



## Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA



Greg G. Sass<sup>a,\*</sup>, Collin Hinz<sup>b</sup>, Anthony C. Erickson<sup>b</sup>, Nerissa N. McClelland<sup>c</sup>, Michael A. McClelland<sup>c</sup>, John M. Epifanio<sup>d</sup>

<sup>a</sup> Wisconsin Department of Natural Resources, Escanaba Lake Research Station, 3110 Trout Lake Station Drive, Boulder Junction, WI 54512, USA

<sup>b</sup> Illinois River Biological Station, Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, 704 North Schrader Avenue, Havana, IL 62644, USA

<sup>c</sup> Illinois Department of Natural Resources, Division of Fisheries, Havana Field Office, Havana, IL 62644, USA

<sup>d</sup> Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, IL 61820, USA

### ARTICLE INFO

#### Article history:

Received 1 April 2014

Accepted 23 July 2014

Available online 23 September 2014

Communicated by Thomas Stewart

#### Index words:

Bighead carp  
Illinois River  
Invasive species  
Silver carp  
Zooplankton

### ABSTRACT

Aquatic invasive species introductions are a global environmental concern. Negative effects of invasive species are often manifested in alterations of food web structure and through competition with and predation upon native species. The Illinois River, Illinois, USA harbors invasive, planktivorous bighead, *Hypophthalmichthys nobilis*, and silver carp, *Hypophthalmichthys molitrix*, and can be a model ecosystem to test for their effects on zooplankton communities. We tested for bighead and silver carp effects on zooplankton communities pre- and post-establishment within one reach of the Illinois River and among river reaches that varied in abundances of these invasive fishes. The establishment of bighead and silver carp was associated with increased rotifer abundances, while cladoceran and copepod abundances were reduced relative to pre-establishment. Cladoceran and copepod abundance and biomass were negatively associated with bighead and silver carp abundances among reaches. Total zooplankton and rotifer abundance and biomass were positively associated with bighead and silver carp abundances. Our results suggest that bighead and silver carp have changed the zooplankton community of the Illinois River which may have implications for the food web, native species, and other ecosystems poised to be invaded, such as the Laurentian Great Lakes.

© 2014 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.

### Introduction

Over the next century, biotic exchange of organisms (including invasive species) is predicted to have the greatest adverse effect on native biodiversity in freshwater ecosystems (Cucherousset and Olden, 2011; Sala et al., 2000). Often, the introduction and establishment of invasive species in novel environments lead to changes in food web structure and the extirpation of native species. For example, zebra, *Dreissena polymorpha*, and quagga mussels, *Dreissena bugensis*, introduced by ballast water in the Laurentian Great Lakes have increased water clarity and suffocated native mussels (Maclsaac, 1996; Ricciardi and Maclsaac, 2000). Invasive rainbow smelt, *Osmerus mordax*, introductions in north temperate inland lakes have led to local extirpations of native walleye, *Sander vitreus*, lake herring (cisco), *Coregonus artedii*, and yellow perch,

*Perca flavescens*, (Hrabik et al., 2001; Krueger and Hrabik, 2005; Mercado-Silva et al., 2007; Roth et al., 2010). Introductions of invasive rusty crayfish, *Orconectes rusticus*, have resulted in the loss of submersed aquatic macrophytes and the decline of native crayfishes (Olsen et al., 1991; Roth and Kitchell, 2005; Wilson, 2002). The rate of new introductions of non-native species is expected to increase in the future, with unknown consequences on native and previously invaded ecosystems (Kolar and Lodge, 2002; Lodge et al., 2006).

The Illinois River, Illinois, USA has long served as a corridor for the inter-basin transfer of species between the Laurentian Great Lakes and the Mississippi River. With the completion of the Chicago Sanitary and Ship Canal (CSSC) in 1910, a manmade waterway was established between Lake Michigan and the Mississippi River (Moy et al., 2011). More recent water quality improvements in the Chicago Area Waterway System (mandated by federal and local laws) have facilitated invasive species transfers to occur in both directions within these formerly hydrologically-separated basins (McClelland et al., 2012). Zebra mussels, round goby, *Neogobius melanostomus*, and white perch, *Morone americana*, have colonized the Illinois River from Lake Michigan through this artificial connection (Irons et al., 2006; Moy et al., 2011). Currently, invasive bighead, *Hypophthalmichthys nobilis*, and silver

\* Corresponding author. Tel.: +1 715 891 1875; fax: +1 715 356 2105.

E-mail addresses: [gregory.sass@wisconsin.gov](mailto:gregory.sass@wisconsin.gov) (G.G. Sass), [collin.hinz@gmail.com](mailto:collin.hinz@gmail.com) (C. Hinz), [aerickson@mail.bradley.edu](mailto:aerickson@mail.bradley.edu) (A.C. Erickson), [Nerissa.McClelland@illinois.gov](mailto:Nerissa.McClelland@illinois.gov) (N.N. McClelland), [Michael.McClelland@illinois.gov](mailto:Michael.McClelland@illinois.gov) (M.A. McClelland), [epifanio@illinois.edu](mailto:epifanio@illinois.edu) (J.M. Epifanio).

carp, *Hypophthalmichthys molitrix*, are threatening to enter Lake Michigan through this corridor following their unintentional introduction to the Middle Mississippi River in the early 1970s (Chick and Pegg, 2001; Kelly et al., 2011).

In 2002, an electric aquatic nuisance species dispersal barrier in the CSSC became operational to decrease the probability of inter-basin transfers of fishes (Moy et al., 2011). Since barrier installation, one individual bighead carp has been captured above this barrier; however, otolith microchemistry suggested that this fish had lived its entire life above the barrier. Several water samples routinely collected and assayed for “environmental” DNA suggest that bighead and silver carp are present above the barrier and able to colonize Lake Michigan (Jerde et al., 2011; Moy et al., 2011). Nevertheless, uncertainty in the analysis of “environmental” DNA may or may not be able to resolve the presence of live fish versus other sources of bighead and silver carp DNA contamination. Despite the dispersal barrier and uncertainty in “environmental” DNA testing, bighead and silver carp are poised to colonize Lake Michigan if they are not already there.

Bighead and silver carp were first documented in the La Grange reach, Illinois River by the U.S. Army Corps of Engineers', Upper Mississippi River Restoration-Environmental Management Program, Long-term Resource Monitoring Program element in 1995 and 1998, respectively (Irons et al., 2007). Since 2000, the silver carp population within this reach, as well as commercial harvest of both species in the Illinois River, have increased exponentially (Irons et al., 2007; Sass et al., 2010). In the late 2000s, the adult and sub-adult silver carp population in the La Grange reach was estimated at over 2500 individuals/river km (Sass et al., 2010). Given their rapid population growth, high fecundities, large adult sizes, capacity to filter very small particles, and ability to disperse long distances quickly, bighead and silver carp have the potential to negatively affect the Illinois River ecosystem and others that have yet to be colonized (e.g., tributaries of the Mississippi River, Laurentian Great Lakes) (DeGrandchamp et al., 2008; Kolar et al., 2007). Perhaps of greatest concern to scientists and managers is the potential for bighead and silver carp to alter energy flows in native aquatic food webs due to their ability to filter very small particles. Bighead and silver carp occupy low trophic levels by feeding upon phytoplankton and zooplankton, thus they have the potential to reduce energy available to upper trophic levels and to compete with native obligate and facultative planktivorous fishes and grazing zooplankton (Irons et al., 2007; Kolar et al., 2007; Milstein et al., 1985). In lentic systems, bighead and silver carp have been observed to reduce total zooplankton abundances and particularly those of larger-bodied zooplankters, such as cladocerans and copepods (Fukushima et al., 1999; Shao et al., 2001; Stone et al., 2000; Yang et al., 1999).

Bighead and silver carp have established robust populations in the Illinois River, pose an imminent threat to invade the Laurentian Great Lakes, and thus may threaten the food webs of these systems and compete with native fishes. The objective of our study was to test for bighead and silver carp effects on zooplankton community composition and biomass within the Illinois River using two complementary comparative studies. First, we tested for differences in zooplankton community samples collected and archived prior to the establishment of bighead and silver carp (1994–2000) with samples collected following the establishment of these invasive fishes (2009–2011) in the La Grange reach, Illinois River. Second, we tested for differences in zooplankton community composition and biomass among six reaches of the Illinois River that varied in bighead and silver carp relative abundances during 2009–2011. We hypothesized that the establishment of bighead and silver carp would result in reduced total zooplankton, rotifer, cladoceran, and copepod abundances relative to the pre-establishment zooplankton community. Similarly, we hypothesized that total zooplankton, rotifer, cladoceran, and copepod abundance and biomass would be reduced in river reaches with greater abundances of bighead and silver carp relative to reaches with low abundances of these invasive species.

