PRIMARY RESEARCH PAPER

Zooplankton community dynamics along the bigheaded carp invasion front in the Upper Mississippi River

Nathan A. Tillotson · Michael J. Weber · Clay L. Pierce

Abstract Invasive Silver *Hypophthalmichthys molitrix* and Bighead Carp *H. nobilis* (collectively bigheaded carp) regularly alter zooplankton communities in lentic systems but dynamics in lotic systems are less understood. Here, we investigated trends in zooplankton communities, densities, and biomass in pools 14–20 of the Upper Mississippi River (UMR) across a gradient of bigheaded carp presence and relative abundance during 2016–2018. We explored the effects of bigheaded carp presence on zooplankton communities using non-metric multidimensional scaling (NMDS) and assessed taxa-specific relationships with bigheaded carp relative abundance using ordinary least-squares regression with an indicator variable for bigheaded carp presence. Zooplankton communities in the UMR were dominated by rotifers and crustacean zooplankton densities were low, making up only 2% of the community density. Zooplankton communities differed where bigheaded carp were present. Density and biomass of cladocerans and copepods were both reduced where bigheaded carp were present but copepods increased with bigheaded carp relative abundance. Ostracod biomass increased in the presence of bigheaded carp whereas rotifers declined with bigheaded carp relative abundance. Low crustacean zooplankton densities in the UMR may limit larval/juvenile fish growth and recruitment regardless of bigheaded carp, but further declines in the crustacean community due to expanding bigheaded carp populations are concerning.

Keywords Zooplankton · Bigheaded carp · Invasive species · Mississippi River

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Introduction

Zooplankton communities are important components of healthy aquatic systems, providing an important link between algal primary production and higher trophic-level consumers. Zooplankton serve as necessary first-food resources for larval fish and continue to be important components of the diet for many juvenile fishes (Siefert, 1972; Pelham et al., 2001; Nunn et al., 2012). Fish recruitment from larvae to juveniles can depend on the availability of appropriately sized zooplankton prey, potentially affecting growth (Bunnell et al., 2003; Dettmers et al., 2003) and year-class strength of some fishes (Hjort, 1914; Welker et al., 1994; Hoxmeier et al., 2004). Zooplankton are also critical for some adult fishes. For instance, American Paddlefish [*Polyodon spathula* (Walbaum, 1792)], Bigmouth Buffalo [*Ictiobus cyprinellus* (Valenciennes, 1844)], and Gizzard Shad [*Dorosoma cepedianum* (Lesueur, 1818)] are important planktivorous

fishes native to North America and exhibit varying degrees of dietary overlap with invasive planktivores (Sampson et al., 2009). Therefore, understanding factors regulating zooplankton communities is important for monitoring native fish populations and maintaining overall ecosystem health.

Expanding ranges of invasive planktivores may disrupt native food webs and reduce zooplankton resources critical for native fishes (Chick et al., 2020). Planktivorous bigheaded carp [Silver Carp *Hypophthalmichthys molitrix* (Valenciennes, 1844) and Bighead Carp *H. nobilis* (Richardson, 1845)] are invasive fishes spreading throughout North American rivers that have the potential to alter zooplankton communities (Domaizon & Dévaux, 1999; Radke & Kahl, 2002; Sass et al., 2014). Bigheaded carp filter water through specialized gill rakers to retain food particles suspended in the water column. Diets of bigheaded carp are frequently comprised of zooplankton, phytoplankton, bacteria, and detritus, but the relative proportion of each of these prey categories can vary (Williamson & Garvey, 2005; Sampson et al., 2009). Furthermore, gill raker morphology differs between Bighead Carp and Silver Carp (Opuszyński, 1981), resulting in a broad range of plankton sizes that are vulnerable to consumption by these species. Silver Carp have fused sponge-like gill rakers, allowing them to consume small prey items like phytoplankton and even particles < 10 μm (Williamson & Garvey, 2005; Görgényi et al., 2016). Bighead Carp have more widely spaced comb-like gill rakers and are primarily zooplanktivorous (Dong & Li, 1994; Kolar et al., 2007) but are capable of producing a mucous that coats their gill rakers, allowing for the consumption of smaller particles like phytoplankton (Jennings, 1988). Despite differences in gill raker morphology, both Silver Carp and Bighead Carp are capable of consuming either phytoplankton or zooplankton depending on their relative availability (Opuszynski et al., 1991; Sampson et al., 2009).

