria were met and the null model likelihood ratio test was significant ( $df = 1, \chi^2 = 108.56, p < 0.001$ ), and all effects within the model were significant ( $F_{1,105} \geq 4.30, p \leq 0.040$ ). A significant positive relationship between temperature and CPUE of juvenile sport fish occurred in control reaches but not in the invaded reaches (Fig. 6b).



**Fig. 6** Trends in abundance of **a** juvenile sport fish through time for the three control reaches [Pool 4 (blue triangle), Pool 8 (blue star), Pool 13 (blue square)], and three invaded reaches [Pool 26 (red inverted triangle), Open River (red circle), La Grange (red diamond)], and **b** juvenile sport fish with water temperature for control (blue circle) and impacted (red circle) reaches sampled by the Long Term Resource Monitoring element of the USACE Upper Mississippi River Restoration Program from 1994 to 2013. Lines indicate a significant ( $p \leq 0.05$ ) linear regression between juvenile sport fish and water temperature

### Discussion

We found empirical evidence of a negative influence of silver carp on the abundance of sport fish in the UMRS. Temporal trends in the abundance of adult sport fish in the control reaches were generally positive, whereas these trends were generally negative in the invaded reaches. None of the three covariates, flood days, water temperature, and suspended solids, had significant effects on the abundance of adult sport fish, even though these variables differed substantially between control and invaded reaches. Although water

temperature was substantially cooler in the control reaches relative to the invaded reaches, all study areas were warming at a similar rate over the 20 years examined and trends in sport fish populations were opposite in invaded and control reaches. Insignificant environmental covariates in our analysis of adult sport fish is not evidence that these factors are unimportant to the population dynamics of sport fish. Our analysis only examined these factors as covariates (i.e., no interactions are included due to limited degrees of freedom). We believe our analysis of 20 years of standardized monitoring data, including multiple control and invaded reaches, and 6 years of data preceding the establishment of silver carp, is one of the strongest empirical assessments of the effects of an invasive species conducted for a large and spatially complex ecosystem. Our results indicate that the association between the abundance of silver carp and adult sport fish was robust despite the inclusion of the three environmental covariates that differed substantially between control and invaded reaches.

Silver carp likely adversely affect adult sport fish by reducing the abundance of zooplankton both through direct consumption of zooplankton and by competing with zooplankton for phytoplankton. Although several of the sport fish included in our index consume zooplankton as adults (e.g., bluegill, yellow perch, white and black crappie), none of these species are exclusively or predominantly zooplanktivorous as adults. Reductions in zooplankton abundance could have a negative influence on the abundance of forage fish, but we found no evidence of such a relationship. A more likely explanation may be that the observed reductions in adult sport fishes result from competition for zooplankton during early life stages of sport fishes.

Our suggestion that silver carp may compete with larval and juvenile sport fish for zooplankton contrasts with early descriptions of silver carp as predominantly consumers of phytoplankton rather than zooplankton (see review in Kolar et al. 2007). This conclusion is based on relatively early studies focused on the evaluating the potential to use silver carp to control algal blooms. Most of these studies examined diet of young-of-the-year or age-1 silver carp stocked in small-artificial ponds fertilized to produce algae blooms (Cremer and Smitherman 1980; Ghosh et al. 1973; Spataru 1977; Spataru et al. 1983). These studies may demonstrate that juvenile silver carp can feed primarily on phytoplankton when reared in ponds

with abundant blooms of phytoplankton, but they may not accurately describe silver carp diet at other life stages or in other ecological contexts. More recent diet and stable isotope studies demonstrate that silver carp diet is plastic and varies with environmental conditions (Coulter et al. 2018; Yao et al. 2016), with silver carp consuming phytoplankton (Calkins et al. 2012; Zhou et al. 2009), zooplankton (Domaizon et al. 2000; Sampson et al. 2009; Sparatu and Gophen 1985; Xu and Xie 2004; Zhou et al. 2009), detritus (Asanka et al. 2015), and even benthic resources (Lubcker et al. 2016), depending on their ontogenetic state (i.e., larvae, juvenile, adult) (Domaizon et al. 2000), trophic state/productivity of the aquatic system (Chen et al. 2011), presence and abundance of competitors (Wang et al. 2018), and season (Spataru and Gophen 1985).