## Methods

### *Bighead and silver carp in the Illinois River*

Although bighead and silver carp were present in the lower Illinois River during the 1990s (Chick and Pegg, 2001; Irons et al., 2007, 2011) (Fig. 1), natural reproduction was not documented in the La Grange reach until 2000. Bighead and silver carp population growth in this reach has been exponential since establishment (Irons et al., 2007; Sass et al., 2010). For the purpose of this study, we define the pre-bighead and silver carp establishment time period as 1994–2000 and the post-establishment time period as 2009–2011 in the La Grange reach, Illinois River.

We used silver carp electrofishing catch-per-unit-effort as an index of both silver and bighead carp relative abundances. Electrofishing is the most efficient gear to capture silver carp; however, is one of the poorest gears for capturing bighead carp (Irons et al., 2011). For example, electrofishing catch-per-unit-effort for bighead carp in the Alton, La Grange, and Peoria reaches of the Illinois River in 2010 was only 0.78/h, 0.03/h, and 0.78/h, respectively (Michaels et al., 2011). Nevertheless, bighead carp abundances have increased concurrently with silver carp abundances as evidenced by catches from a long-term, standardized multiple-gear fisheries monitoring program on the La Grange reach, Illinois River (Irons et al., 2007, 2011) and in commercial fishery trammel net landings, which primarily consist of bighead carp captured in the lower three reaches (Alton, La Grange, Peoria) of the Illinois River (Irons et al., 2007). Therefore, we used the relative abundance of silver carp as a measure of the magnitude of bighead and silver carp establishment.

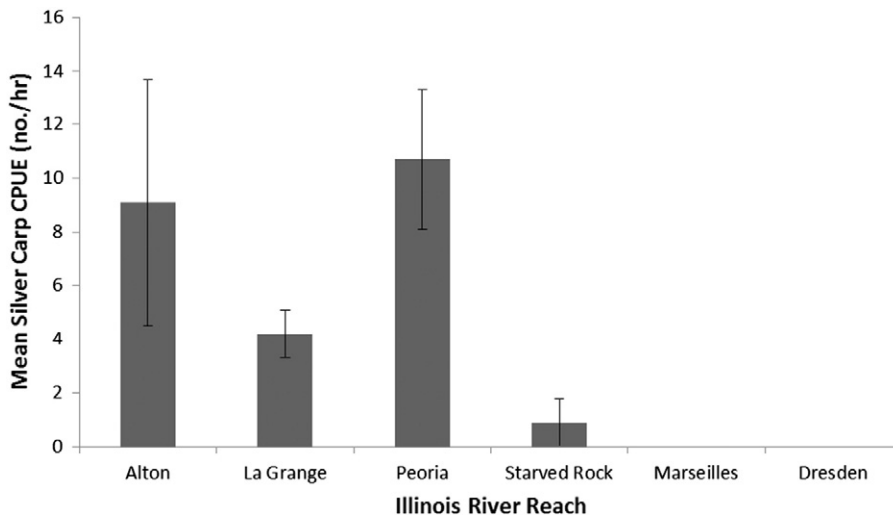
During 2009–2011, electrofishing catch-per-unit-effort (i.e., relative abundance) of silver carp differed among six reaches of the Illinois River (Figs. 1, 2). Various relative abundances of silver carp were collected by the Long-term Illinois, Mississippi, Ohio, and Wabash River Fish Population Monitoring Program (LTFP) in the lower four reaches of the Illinois River (Alton, La Grange, Peoria, Starved Rock) in 2010 (Michaels et al., 2011) (Fig. 2). No bighead or silver carp were collected by this standardized fish monitoring program in the Marseilles and Dresden reaches in 2010 (Michaels et al., 2011) (Fig. 2). Detailed protocols for the LTFP can be found in Michaels et al. (2011). Briefly, pulsed-DC boat electrofishing is conducted at stratified-random sampling sites in each reach during three time periods (June 15–July 31, August 1–September 15, September 16–October 31) annually using Long-term Resource Monitoring Program protocols found in Gutreuter et al. (1995). The number of 15 min electrofishing runs conducted in each reach during each time period is standardized by reach length. All sampled fishes were identified, measured for length and weight, and returned to the water unharmed. For the purpose of this study, we separated the lower four and upper two reaches of the Illinois River into two treatment groups to allow for comparisons based upon the relative abundances of bighead and silver carp in each section of the Illinois River.

### *Pre- and post-bighead and silver carp establishment*

We assessed zooplankton community composition and abundance within the La Grange reach of the Illinois River at a single, fixed, main channel site near Havana, Illinois (river km 193) pre-bighead and silver carp establishment (1994–2000) and post-establishment (2009–2011). The Illinois River Biological Station has maintained an archived historical collection of zooplankton samples since 1994; however, this standardized zooplankton monitoring program was eliminated during 2001–2008 due to funding constraints. In each year of sampling, monthly zooplankton collections were conducted during May–November with an identical sampling protocol between time periods. For each sample, 30 L of water was pumped through a 55 µm filter and this procedure was replicated three times. We examined the integrated zooplankton community and abundance throughout the entire water column by



**Fig. 1.** Map of Illinois and the Illinois River, USA illustrating the six reaches sampled for zooplankton during 1994–2000 and 2009–2011. White dots within reaches denote zooplankton sampling locations.



**Fig. 2.** Mean ( $\pm$ S.E.) pulsed-DC electrofishing relative abundances (catch-per-unit-effort, CPUE, no./h) of silver carp, *Hypophthalmichthys molitrix*, collected in six reaches of the Illinois River by the Long-term Illinois, Mississippi, Ohio, and Wabash River Fish Population Monitoring Program in 2010.

attaching a weight to a hose and lifting that hose from the bottom to the surface of the water while pumping. Zooplankton samples were preserved in a sugar-buffered formalin solution and transported to the Illinois River Biological Station for analysis.

Macrozooplankters (55  $\mu\text{m}$  filter) were counted and identified as rotifers to genus, cladocerans to genus, and copepods to family (Appendix 1). An estimate of the number of zooplankton in each sample was determined by dividing the sample concentrate volume, by the volume of subsamples required to reach 100 zooplankton, and multiplied by the number of zooplankton counted in the subsample(s). This number was then divided by the volume filtered to get an estimate of the number of zooplankton in 1 L of river water for each sample.

We used t-tests to test for differences in the mean abundance of total zooplankton, rotifers, cladocerans, and copepods between pre- and post-bighead and silver carp establishment periods. We used the null hypothesis of no difference in the mean abundance between pre- and post-bighead and silver carp establishment time periods at the  $\alpha = 0.05$  level using four pair-wise comparisons.

#### *Zooplankton abundance and biomass between lower and upper reaches*

We also assessed zooplankton community composition and abundance across six reaches of the Illinois River that varied in bighead and silver carp relative abundances during 2009–2011. From downstream to upstream in the Illinois River, we sampled the Alton, La Grange, Peoria, Starved Rock, Marseilles, and Dresden reaches (Fig. 1). In 2009 and 2010, a single, fixed, main channel site was sampled in each reach. Sampling sites included Florence (Alton reach, river km (rkm) 89), Havana (La Grange reach, rkm 193), Chillicothe (Peoria reach, rkm 290), Ottawa (Starved Rock reach, rkm 386), Morris (Marseilles reach, rkm 424), and Channahon (Dresden reach, rkm 448). In 2011, we expanded the spatial extent of zooplankton sampling within the Alton, La Grange, and Peoria reaches. In addition to the sites sampled in 2009–2010, we added: Grafton, Hardin, and Merodosia (Alton reach, rkm's 0, 35, 114); Lily Lake (backwater lake), Frederick, Bath Chute (side channel), Matanzas Lake (backwater lake), and the Peoria Lock and Dam (La Grange Reach, rkm's 134, 157, 177, 192, 252); and Upper Peoria Lake, Henry, and Hennepin (Peoria reach, rkm's 278, 315, 334). All zooplankton collections were conducted monthly during May–November in each year. Macrozooplankton (55  $\mu\text{m}$  filter) sampling protocols were identical to those described above. In 2009 and 2010, we also pumped 3.6 L of surface water (1 m depth) through a 20  $\mu\text{m}$  filter and only collected one sample at each site to assess the microzooplankton community (Chick et al., 2010). In 2011, a single integrated water column assessment of the microzooplankton community was collected by pumping 10 L of water through a 20  $\mu\text{m}$  filter at each site. Zooplankton samples were preserved in a sugar-buffered formalin solution and transported to the Illinois River Biological Station for analysis.

We analyzed the macrozooplankton (55  $\mu\text{m}$  filter) samples as described above. The microzooplankton community was assessed using a Sedgewick Rafter counting cell, which held 1 mL of the sample. For the microzooplankton, we used the volume of subsamples required to reach a count of 400 zooplankton. This number was then divided by the volume filtered to get an estimate of the number of zooplankton in 1 L of river water for each sample. In 2011, we also estimated the zooplankton biomass of each sample using carapace length–biomass relationships developed by the United States Environmental Protection Agency (2003) and Dumont et al. (1975).