Bigheaded carp can alter the density, biomass, and size structure of zooplankton that can have cascading effects throughout the ecosystem (Radke & Kahl, 2002; DeBoer et al., 2018). Bigheaded carp frequently reduce the density and biomass of large-bodied cladocerans (Domaizon & Dévaux, 1999; Radke & Kahl, 2002; Cooke et al., 2009; Collins & Wahl, 2018); however, the dynamics of copepods, rotifers, and other zooplankton in the presence of bigheaded

carp vary. Cyclopoid and calanoid copepod densities also decline in the presence of bigheaded carp (Sass et al., 2014; DeBoer et al., 2018) but sometimes in differential proportions (Xie & Yang, 2000) and generally to a lesser extent than large-bodied cladocerans (Domaizon & Dévaux, 1999) that can lead to a more copepod-dominated zooplankton community (Cooke et al., 2009). In contrast, rotifer community response to bigheaded carp is more variable (Sass et al., 2014; Collins & Wahl, 2018; Collins et al., 2018) even though rotifers are important dietary components for both Silver Carp and Bighead Carp (Williamson & Garvey, 2005; Sampson et al., 2009). Conversely, ostracod biomass may increase in the presence of Bighead Carp (Cooke et al., 2009), potentially because they can survive ingestion by fish (Vinyard, 1979) and may be able to take advantage of competitive release from other zooplankton. Although it is hypothesized zooplankton populations will decline following bigheaded carp invasion and some information is available regarding the effects of bigheaded carp on zooplankton communities in mesocosms, enclosures, and lentic systems (Radke & Kahl, 2002; Cooke et al., 2009; Collins & Wahl, 2018), little work is available evaluating the effect of bigheaded carp on zooplankton in lotic systems (but see Sass et al., 2014; DeBoer et al., 2018; Chara-Serna & Casper, 2021). Experimental research in lentic environments provides useful information describing possible ways invasive planktivores can affect zooplankton but more information is needed to understand their effects within dynamic large rivers given inherent differences due to flow and related processes.

The invasion front for bigheaded carp in the Upper Mississippi River (UMR) spans from Pool 20 where bigheaded carp were first detected in the 1980s (Irons et al., 2009) and are abundant to Pool 14 where bigheaded carp were not detected until 2010 (Gritters et al., 2015) and are scarce. Pool 20 is immediately downstream of Lock and Dam 19 (LD19), the southernmost high-head dam on the Mississippi River that restricts water levels at all flows and significantly inhibits fish passage (Tripp et al., 2014). Bigheaded carp are not exempt from passage restrictions posed by LD19 and are likewise precluded from upstream travel except through the navigational lock operated during routine river traffic which has limited their spatial spread and abundance further upstream. This gradient of invasive bigheaded carp abundance from

pools 20–14 provides a unique opportunity to study their effects on zooplankton communities in large-river systems, building and expanding on the results from the Illinois River (Sass et al., 2014; Chara-Serna & Casper, 2021).

The objective of this study was to investigate spatial and temporal variation in zooplankton communities associated with bigheaded carp presence and across a gradient of bigheaded carp relative abundance in the UMR. We measured density and biomass of zooplankton at varying taxonomic resolutions along the bigheaded carp invasion front to assess the extent various taxa were affected by bigheaded carp. Broadly, we predicted zooplankton communities would differ relative to bigheaded carp presence or absence. Specifically, we hypothesized a negative relationship between bigheaded carp relative abundance and density and biomass of crustacean zooplankton (combined cladocerans and adult copepods), cladocerans (each taxa therein and as a group), copepods (each taxa therein and as a group), and copepod nauplii. Conversely, we hypothesized bigheaded carp would have a positive association with the density and biomass of rotifers and ostracods given their potential for competitive release (Neill, 1975; Sass et al., 2014; Collins et al., 2018). Increasing rotifer and ostracod density while crustacean zooplankton decline may offset and result in negligible differences for total zooplankton density. Therefore, we predicted no discernable relationship between bigheaded carp and total zooplankton density.