Although there is substantial variation and flexibility in the diet of silver carp, studies have consistently demonstrated that silver carp reduce the abundance of zooplankton and shift the community composition of zooplankton. Research conducted in artificial ponds (Burke et al. 1986; Milstein et al. 1985) natural lakes (Lu et al. 2002; Wu et al. 1997), reservoirs (Radke and Kahl 2002; Zhou et al. 2011), and rivers (Sass et al. 2014), all demonstrate that silver carp can substantially reduce the abundance of crustacean zooplankton (e.g., cladocerans and copepods). Silver carp also shift the composition of crustacean zooplankton to smaller-sized taxa (Wu et al. 1997). Because most native sport fish feed heavily on crustacean zooplankton during their larval and juvenile stages (Chick and Van Den Avyle 1999; Sampson et al. 2009; Sass et al. 2014), reductions in the abundance of these important food resources by silver carp is a viable hypothesis for the negative empirical relationship between sport fish and silver carp found in this study. Sass et al. (2014) demonstrated that zooplankton abundance in the Illinois River (including the La Grange Reach) declined and the composition shifted to smaller taxa after bigheaded carps became established, further supporting our hypothesis. The effects of silver carp on zooplankton may be a combination of both predation and competition for phytoplankton, but there can be little doubt that their direct predation on zooplankton contributes to this decline.

Silver carp appear to be constraining the recruitment of juvenile sport fish, but the relationship interacts with water temperature. Water temperature was the only significant variable in the full mixed-

model with an overall positive relationship between temperature and juvenile sport fish. Using a simplified mixed model, we found significant interaction between the effects of silver carp and water temperature on juvenile sport fish. The overall positive relationship between juvenile sport fish and temperature was driven by the three control reaches, whereas there was no relationship between temperature and juvenile sport fish in the three reaches invaded by silver carp. Recruitment success of many fish species is positively related to water temperature during the growing season (Chick et al. 2013; Houde 1987). The positive relationship between water temperature and the abundance of juvenile sport fish in control, but not in invaded, reaches suggests silver carp may be restricting recruitment of sport fish. This pattern is consistent with the Biotic–Abiotic Constraining Hypothesis, whereby certain biotic interactions can constrain recruitment of fishes even when abiotic conditions are favorable (Quist et al. 2003; Quist and Hubert 2005). Under this model, silver carp is a plausible biotic factor that could constrain recruitment of sport fish in reaches invaded by silver carp. Moreover, this mechanism might operate similarly for sport fish in the Great Lakes should silver carp ever become established there.

Our analysis of the effects of invasive silver carp on native sport fish using multi-species indices has at least three advantages. First, sport fish are economically important natural resources (Southwick Associates 2012) as well as important predators of fish and invertebrates in freshwater ecosystems. By one widely accepted definition (Clinton 1999), an invasive species is a non-native species that does ecological and/or economic harm, or harm to human health. Our finding that adult sport fish are declining in reaches invaded by silver carp, and that this decline is empirically related to the abundance of silver carp, suggests both ecological and economic damage from the invasion of silver carp. Finally, multispecies indices have been suggested to be more sensitive to environmental impacts, especially where the population dynamics of individual species typically show substantial variation (Niemi and McDonald 2004; Noss 1990). For example, gizzard shad, which were the dominant forage species in the invaded reaches (e.g., 62.9–78/9% of the forage fish index; Table S5) are well known to have large inter-annual variation in recruitment and overall population levels (Bremigan and Stein 1999, 2001;

Wuellner et al. 2008). Even though gizzard shad can have substantial dietary overlap with silver carp (Sampson et al. 2009; Wang et al. 2018), this large inter-annual variation in population size and recruitment may have contributed to the lack of any relationship between the multispecies index of forage fish and the abundance of silver carp. Additionally, since adult sport fish are declining, this may be releasing forage fish from predation.

Our study provides empirical evidence of an adverse relationship between silver carp and economically valuable sport fish in the UMRS. Great concern has been raised over the potential for bigheaded carps to invade the Great Lakes (Jerde et al. 2011, 2013; Kolar and Lodge 2002), including the appointment of an Asian Carp Director for the Council of Environmental Quality to oversee the United States Government's efforts to prevent the spread of bigheaded carps to new areas. These concerns are valid, but the effects of bigheaded carp on economically valuable outdoor recreational activities on the UMRS is less frequently discussed. Silver carp not only threaten sport fishing, but also are detrimental to recreational activities involving boating on UMRS waters due to their propensity to jump and impact boaters. Outdoor recreation on the UMRS was estimated to have an economic value of \$1.2 billion annually in 1990 (equivalent to \$2.2 billion in 2018 dollars), which is not a trivial resource for the U.S. economy (Carlson et al. 1995). Our study suggests that in addition to focusing on the Great Lakes, efforts to prevent the spread of silver carp to new areas throughout the United States and to reduce their abundance in areas where they have already become established are worthy of federal consideration and investment to minimize ecological and economic impacts.

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[other/ltrmp\\_monitoring.html](#)). River stage data are available through the United States Geological Survey National Water Information System: Web Interface (<http://waterdata.usgs.gov/nwis/sw>), and United States Army Corps of Engineers (<https://www.rivergages.com>).

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