We compared zooplankton community composition (rotifers, cladocerans, and copepods) among the six reaches of the Illinois River by dividing the abundance of each zooplankton taxon by the total zooplankton abundance in each reach during 2009–2011. We used t-tests to test for differences in the mean abundance and biomass of total zooplankton, rotifers, cladocerans, and copepods collected with the 55  $\mu\text{m}$  filter between the four lower and two upper river reaches during 2009–2011. Similarly, t-tests were used to test for

differences in the mean abundance and biomass of total zooplankton and rotifers collected with the 20  $\mu\text{m}$  filter between the four lower and two upper river reaches during 2009–2011. Cladocerans and copepods were excluded from the 20  $\mu\text{m}$  statistical tests because this gear samples macrozooplankton poorly (Chick et al., 2010). Tests for differences in mean abundances of zooplankton between the lower and upper Illinois River included all data from 2009 to 2011. Tests for differences in biomass only used data from 2011 because this was the first sampling period where biomass was quantified. We used the null hypothesis of no difference in the mean abundance or biomass between the lower four and upper two reaches of the Illinois River at the  $\alpha = 0.05$  level. Due to the number of pair-wise comparisons in our lower versus upper river statistical analyses ( $n = 12$ ), we applied a Bonferroni correction ( $\alpha = 0.05/12 = 0.004$ ) to reduce the probability of committing Type I errors (Rice, 1989).

## Results

### *Pre- and post-bighead and silver carp establishment*

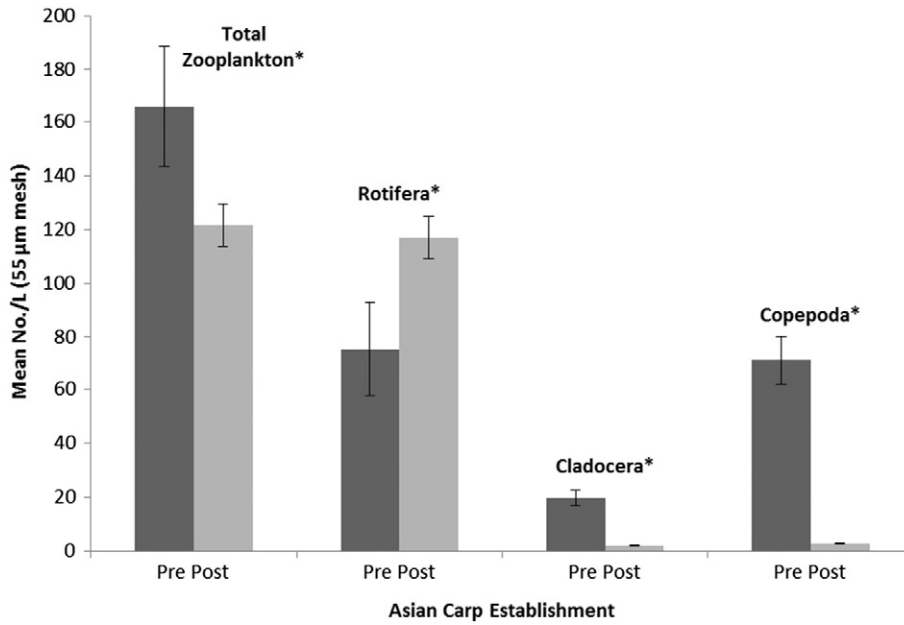
Mean total zooplankton, cladoceran, and copepod abundances (55  $\mu\text{m}$  filter) decreased significantly between pre- and post-bighead and silver carp establishment time periods in the La Grange reach, Illinois River (Fig. 3). Mean rotifer abundance (55  $\mu\text{m}$  filter) increased significantly among time periods (Fig. 3). Mean total zooplankton abundance decreased from 166.1 to 121.7/L before and after bighead and silver carp establishment, respectively ( $N = 257$ ,  $T_{255} = 2.17$ ,  $P = 0.03$ ). Between time periods, the mean rotifer abundance increased from 75.2 to 117.0/L ( $N = 257$ ,  $T_{255} = 2.16$ ,  $P = 0.03$ ). Mean cladoceran and copepod abundances declined significantly from 19.7 to 2.0 and from 71.2 to 2.7/L, respectively prior to and after bighead and silver carp establishment in the La Grange reach, Illinois River (cladocerans,  $N = 257$ ,  $T_{255} = 13.15$ ,  $P < 0.001$ ; copepods,  $N = 257$ ,  $T_{255} = 16.52$ ,  $P < 0.001$ ).

### *Zooplankton community composition between lower and upper reaches*

Zooplankton community composition (55  $\mu\text{m}$  filter) in the lower four reaches of the Illinois River was dominated by rotifers; greater proportions of cladocerans and copepods relative to rotifers were observed in the upper two reaches in 2009–2011. In the lower four reaches, rotifers comprised 94–98% of the zooplankton community compared to only 2–6% cladocerans and copepods. In the upper two reaches, cladocerans and copepods were 12–31% and rotifers 69–88% of the total zooplankton community. Percentage of community composition for rotifers, cladocerans, and copepods by river reach were: Alton reach (95.1% rotifers, 2.7% cladocerans, 2.2% copepods); La Grange reach (98.2, 1.7, 0.1), Peoria reach (97.4, 0.7, 1.9), Starved Rock reach (94.4, 2.1, 3.5), Marseilles reach (87.5, 6.1, 6.4), and Dresden reach (68.4, 11.3, 20.3).

### *Zooplankton abundances between lower and upper reaches*

Mean abundances (55  $\mu\text{m}$  filter) of total zooplankton and rotifers were significantly lower in the upper compared to the lower reaches. Mean cladoceran and copepod abundances were significantly greater in the upper reaches compared to the lower reaches in 2009–2011 (Fig. 4). Mean total zooplankton abundance was nearly threefold less in the upper reaches compared to the lower reaches (lower = 112.5/L, upper = 37.8/L;  $N = 606$ ,  $T_{604} = 6.6$ ,  $P < 0.001$ ). Mean rotifer abundances in the lower and upper reaches were 108.0 and 29.4/L, respectively ( $N = 606$ ,  $T_{604} = 7.0$ ,  $P < 0.001$ ). Mean cladoceran abundances in the upper reaches (3.3/L) were significantly greater than in the lower reaches (1.9/L) ( $N = 601$ ,  $T_{599} = 4.1$ ,  $P < 0.001$ ). Mean copepod abundance in the upper reaches (5.0/L) was double that of the lower reaches (2.5/L) ( $N = 603$ ,  $T_{601} = 6.2$ ,  $P < 0.001$ ).

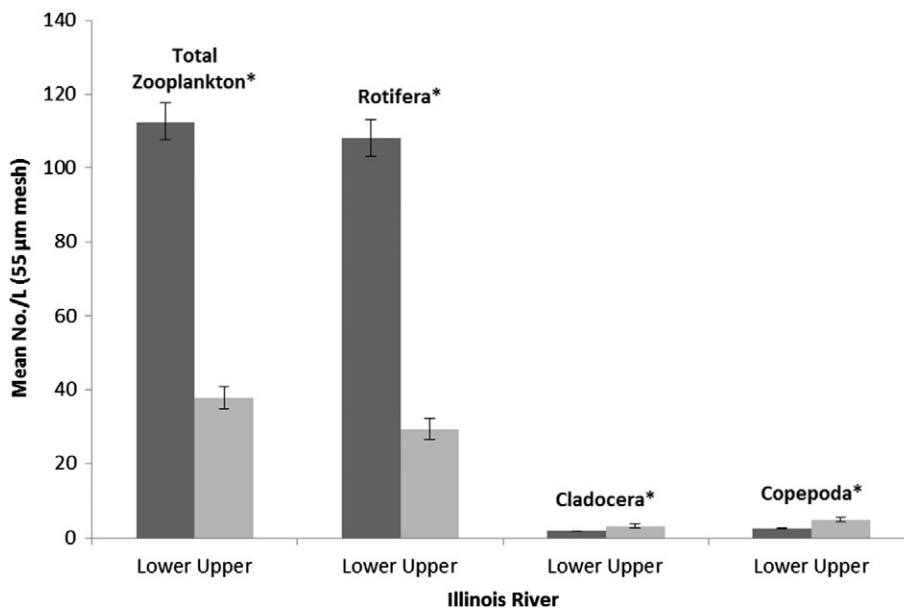


**Fig. 3.** Mean ( $\pm$  S.E.) abundance (no./L) of total zooplankton, rotifers, cladocerans, and copepods collected with a 55  $\mu$ m filter in the La Grange reach of the Illinois River prior to (pre-, 1994–2000) and after (post-, 2009–2011) the establishment of invasive bighead, *Hypophthalmichthys nobilis*, and silver carp, *Hypophthalmichthys molitrix*. Asterisks denote statistically significant differences between time periods ( $\alpha = 0.05$ ).