Methods

Field sampling

We sampled zooplankton at five major locations from 15 sites spanning Pool 14–Pool 20 within the UMR in 2016, 2017, and 2018 (Fig. 1). Sampling locations were spatially standardized with respect to the five major tributaries (Des Moines River, Skunk River, Iowa River, Rock River, and Wapsipinicon River) in this reach and each location was unique to a navigational pool of the UMR (Pools 20, 19, 18, 16, and 14). Hereafter, we refer to these major sampling locations as the navigational pool of the UMR where they reside. We selected three sites at each pool that were approximately 1 km downstream, within, and

upstream of the mouths of each tributary. At each site, we sampled three habitats (backwater, thalweg, and channel border) to capture potential variability in zooplankton communities within a site. Backwater habitats were designated as areas with little to no apparent flow whereas thalweg habitats were designated as locations with the highest flow throughout the river channel. Channel border sites were located on the outside edges of the main river channel and characterized by areas of intermediate flow. We collected triplicate zooplankton samples at each site using an integrated tube sampler (5 cm diameter, 50 cm length). We combined contents of the three samples (approximately 2-3L), filtered it through a 63-μm mesh sieve, and preserved in Lugol's solution. We conducted sampling from May through August of 2016, 2017, and 2018 and revisited sites approximately every 10 days for a total of 12 sampling events per year and 1,620 total zooplankton samples collected annually.

In fall 2016, 2017, and 2018, we conducted daytime boat electrofishing (Smith-Root; 4–13 A, 100–500 V DC, 25% duty cycle, 25% frequency, 60 pulses/s; with two netters) to estimate bigheaded carp relative abundance as catch-per-unit-effort (CPUE in fish/h) in each of the sampled pools. Electrofishing transects were conducted parallel to shore at each site and we focused sampling effort on backwater and channel border habitats generally < 4 m deep. We conducted one transect 15 min in duration per tributary mouth site per year (three transects per pool per year). We identified bigheaded carp to species (Bighead or Silver Carp) but catch data for both species was combined for our analyses. Given the close proximity of sites within UMR pools, estimates of bigheaded carp CPUE were averaged across sites within pools each year.

Sample processing

In the laboratory, we processed zooplankton samples under a dissecting microscope using a Ward Counting Wheel. We rinsed and concentrated sample contents into a known volume of distilled water (approximately 50 ml) and subsampled using a 1-ml Hensen Stempel Pipette. We continually processed subsamples (1 ml aliquots) until at least 60 total individuals were counted from the sample (similar to Weber et al., 2020). If fewer than four individuals