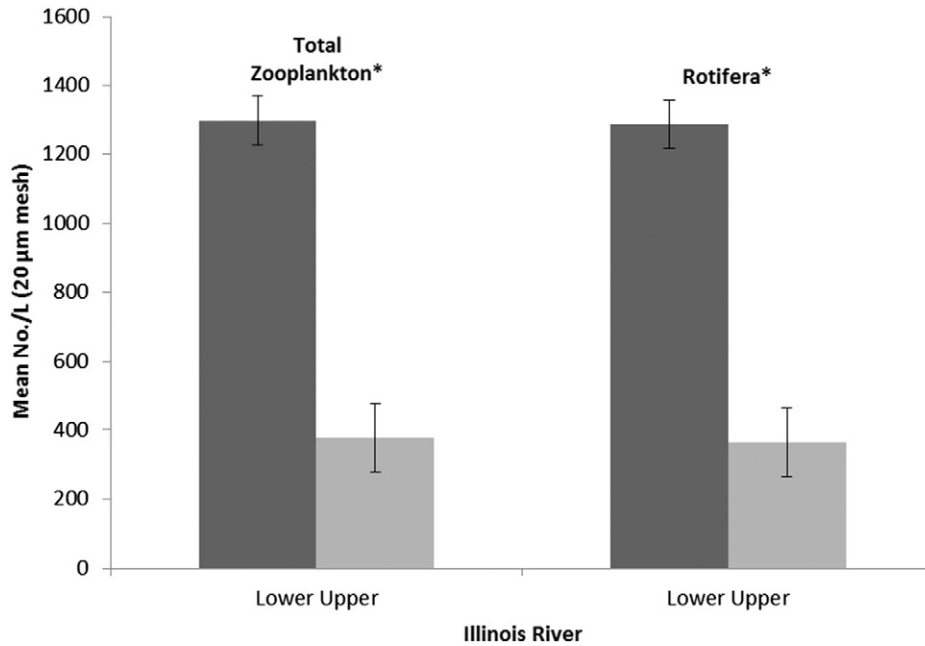
Mean abundances (20  $\mu$ m filter) of total zooplankton and rotifers were significantly lower in the upper reaches compared to the lower reaches in 2009–2011 (Fig. 5). Mean abundance of total zooplankton between the lower and upper reaches was 1298.0 and 376.8/L, respectively (N = 198,  $T_{196} = 5.0$ ,  $P < 0.001$ ). Mean rotifer abundance was significantly greater in the lower reaches (1288.0/L) compared to the upper reaches (364.9/L) (N = 198,  $T_{196} = 5.0$ ,  $P < 0.001$ ).

*Zooplankton biomass between lower and upper reaches*

Mean biomass ( $\mu$ g/L, 55  $\mu$ m filter) of total zooplankton and rotifers were significantly lower in the upper reaches compared to the lower reaches, while copepod biomass showed a significant reciprocal relationship in 2011 (Fig. 6). Mean cladoceran biomass did not differ between the lower and upper reaches ( $P > 0.05$ ). Mean biomass of total



**Fig. 4.** Mean ( $\pm$  S.E.) abundance (no./L) of total zooplankton, rotifers, cladocerans, and copepods collected with a 55  $\mu$ m filter in the Alton, La Grange, Peoria, and Starved Rock reaches (Lower) versus the Marseilles and Dresden reaches (Upper) of the Illinois River in 2009–2011. The lower and upper Illinois River groups were delineated based upon relative abundances of silver carp, *Hypophthalmichthys molitrix* (Fig. 2). Asterisks denote statistically significant differences between the lower and upper Illinois River ( $\alpha = 0.004$ ).



**Fig. 5.** Mean ( $\pm$ S.E.) abundance (no./L) of total zooplankton and rotifers collected with a 20  $\mu$ m filter in the Alton, La Grange, Peoria, and Starved Rock reaches (Lower) versus the Marseilles and Dresden reaches (Upper) of the Illinois River in 2009–2011. The lower and upper Illinois River groups were delineated based upon relative abundances of silver carp, *Hypophthalmichthys molitrix* (Fig. 2). Asterisks denote statistically significant differences between the lower and upper Illinois River ( $\alpha = 0.004$ ). Mean abundance of cladocerans and copepods from 20  $\mu$ m mesh net sampling was excluded based upon the recommendation of Chick et al. (2010).

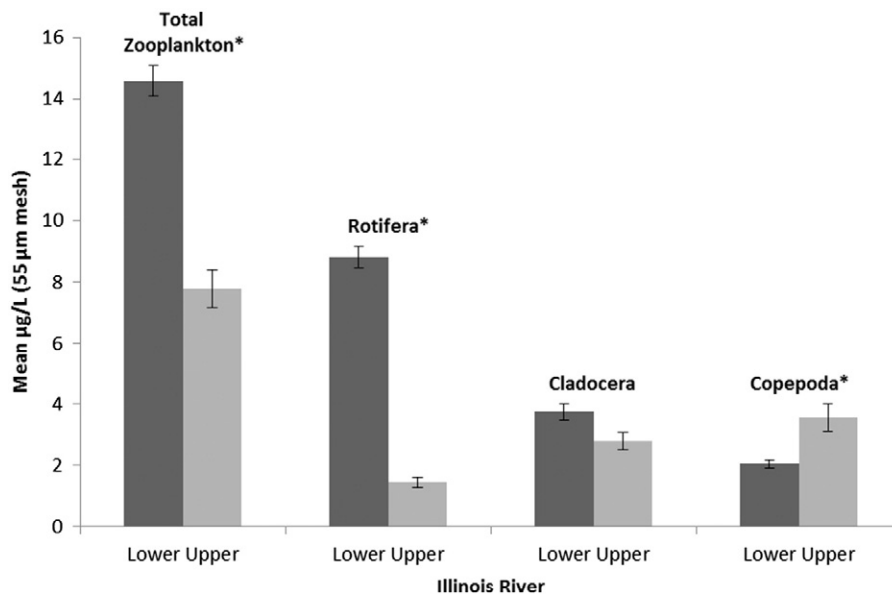
zooplankton in the upper reaches (7.8  $\mu$ g/L) was about half that of the lower reaches (14.6  $\mu$ g/L) ( $N = 498$ ,  $T_{496} = 5.25$ ,  $P < 0.001$ ). Mean rotifer biomass in the upper reaches (1.5  $\mu$ g/L) was significantly lower than that observed in the lower reaches (8.8  $\mu$ g/L) ( $N = 498$ ,  $T_{496} = 8.4$ ,  $P < 0.001$ ). Mean copepod biomass in the upper and lower reaches was 3.6 and 2.0  $\mu$ g/L, respectively ( $N = 498$ ,  $T_{496} = 4.2$ ,  $P < 0.001$ ).

Mean biomass ( $\mu$ g/L, 20  $\mu$ m filter) of total zooplankton and rotifers were significantly lower in the upper compared to the lower reaches in 2011 (Fig. 7). Mean total zooplankton biomass was 65.5  $\mu$ g/L in the

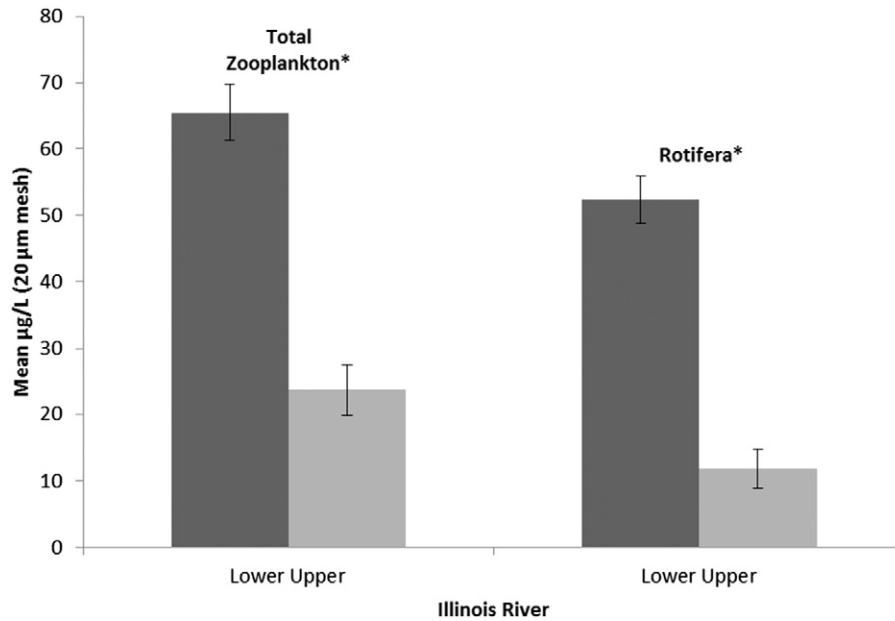
lower four reaches of the Illinois River and 23.7  $\mu$ g/L in the upper two reaches ( $N = 177$ ,  $T_{175} = 3.55$ ,  $P < 0.001$ ). Mean biomass of rotifers in the upper reaches (11.8  $\mu$ g/L) was significantly lower than in the lower reaches (52.3  $\mu$ g/L) ( $N = 177$ ,  $T_{175} = 4.2$ ,  $P < 0.001$ ).