Fig. 1 Sites sampled for zooplankton and bigheaded carp in 2016, 2017, and 2018 in Pools 14, 16, 18, 19, and 20 in the Upper Mississippi River. Major sampling locations are groups of three sites associated with the mouths of tributaries to the Upper Mississippi River and are referred to by the navigational pool where they reside. Pools that did not contain tributaries were not included (pools 15 and 17)
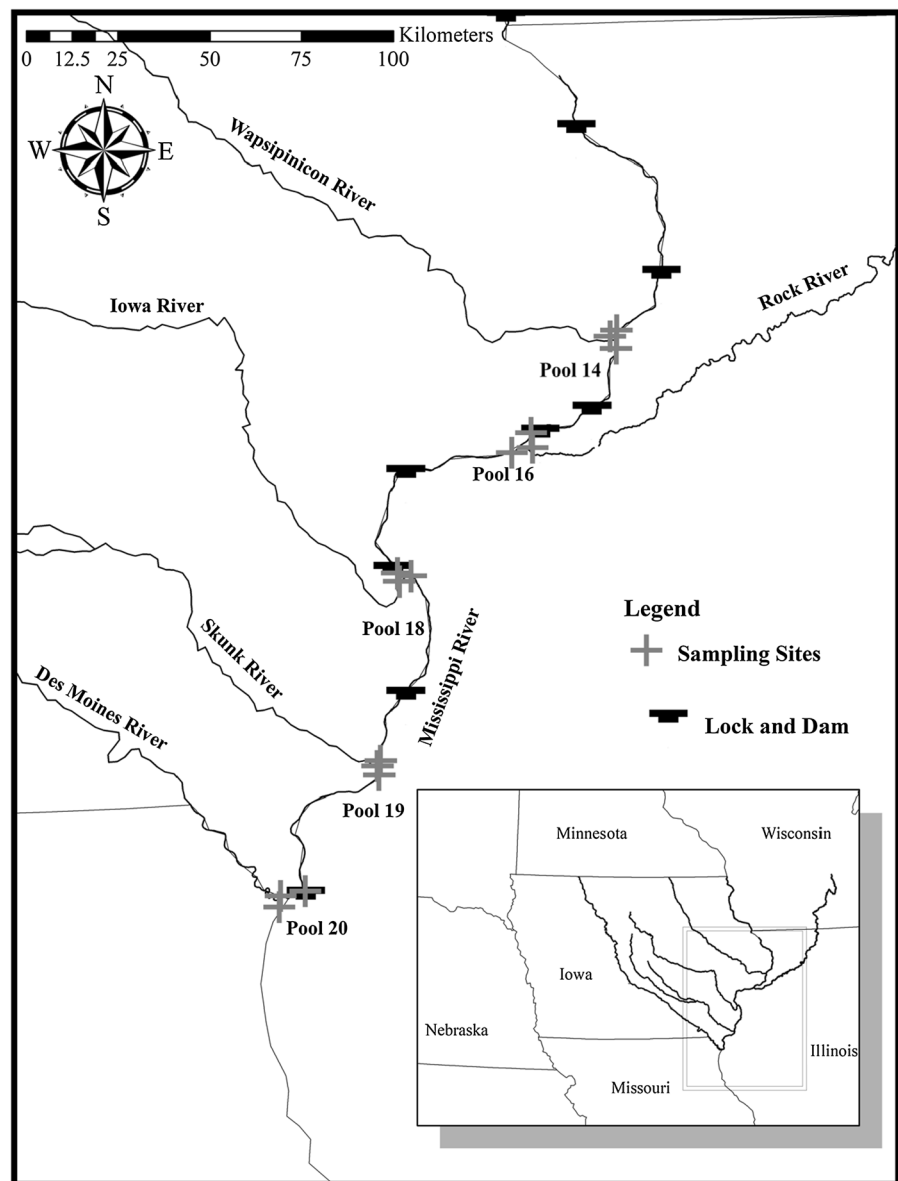
were found in any given 1 ml aliquot, we processed the sample in its entirety. To optimize time spent identifying zooplankton with the biological importance of a given taxonomic specificity, we identified zooplankton to varying taxonomic levels. Most cladocerans were identified to genus, except Chydoridae and Sididae were identified to family. Copepods were identified to order (Cyclopoida, Calanoida, Harpacticoida), rotifers were identified to the phylum Rotifera, and ostracods were identified to the class Ostracoda. We measured the first 30 individuals encountered of each taxon in a sample using an ocular micrometer

and estimated biomass (excluding ostracods) using length-dry-weight equations (Dumont et al., 1975; McCauley, 1984; Culver et al., 1985). There is no published length-dry-weight regression equation for ostracods, so we approximated their shapes as cylinders, calculated their body volume, and converted it to dry-weight using a specific gravity of 1.05 and dry-weight:wet-weight ratio of 15% (Strayer, 1986). Given the biomass of ostracods was calculated in a different manner than the rest of the taxa, ostracods were not included in the biomass estimates for total zooplankton, as direct comparisons with other groups

were not possible. Finally, we calculated density (individuals/l) and biomass density (μg/l; hereafter referred to as biomass) of each zooplankton taxa for each sample.