## Discussion

Samples collected before and after bighead and silver carp establishment afforded us a unique opportunity to test for lower trophic level



**Fig. 6.** Mean ( $\pm$ S.E.) biomass ( $\mu$ g/L) of total zooplankton, rotifers, cladocerans, and copepods collected with a 55  $\mu$ m filter in the Alton, La Grange, Peoria, and Starved Rock reaches (Lower) versus the Marseilles and Dresden reaches (Upper) of the Illinois River in 2011. The lower and upper Illinois River groups were delineated based upon relative abundances of silver carp, *Hypophthalmichthys molitrix* (Fig. 2). Asterisks denote statistically significant differences between the lower and upper Illinois River ( $\alpha = 0.004$ ).



**Fig. 7.** Mean ( $\pm$  S.E.) biomass ( $\mu\text{g/L}$ ) of total zooplankton and rotifers collected with a 20  $\mu\text{m}$  filter in the Alton, La Grange, Peoria, and Starved Rock reaches (Lower) versus the Marseilles and Dresden reaches (Upper) of the Illinois River in 2011. The lower and upper Illinois River groups were delineated based upon relative abundances of silver carp, *Hypophthalmichthys molitrix* (Fig. 2). Asterisks denote statistically significant differences between the lower and upper Illinois River ( $\alpha = 0.004$ ). Mean biomass of cladocerans and copepods from 20  $\mu\text{m}$  mesh net sampling was excluded based upon the recommendation of Chick et al. (2010).

effects of these invasive, planktivorous fishes on zooplankton community composition, abundance, and biomass in one reach of a large, dynamic river. The current relative abundance gradient of bighead and silver carp within the Illinois River also allowed us to test for differences in the zooplankton community among reaches post-establishment. We provide multiple lines of evidence to suggest that these invasive fishes are associated with changes in the zooplankton community of the Illinois River. These changes may have negative implications for invaded and yet to be invaded ecosystems, including the Laurentian Great Lakes. To our knowledge, this study is the first to document broad-scale changes in a zooplankton community associated with the invasion of bighead and silver carp in a large river ecosystem.

#### Pre- and post-bighead and silver carp establishment

In the La Grange reach, Illinois River, the establishment of bighead and silver carp was associated with significantly lower mean abundances of total zooplankton, cladocerans, and copepods. The mean abundance of rotifers increased significantly – failing to support our hypothesis. Because bighead and silver carp population growth in the La Grange reach has been exponential and these species are planktivorous, our results suggest that high and taxa-specific consumption of zooplankton is a plausible mechanism explaining our observed patterns (Irons et al., 2007; Sass et al., 2010; Williamson and Garvey, 2005). Our results also suggest that the establishment of these invasive fishes may create a positive feedback loop favoring rotifers over cladocerans and copepods. Rotifers are a primary prey item for bighead and silver carp, but are generally not favored or able to be filtered by many other native facultative or obligate planktivorous fishes besides gizzard shad, *Dorosoma cepedianum*, and bigmouth buffalo, *Ictiobus cyprinellus* (Sampson et al., 2009; Williamson and Garvey, 2005).

Bighead carp are primarily zooplanktivorous, but may switch to phytoplankton, algae, and detritus if zooplankton is limited (Burke et al., 1986; Cremer and Smitherman, 1980; Dong and Li, 1994; Lazareva et al., 1977). Bighead carp have been observed to consume prey items

as small as 50  $\mu\text{m}$  and preferentially select for larger-bodied zooplankton, such as cladocerans and copepods (Borutskiy, 1973; Cremer and Smitherman, 1980; Nikol'skiy and Aliyev, 1974; Opuszynski and Shireman, 1991; Spataru et al., 1983). Silver carp are typically phytoplanktivorous and can filter particles as small as 3  $\mu\text{m}$  (Calkins et al., 2012; De-Shang and Shuang-Lin, 1996; Ghosh et al., 1973; Williamson and Garvey, 2005). Silver carp undergo an ontogenetic diet shift from preference of zooplankton to phytoplankton, but may switch back to zooplankton when phytoplankton is limited (Burke et al., 1986; Opuszynski, 1979; Spataru and Gophen, 1985). Our results suggest that larger-bodied zooplankton were abundant in the La Grange reach, Illinois River prior to the establishment of bighead and silver carp. After their establishment and with the current high densities of these invasive fishes within this reach, our results suggest that selective foraging by bighead and silver carp has likely reduced cladoceran and copepod abundances, while rotifer abundances have increased.

Bighead and silver carp have reduced cladoceran and copepod abundances in lentic systems (Fukushima et al., 1999; Shao et al., 2001; Stone et al., 2000; Yang et al., 1999). Rotifer abundances have also declined in the presence of these invasive fishes (Fukushima et al., 1999; Lieberman, 1996). Rotifers dominated the main channel zooplankton community of the lowermost portion of Illinois River, which may have been a consequence of the presence of bighead and silver carp, but those previous studies did not specifically test for their effects (Chick and Pegg, 2001; Wahl et al., 2008). Our results are consistent with previously observed effects of bighead and silver carp on larger-bodied zooplankton, but not so for rotifers. Our observations suggest that these invasive fishes have had a positive influence on rotifer abundances, which contrasts patterns observed in lentic systems, but potentially supports the findings of Wahl et al. (2008). However, the microzooplankton communities could have been inadequately sampled in these previous studies (Chick et al., 2010). Although rotifers have often dominated bighead and silver carp diets (Sampson et al., 2009; Williamson and Garvey, 2005), the life histories of rotifers appear to make them resilient to high predation pressures from these invasive species (Stemberger and Gilbert, 1985).

### Zooplankton community composition between lower and upper reaches

During 2009–2011, rotifer abundances were positively associated with bighead and silver carp relative abundances among the six reaches of the Illinois River sampled. Cladoceran and copepod abundances were negatively associated with bighead and silver carp relative abundances. In the lower four reaches of the Illinois River, where these invasive fishes are most abundant, rotifers dominated zooplankton community composition. Bighead and silver carp are present within the Marseilles and Dresden reaches; however, their abundances have often been below detection limits using traditional fisheries gears (e.g., electrofishing, trammel netting). Rotifers still dominated in the Marseilles and Dresden reaches, but cladocerans and copepods comprised a greater proportion of the community compared to the lower four reaches of the Illinois River. Similar to previous studies and our pre- versus post-bighead and silver carp establishment comparison, high densities of these invasives tend to decrease the abundance of cladocerans and copepods. At lower bighead and silver carp densities (i.e., Marseilles and Dresden reaches), predation pressure appears weaker and may allow for the persistence of greater cladoceran and copepod abundances than at high densities of these invasive fishes. Consumption of cladocerans by bighead and silver carp may also release rotifers from competition with these larger-bodied zooplankters for food particles and decrease mortality rates on rotifers from incidental ingestion (Gilbert, 1988). Still, rotifers dominated zooplankton community composition in the six reaches of the Illinois River, which may suggest that the food webs of lentic systems respond differently to the presence and abundance of bighead and silver carp (Fukushima et al., 1999; Lieberman, 1996).

### Zooplankton abundances between lower and upper reaches

We observed significantly lower mean abundances of total zooplankton and rotifers in the upper river compared to the lower river using 55 and 20  $\mu\text{m}$  filters during 2009–2011. Significantly greater mean abundances of cladocerans and copepods were observed in the upper river, where bighead and silver carp are less abundant, using only the 55  $\mu\text{m}$  filter. We did not test for differences in cladoceran and copepod abundances between the upper and lower river using the 20  $\mu\text{m}$  filter because this mesh size does not sample macrozooplankton assemblages adequately (Chick et al., 2010). Our results suggest that rotifer abundances were positively associated with bighead and silver carp abundances in the Illinois River. Cladoceran and copepod abundances were negatively associated with the abundance of these invasive fishes.

Our results suggest that size-selective predation pressure by bighead and silver carp in the lower four reaches of the Illinois River may have caused the decline in cladoceran and copepod abundances. Natural recruitment of bighead and silver carp in the Starved Rock, Marseilles, and Dresden reaches has not been observed. Therefore, zooplanktivory by juvenile silver carp in the lower three reaches of the river may also contribute to the low abundances of cladocerans and copepods observed (Burke et al., 1986; Opuszynski, 1979; Spataru and Gophen, 1985). Native fishes also rely upon larger-bodied zooplankton at various life stages, which may also reduce cladoceran and copepod abundances.

Previous studies have suggested that rotifer abundances were reduced in the presence of these invasive fishes (but see Wahl et al., 2008). Lieberman (1996) observed a >80% reduction in rotifers in a small pond after bighead and silver carp were introduced. In an experiment by Fukushima et al. (1999), rotifers were abundant in fishless enclosures, but not in enclosures containing silver carp. Gut contents of bighead and silver carp are often dominated by rotifers, which would suggest that high densities of these invasive species may reduce rotifer abundances (Sampson et al., 2009; Williamson and Garvey, 2005). Rotifers may also be a dominant prey item for larval silver carp

(Kouril et al., 1982; Krykhtin and Gorbach, 1981; Marciak and Bogdan, 1979). Nevertheless, rotifer abundances may be more easily depleted by bighead and silver carp in lentic systems where rotifer food resources may become limited, which is not often the case in lotic systems where food resources are continually supplied.

Our findings are generally inconsistent with previous studies describing the relationship between bighead/silver carp and rotifers (but see Wahl et al., 2008). Possible mechanisms leading to differences in our observations with previous studies include lotic versus lentic aquatic ecosystems, main channel sampling of the zooplankton community, the life history of rotifers, and predatory release of rotifers with low abundances of cladocerans and copepods (Stemberger and Gilbert, 1985; Gilbert, 1988). Most studies testing for the effects of bighead and silver carp on zooplankton community composition have been conducted in lentic systems. It is plausible that the influence of bighead and silver carp on rotifers in large, dynamic rivers is different. Our finding is supported by Wahl et al. (2008), but bighead and silver carp effects were not directly tested for in that study. We conducted the majority of our zooplankton sampling at main channel sites; however, a side channel and two backwater lakes were also sampled in 2011. Bighead and silver carp are known to avoid main channel habitats within rivers (Calkins et al., 2012; DeGrandchamp et al., 2008). It is possible that rotifer abundances were locally elevated within this habitat of the river compared to others. Given the dynamic hydrology, flow regime, the level of mixing that occurs within the water column of the Illinois River, and the inclusion of backwater lakes and a side channel to our sampling protocols in 2011, it is not likely that our main channel sampling protocols influenced our observations. Rotifer generation times are much more rapid than those of cladocerans and copepods, thus making rotifers potentially more resilient to high predation pressures from bighead and silver carp (Stemberger and Gilbert, 1985; Pennak, 1989). Some predaceous cladocerans and copepods feed upon rotifers, which may also act to increase rotifer abundances in the presence of bighead and silver carp (Gilbert, 1988; Pennak, 1989).

### Zooplankton biomass between lower and upper reaches

The mean biomass of rotifers was significantly lower in the upper two reaches of the Illinois River using a 55 and 20  $\mu\text{m}$  filter. Our observation provides further evidence to suggest that rotifers comprise the majority of zooplankton individuals and biomass in the presence of robust bighead and silver carp populations. Copepod biomass was significantly greater in the upper two reaches of the Illinois River where these invasive fishes are less abundant. We found no significant difference in the mean cladoceran biomass between the upper and lower river.

Few studies have tested for the influence of bighead/silver carp on zooplankton biomass. Lu et al. (2002) found that crustacean zooplankton biomass was negatively correlated with bighead and silver carp biomass. Small crustacean zooplankton were more persistent in the presence of these invasive fishes compared to larger cladocerans and copepods (Lu et al., 2002). Biomass of cladocerans between the lower and upper Illinois River did not differ, which may suggest that smaller-bodied crustaceans were more prevalent in the lower river. Although selective predation pressure on larger-bodied cladocerans and copepods by robust populations of bighead and silver carp provides the most plausible explanation for our observed patterns, other complex and indirect pathways are also possible. For example, silver carp have been observed to consume calanoid copepod nauplii thus limiting adult abundances, change the growth trajectories of zooplankters, and may potentially compete with zooplankton for food resources (Burke et al., 1986; Lu et al., 2002; Milstein et al., 1985; Radke and Kahl, 2002).

### Conclusion

Our results suggest that establishment and population growth of invasive bighead and silver carp is associated with changes in



zooplankton community composition and biomass across a pre- versus post-establishment comparison and a gradient of abundances in the Illinois River. Similar to previous studies, bighead and silver carp have the ability to significantly reduce cladoceran and copepod abundances and biomass. Unexpectedly and generally contrary to previous lentic studies, our results suggest that high densities of these invasive fishes are associated with increased abundances and biomass of rotifers. Because rotifers are a dominant prey item in bighead and silver carp diets, (Sampson et al., 2009; Williamson and Garvey, 2005), strong potential for competition exists between these invasives and native obligate and/or facultative planktivorous fishes. Sampson et al. (2009) found high dietary overlap between bighead and silver carp and native gizzard shad and bigmouth buffalo, but less overlap with paddlefish, *Polyodon spathula*. Irons et al. (2007) reported reduced body condition of gizzard shad and bigmouth buffalo following the establishment of bighead and silver carp in the La Grange reach, Illinois River suggesting potential competition and reduced fitness of these native fishes. Schrank et al. (2003) observed reduced growth of age-0 paddlefish in the presence of bighead carp in experimental ponds suggesting that competition could occur. Native juvenile fish survival may also be reduced over time in the presence of bighead and silver carp. If cladocerans are unavailable at critical life stages, such as during the transition from intrinsic to exogenous sources of food, native juvenile fish mortality rates may increase (Cushing, 1990). Given the current population growth trajectories of bighead and silver carp in the Illinois River, it is plausible that macrozooplankton may become even more limited over time resulting in negative effects on native fishes.

Our results suggest that the establishment of invasive bighead and silver carp is correlated with an alteration of the zooplankton community to potentially benefit themselves. Increases in rotifer abundances directly benefit bighead and silver carp because their capacities to filter very small particles far exceed those of many native fishes and rotifers are a dominant prey item in their diets (Sampson et al., 2009; Williamson and Garvey, 2005). Bighead and silver carp present an imminent threat for colonizing the Laurentian Great Lakes through the CSSC (Jerde et al., 2011). Cooke and Hill (2010) postulated that zooplankton were insufficient in most regions of the Laurentian Great Lakes to support bighead and silver carp. We argue that the conclusions of Cooke and Hill (2010) may be unfounded and not precautionary in regard to the colonization potential of bighead and silver carp in the Laurentian Great Lakes. Cooke and Hill (2010) did not consider rotifer abundances in their bioenergetics modeling exercises, nor the potential for bighead and silver carp to alter zooplankton community composition, as we have shown here for a large, dynamic river. Because bighead and silver carp may have the ability to alter food webs to potentially benefit their range expansion and fitness, we recommend that additional measures to reduce the risk of invasion to the Laurentian Great Lakes be implemented immediately and with the greatest certainty to prevent introductions. Ecological separation of the Lake Michigan and Upper Mississippi River basins remains the most reliable management action to reduce the probability of bighead and silver carp invading the Laurentian Great Lakes (Rasmussen et al., 2011). Such separation would restore these basins to their natural watersheds and permanently prevent inter-basin invasive species transfers through this corridor.

## Acknowledgments

We thank all of the current and former employees of the Illinois River Biological Station that aided in the field collections of zooplankton. Kenny Lookingbill, James Stoeckel, Lori Soeken-Gittinger, John Chick, and Steve Tyszko deserve special recognition for the technical, field, and laboratory support they provided for this project. Funding for this project was provided by the National Great Rivers Research and Education Center to GGS and ACE and by Cooperative Agreement No. 30181AJ071 between the U.S. Fish and Wildlife Service and the Illinois Department of Natural Resources to GGS and JME.

## Appendix 1

Taxonomic information for Rotifera, Cladocera, and Copepoda collected from the Illinois River, Illinois, USA pre- (1994–2000) (Pre-) and post-bighead, *Hypophthalmichthys nobilis*, and silver carp, *Hypophthalmichthys molitrix*, establishment (2009–2011) (Post-) in the La Grange reach and during 2009–2011 in the Alton, Peoria, Starved Rock, Marseilles, and Dresden reaches. X's denote presence.