Data analysis

First, we averaged bigheaded carp CPUE among sites within pools each year. We evaluated differences in bigheaded carp relative abundance each year between pools via one-way analysis of variance (ANOVA) and compared using a pairwise post hoc test (Tukey's honest significant difference, R version 3.5.2). Next, we explored patterns in zooplankton community structure among UMR pools and years with non-metric multidimensional scaling (NMDS) ordination of the zooplankton density data ("metaMDS" function in "vegan" package) using Bray–Curtis similarities. To avoid underestimating the effects of some of the less abundant taxa and to account for zeros in the community data, we $\ln(X+1)$ transformed the raw data prior to calculating the Bray–Curtis similarity matrix. We used yearly electrofishing data of bigheaded carp captures to categorize ordination points (pool:year) into bigheaded carp presence or absence groups and constructed 90% confidence ellipses around each group. Additionally, we conducted an analysis of similarity (ANOSIM) of zooplankton communities based on bigheaded carp presence/absence groups using Bray–Curtis similarities of the $\ln(X+1)$ transformed zooplankton community density data (999,999 permutations, "anosim" function in "vegan" package).

To match the single estimate of bigheaded carp relative abundance generated for each pool-year combination, all zooplankton density and biomass data were also averaged by pool-year combinations. Scatterplots of the relationship between bigheaded carp CPUE (individuals/hr) and zooplankton density and biomass revealed both negative and positive nonlinear associations with certain zooplankton taxa. We assessed these relationships using ordinary least-squares regression models with a common indicator variable,

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2$$

where Y is our taxa-specific zooplankton response variable (density or biomass), β_0 is the intercept (estimate of zooplankton density or biomass when bigheaded carp are absent), X_1 is bigheaded carp CPUE, X_2 is an indicator variable for bigheaded carp presence ($X_2 = 0$ if bigheaded carp are not captured at a site, $X_2 = 1$ if bigheaded carp are captured), β_1 is the effect of increasing bigheaded carp CPUE on the zooplankton response, and β_2 is the effect of the bigheaded carp presence or absence indicator variable. When $X_2 = 1$ (i.e., when bigheaded carp are present), the model becomes

$$Y = (\beta_0 + \beta_2) + \beta_1 X_1$$

where the effect of bigheaded carp presence is accounted for in the model intercept. This approach allowed us to observe multiple kinds of relationships between bigheaded carp (i.e., presence/absence and relative abundance) and zooplankton taxa while also accounting for potential nonlinear relationships that can occur between abundances of invasive and native species (Weber & Brown, 2011). To better approximate a linear relationship and control for variability in the data, we applied natural logarithm (ln) transformations to all data and a constant (1) was added to species vectors where zeros were present in the raw data (bigheaded carp CPUE, calanoid copepod density, calanoid copepod biomass, *Ceriodaphnia* density, and *Ceriodaphnia* biomass). We then evaluated regression model significance with t-tests using a strength of evidence approach where $P < 0.05$ has 'strong evidence,' $P = 0.05$–0.10 has moderate evidence, and $P > 0.10$ has weak evidence of an effect instead of a strict $\alpha = 0.05$ threshold (e.g., McBride et al. 2014). All analyses were performed in R (Version 3.5.1).

Results

Bigheaded carp were captured in all sampled pools (Pools 20, 19, 18, and 16) of the UMR but one (Pool 14). Catches in Pool 20 were as high as 494 fish/h in 2018 and was generally greater than in the other pools (ANOVA, $P < 0.05$; Fig. 2). Catches in Pools 19 (mean CPUE = 3 fish/h) and 18 (mean CPUE = 2 fish/h) tended to be numerically intermediate compared to Pools 20, 16, and 14 (Fig. 2). Bigheaded carp were not captured in Pool 14 and only one individual was captured in Pool 16 across all three years of sampling (Fig. 2). However, there was no evidence

Fig. 2 Catch-per-unit-effort (CPUE; mean fish/h ± SE) of bigheaded carp captured via daytime boat electrofishing from five pools of the Upper Mississippi River in 2016, 2017, and 2018. Letters indicate differences ($P < 0.05$) in mean bigheaded carp CPUE among pools
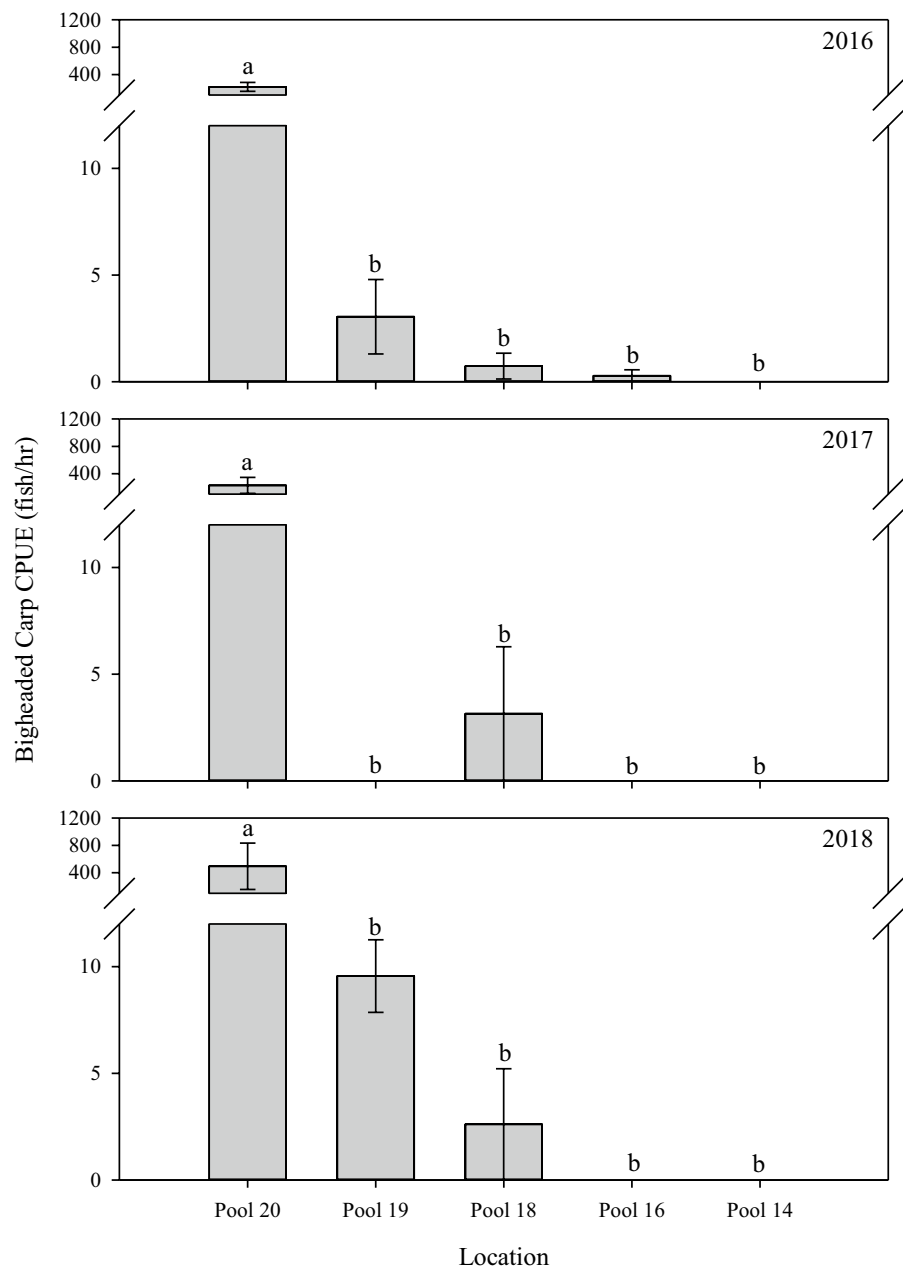

bigheaded carp abundance in Pools 14 and 16 were different from Pools 19 and 18 (ANOVA, $P > 0.99$).