	La Pre-	Grange Post-	Alton	Peoria	Starved Rock	Marseilles	Dresden
<b>Rotifera</b>							
<i>Anuraeopsis</i>		X	X	X	X	X	X
<i>Ascomorpha</i>	X	X	X	X	X	X	X
<i>Asplanchna</i>	X	X	X	X	X	X	X
<i>Asplanchnopus</i>					X	X	X
<i>Belloid</i>	X	X	X	X	X	X	X
<i>Birgea</i>		X					
<i>Brachionus</i>	X	X	X	X	X	X	X
<i>Cephalodella</i>	X	X	X	X	X	X	X
<i>Chromogaster</i>		X					
<i>Collotheca</i>	X	X	X	X	X		
<i>Colurella</i>	X	X	X	X	X	X	X
<i>Conchilus</i>	X	X	X	X	X	X	X
<i>Conochiloides</i>			X	X	X	X	X
<i>Dicranophorus</i>	X	X	X	X	X	X	X
<i>Encentrum</i>		X	X	X	X	X	X
<i>Eothinia</i>		X					
<i>Epiphanes</i>		X	X	X	X	X	X
<i>Euchlanis</i>		X	X	X	X	X	X
<i>Filinia</i>	X	X	X	X	X	X	
<i>Gastropus</i>	X	X	X	X	X	X	X
<i>Habrotrocha</i>		X					
<i>Heneceros</i>			X				
<i>Hexartha</i>		X	X	X	X	X	X
<i>Kellicottias</i>	X	X	X	X	X	X	X
<i>Keratella</i>	X	X	X	X	X	X	X
<i>Lecane</i>	X	X	X	X	X	X	X
<i>Lepadella</i>	X	X	X	X	X	X	X
<i>Monostyla</i>		X	X	X	X	X	X
<i>Microdon</i>		X					
<i>Mytilimia</i>	X	X	X	X	X	X	X
<i>Notholoca</i>	X	X	X	X	X	X	X
<i>Playtias</i>	X	X	X	X	X	X	X
<i>Ploesoma</i>	X	X	X	X	X	X	X
<i>Polyartha</i>	X	X	X	X	X	X	X
<i>Rotaria</i>	X	X	X				
<i>Squatinella</i>		X					
<i>Synchaeta</i>	X	X	X	X	X	X	X
<i>Testudinella</i>	X	X	X	X	X	X	X
<i>Trichocerca</i>	X	X	X	X	X	X	X
<i>Trichotria</i>	X	X	X	X	X	X	X
<b>Cladocera</b>							
<i>Acroperus</i>				X	X		X
<i>Alona</i>		X	X	X	X	X	X
<i>Allonella</i>			X		X	X	X
<i>Alonopsis</i>		X		X			
<i>Anchistorpus</i>			X				
<i>Bosmina</i>	X	X	X	X	X	X	X
<i>Camptocerus</i>					X	X	
<i>Ceriodaphnia</i>	X	X	X	X			X
<i>Chydorus</i>	X	X	X	X	X	X	X
<i>D. ambigua</i>	X						X
<i>D. dubia</i>	X					X	X
<i>D. lumholtzi</i>	X					X	X
<i>D. mendotae</i>	X						
<i>D. parvula</i>	X	X		X			
<i>D. pulex</i>	X	X		X	X	X	X
<i>D. retrocurva</i>							X
<i>D. spp.</i>	X	X	X	X	X	X	X
<i>Diaphanosoma</i>	X	X	X	X	X	X	X
<i>Euryceras</i>				X			X
<i>Illiocryptus</i>	X	X		X	X	X	X
<i>Leptodora</i>	X						
<i>Macrothrix</i>		X		X			
<i>Megafenestra</i>							X

(continued on next page)

## Appendix 1 (continued)

	La Pre-	Grange Post-	Alton	Peoria	Starved Rock	Marseilles	Dresden
Cladocera							
<i>Moina</i>	X	X	X	X	X	X	X
<i>Moinodaphnia</i>						X	
<i>Scapholeberis</i>				X			
<i>Sida</i>	X	X	X	X	X	X	X
<i>Simocephalus</i>	X	X		X		X	
Copepoda							
Calanoida	X	X	X	X	X	X	X
Cyclopoida	X	X	X	X	X	X	X
Harpacticoida	X	X	X	X	X	X	X
Naplius	X	X	X	X	X	X	X