Zooplankton communities throughout all pools and years were dominated by rotifers (74% density, 67% biomass), ostracods (21% density), and copepod nauplii (3% density, 3% biomass) with the remainder of the community (2% density, 30% biomass) comprised of cladoceran and adult copepod taxa (Fig. 3). Within the crustacean zooplankton community, cladocerans

were slightly more abundant (55%) than copepods (45%) but cladocerans made up less of the biomass (32%) than copepods (68%; Fig. 3). By density, the most dominant cladoceran taxa was *Bosmina* (46%), followed by Chydoridae (33%), *Daphnia* (12%), Sididae (5%), and *Ceriodaphnia* (4%; Fig. 3). However, *Daphnia* dominated cladoceran biomass (41%), followed by *Bosmina* (26%), Chydoridae (23%), Sididae (8%), and *Ceriodaphnia* (2%). Cyclopoid, calanoid,

Fig. 3 Density (mean individuals/l±SE) of zooplankton taxa collected from five pools of the Upper Mississippi River in 2016 (top), 2017 (middle), and 2018 (bottom). Pool-specific taxa are in consistent left to right order respective to the descending order of taxa in the figure legend
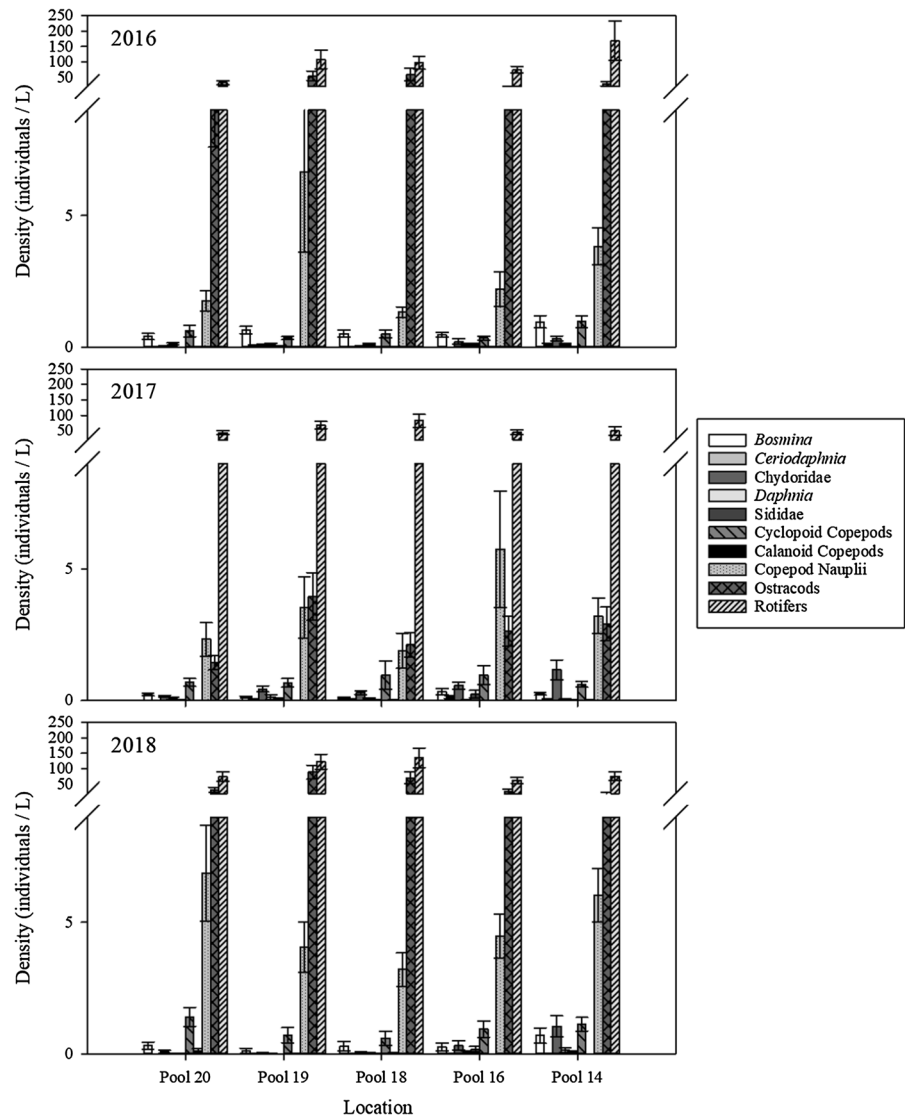
and harpacticoid copepods were all present in the UMR, but the copepod community was largely represented by cyclopoids (98% density, 96% biomass; Fig. 3). Calanoid (2% density) and harpacticoid (<1% density) copepods were encountered less frequently in our samples and comprised 4% and <1% of the remaining copepod biomass, respectively (Fig. 3).