## References

- Borutskiy, Y.V., 1973. The food of the bighead carp and the silver carp in the natural waters and ponds of the USSR. *Trofologiya vodnykh zhivotnykh* (The trophology of aquatic animals). Nauka Press, Moscow.
- Burke, J.S., Bayne, D.R., Rea, H., 1986. Impact of silver and bighead carps on plankton communities on channel catfish ponds. *Aquaculture* 55, 59–68.
- Calkins, H.A., Tripp, S.J., Garvey, J.E., 2012. Linking silver carp habitat selection to flow and phytoplankton in the Mississippi River. *Biol. Invasions* 14, 949–958.
- Chick, J.H., Pegg, M.A., 2001. Invasive Asian carp in the Mississippi River basin. *Science* 292, 2250–2251.
- Chick, J.H., Levchuk, A.P., Medley, K.A., Havel, J.H., 2010. Underestimation of rotifer abundance a much greater problem than previously appreciated. *Limnol. Oceanogr. Methods* 79–87.
- Cooke, S.L., Hill, W.R., 2010. Can filter-feeding Asian carp invade the Laurentian Great Lakes? A bioenergetics modeling exercise. *Freshw. Biol.* 55, 2138–2152.
- Cremer, M.C., Smitherman, R.O., 1980. Food habits and growth of silver and bighead carp in cages and ponds. *Aquaculture* 20, 57–64.
- Cucherousset, J., Olden, J.D., 2011. Ecological impacts of nonnative freshwater fishes. *Fisheries* 36, 215–230.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Adv. Mar. Biol.* 26, 249–293.
- DeGrandchamp, K.A., Garvey, J.E., Colombo, R.E., 2008. Movement and habitat selection by invasive Asian carps in a large river. *Trans. Am. Fish. Soc.* 137, 45–56.
- De-Shang, L., Shuang-Lin, D., 1996. The structure and function of the filtering apparatus of silver carp and bighead carp. *Acta Zool. Sin.* 42, 10–14.
- Dong, S., Li, D., 1994. Comparative studies of the feeding selectivity of silver carp, *Hypophthalmichthys molitrix*, and bighead carp, *Aristichthys nobilis*. *J. Fish Biol.* 44, 621–626.
- Dumont, H.J., Van de Velde, I., Dumont, S., 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19, 75–97.
- Fukushima, M., Takamura, N., Sun, L., Nakagawa, M., Matsushige, K., Xie, P., 1999. Changes in the plankton community following introduction of filter-feeding planktivorous fish. *Freshw. Biol.* 42, 719–735.
- Ghosh, A., Banenjek, M.K., Nanumantha, L., 1973. Some observations on the cultural prospects of silver carp, *Hypophthalmichthys molitrix* (Valenciennes) in sewage-feed ponds. *J. Inland Fish. Soc. India* 5, 131–133.
- Gilbert, J.J., 1988. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnol. Oceanogr.* 33, 1286–1303.
- Gutreuter, S., Burkhardt, R., Lubinski, K., 1995. Long Term Resource Monitoring Program Procedures: Fish Monitoring. National Biological Service, Environmental Management Technical Center, Onalaska, Wisconsin.
- Hrabik, T.R., Carey, M.P., Webster, M.S., 2001. Interactions between young-of-the-year exotic rainbow smelt and native yellow perch in a northern temperate lake. *Trans. Am. Fish. Soc.* 130, 568–582.
- Irons, K.S., McClelland, M.A., Pegg, M.A., 2006. Expansion of round goby in the Illinois waterway. *Am. Midl. Nat.* 156, 198–200.
- Irons, K.S., Sass, G.G., McClelland, M.A., Stafford, J.D., 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, U.S.A.: is this evidence for competition and reduced fitness? *J. Fish Biol.* 71, 258–273.
- Irons, K.S., Sass, G.G., McClelland, M.A., O'Hara, T.M., 2011. Bigheaded carp invasion of the La Grange Reach of the Illinois River: insights from the Long Term Resource Monitoring Program. In: Chapman, D.C., Hoff, M.H. (Eds.), Asian carps in North America American Fisheries Society Symposium 74. American Fisheries Society, Bethesda, Maryland, pp. 31–50.
- Jerde, C.L., Mahon, A.R., Chadderton, W.L., Lodge, D.M., 2011. "Sight-unseen" detection of rare aquatic species using environmental DNA. *Conserv. Lett.* 4, 150–157.
- Kelly, A.M., Engle, C.R., Armstrong, M.L., Freeze, M., Mitchell, A.J., 2011. History of introductions and governmental involvement in promoting the use of grass, silver, and bighead carps. In: Chapman, D.C., Hoff, M.H. (Eds.), Asian carps in North America American Fisheries Society Symposium 74. American Fisheries Society, Bethesda, Maryland, pp. 163–174.
- Kolar, C.S., Lodge, D.M., 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* 298, 1233–1236.
- Kolar, C.S., Chapman, D.C., Courtenay Jr., W.R., Housel, C.M., Williams, J.D., Jennings, D.P., 2007. Bigheaded carps: a biological synopsis and environmental risk assessment. American Fisheries Society Special Publication 33. American Fisheries Society, Bethesda, Maryland.
- Kouril, J., Skacelova, O., Hamackova, J., 1982. Feeding of silver carp fry (*Hypophthalmichthys molitrix*) with plankton and dry feeds Ewos Larvstart C 10. Proceedings of the Second International Symposium on Herbivorous Fish, Yugoslavia.
- Krueger, D.M., Hrabik, T.R., 2005. Food web alterations that promote native species: the recovery of cisco (*Coregonus artedii*) populations through management of native piscivores. *Can. J. Fish. Aquat. Sci.* 62, 2177–2188.
- Krykhtin, M.L., Gorbach, E.L., 1981. Reproductive ecology of the grass carp, *Ctenopharyngodon idella*, and the silver carp, *Hypophthalmichthys molitrix*, in the Amur Basin. *J. Ichthyol.* 21, 109–123.
- Lazareva, L.P., Omarov, M.O., Lezina, A.N., 1977. Feeding and growth of the bighead, *Aristichthys nobilis*, in the waters of Dagestan. *J. Ichthyol.* 17, 65–71.
- Lieberman, D.M., 1996. Use of silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) for algae control in a small pond: changes in water quality. *J. Freshw. Ecol.* 11, 391–397.
- Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K.R., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T., McMichael, A., 2006. Biological invasions: recommendations for U.S. policy and management. *Ecol. Appl.* 16, 2035–2054.
- Lu, M., Xie, P., Tang, H., Shao, Z., Xie, L., 2002. Experimental study of trophic cascade effect of silver carp (*Hypophthalmichthys molitrix*) in a subtropical lake, Lake Donghu: on plankton community and underlying mechanisms of changes of crustacean community. *Hydrobiologia* 487, 19–31.
- MacIsaac, H.J., 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *Am. Zool.* 36, 287–299.
- Marciak, Z., Bogdan, E., 1979. Food requirements of juvenile stages of grass carp, *Ctenopharyngodon idella* Val., silver carp, *Hypophthalmichthys molitrix* Val., and bullhead carp, *Aristichthys nobilis* Rich. *EMS Spec. Publ.* 4, 139–157.
- McClelland, M.A., Sass, G.G., Cook, T.R., Irons, K.S., Michaels, N.N., O'Hara, T.M., Smith, C.S., 2012. The long-term Illinois River fish population monitoring program. *Fisheries* 37, 340–350.
- Mercado-Silva, N., Sass, G.G., Roth, B.M., Gilbert, S., Vander Zanden, M.J., 2007. Impact of rainbow smelt (*Osmerus mordax*) invasion on walleye (*Sander vitreus*) recruitment in Wisconsin lakes. *Can. J. Fish. Aquat. Sci.* 64, 1543–1550.
- Michaels, N.N., Tyszko, S., McClelland, M.A., Sass, G.G., 2011. The long-term Illinois, Mississippi, Ohio, and Wabash River fish population monitoring program. Project F-101-R-22 Annual Report to the Illinois Department of Natural Resources, Prairie Research Institute Technical Report 23, Illinois Natural History Survey, Champaign, Illinois.
- Milstein, A., Hefner, B., Teltsch, B., 1985. Principal component analysis of interactions between fish species and the ecological conditions in fish ponds. II. Zooplankton. *Aquacult. Fish. Manag.* 16, 319–330.
- Moy, P.B., Polls, I., Dettmers, J.M., 2011. The Chicago Sanitary and Ship Canal aquatic nuisance species dispersal barrier. In: Chapman, D.C., Hoff, M.H. (Eds.), Asian carps in North America American Fisheries Society Symposium 74. American Fisheries Society, Bethesda, Maryland, pp. 121–138.
- Nikol'skiy, G.V., Aliyev, D.D., 1974. The role of far-eastern herbivorous fishes in the ecosystem of natural waters in which they are acclimatized. *J. Ichthyol.* 14, 842–847.
- Olsen, T.M., Lodge, D.M., Capelli, G.M., Houlihan, R.J., 1991. Mechanisms of impact of introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can. J. Fish. Aquat. Sci.* 48, 1853–1861.
- Opuszynski, K., 1979. Silver carp, *Hypophthalmichthys molitrix* (Val.) in carp ponds. 3. Influences on ecosystem. *Ekologia Pol.* 27, 117–133.
- Opuszynski, K., Shireman, J.V., 1991. Food passage time and daily ration of bighead carp, *Aristichthys nobilis*, kept in cages. *Environ. Biol. Fish.* 30, 387–393.
- Pennak, R.W., 1989. Fresh-water Invertebrates of the United States: Protozoa to Mollusca, Third edition. Wiley and Sons, New York.
- Radke, R.J., Kahl, U., 2002. Effects of a filter-feeding fish [silver carp, *Hypophthalmichthys molitrix* (Val.)] on phyto- and zooplankton in a mesotrophic reservoir: results from an enclosure experiment. *Freshw. Biol.* 47, 2337–2344.
- Rasmussen, J.L., Regier, H.A., Sparks, R.E., Taylor, W.W., 2011. Dividing the waters: the case for hydrologic separation of the North American Great Lakes and Mississippi River basins. *J. Great Lakes Res.* 37, 588–592.
- Ricciardi, A., MacIsaac, H.J., 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends Ecol. Evol.* 15, 62–65.
- Rice, W.R., 1989. Analyzing tables of statistical tests. *Evolution* 43, 223–225.
- Roth, B.M., Kitchell, J.F., 2005. The role of size-selective predation in the displacement of *Orconectes* crayfishes following rusty crayfish invasion. *Crustaceana* 78, 297–310.
- Roth, B.M., Hrabik, T.R., Solomon, C.T., Mercado-Silva, N., Kitchell, J.F., 2010. A simulation of food-web interactions leading to rainbow smelt (*Osmerus mordax*) dominance in Sparkling Lake, Wisconsin. *J. Fish Biol.* 77, 1379–1405.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Sampon, S.J., Chick, J.H., Pegg, M.A., 2009. Dietary overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biol. Invasions* 11, 483–496.
- Sass, G.G., Cook, T.R., Irons, K.S., McClelland, M.A., Michaels, N.N., O'Hara, T.M., Stroub, M.R., 2010. A mark-recapture population estimate for invasive silver carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. *Biol. Invasions* 12, 433–436.

- Schrank, S.J., Guy, C.S., Fairchild, J.F., 2003. Competitive interactions between age-0 bighead carp and paddlefish. *Trans. Am. Fish. Soc.* 132, 1222–1228.
- Shao, Z., Xie, P., Zhuge, Y., 2001. Long-term changes of planktonic rotifers in a subtropical Chinese lake dominated by filter-feeding fishes. *Freshw. Biol.* 46, 973.
- Spataru, P., Gophen, M., 1985. Feeding behavior of silver carp, *Hypophthalmichthys molitrix* Val. and its impact on the food web in Lake Kinneret, Israel. *Hydrobiologia* 120, 53–61.
- Spataru, P., Wohlfarth, G.W., Hulata, G., 1983. Studies on the natural food of different fish species in intensively manured polyculture ponds. *Aquaculture* 35, 283–298.
- Stemberger, R.S., Gilbert, J.J., 1985. Body size, food concentration, and population growth in planktonic rotifers. *Ecology* 66, 1151–1159.
- Stone, N., Engle, C., Heikes, D., Freeman, D., 2000. Bighead carp. Southern Regional Aquaculture Center (SRAC), Stoneville, Mississippi, September 2000, Southern Regional Aquaculture Center Publication 438.
- United States Environmental Protection Agency, 2003. Standard Operating Procedure for Zooplankton Analysis. p. LG403.
- Wahl, D.H., Goodrich, J., Nannini, M.A., Dettmers, J.M., Soluk, D.A., 2008. Exploring riverine zooplankton in three habitats of the Illinois River ecosystem: where do they come from? *Limnol. Oceanogr.* 53, 2583–2593.
- Williamson, C.J., Garvey, J.E., 2005. Growth, fecundity, and diets of newly established silver carp in the middle Mississippi River. *Trans. Am. Fish. Soc.* 134, 1423–1430.
- Wilson, K.A., 2002. Impacts of the Invasive Rusty Crayfish (*Orconectes rusticus*) in Northern Wisconsin Lakes (Dissertation) University of Wisconsin-Madison.
- Yang, Y., Huang, X., Liu, J., 1999. Long-term changes in zooplankton and water quality in a shallow, eutrophic Chinese lake densely stocked with fish. *Hydrobiologia* 391, 195–203.