Ordination of zooplankton density data using NMDS revealed patterns in pool:years and zooplankton communities based on bigheaded carp presence (Fig. 4). Cyclopoid copepods, copepod nauplii, and *Bosmina* were most associated with pool:years where bigheaded carp were not captured whereas rotifers and ostracods were associated with pool:years where

bigheaded carp were captured (90% confidence ellipses; Fig. 4). Calanoid copepods fell within 90% confidence ellipses for both bigheaded carp presence groups (Fig. 4). Sididae, Chydoridae, *Ceriodaphnia*, and *Daphnia* were all outside of 90% confidence ellipses for both bigheaded carp presence groups but Sididae, Chydoridae, and *Ceriodaphnia* were all most associated with pool:years where bigheaded carp were absent whereas *Daphnia* were most associated with pool:years where bigheaded carp were present (Fig. 4). Although 90% confidence ellipses around bigheaded carp presence groups displayed a small degree of overlap (Fig. 4; NMDS: stress=0.070), there was moderate evidence ellipses were mostly
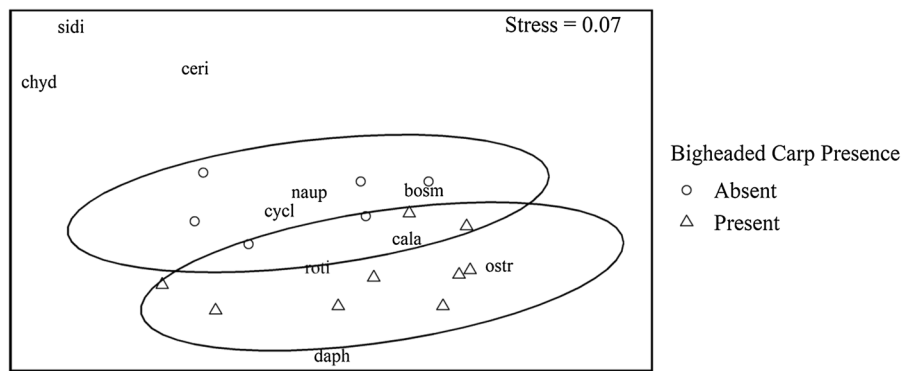
Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of mean zooplankton density in the Upper Mississippi River pools sampled in 2016, 2017, and 2018 where adult bigheaded carp are present (triangle) and absent (circle). Zooplankton density data were ln(X+1) transformed and ordina-

tions used Bray–Curtis similarities. Ellipses represent 90% confidence intervals based on bigheaded carp presence at a given pool during yearly sampling. Zooplankton taxa scores are overlaid and indicated by four-letter prefixes of the full taxa name

distinct between locations where bigheaded carp were present versus absent (ANOSIM: R-statistic = 0.18, P = 0.07).

Relationships between bigheaded carp relative abundance and zooplankton density in the UMR varied among groups and individual taxa (Table 1; Figs. 5, 6 and 7). Of the 14 taxanomic zooplankton groups (including individual taxa and nested groups), there was evidence bigheaded carp presence was positively related to one group, negatively related to five groups, and not related to eight groups. Of the same zooplankton groups, bigheaded carp relative abundance was positively related to five groups, negatively related to two groups, and not related to seven groups. Total zooplankton, crustacean zooplankton, total cladocerans, Chydoridae, total copepods, cyclopoid copepod, and rotifer density were all associated with bigheaded carp presence and/or relative abundance in the UMR (Table 1). Evidence suggested bigheaded carp presence tended to be positively related (P = 0.08) whereas bigheaded carp CPUE tended to be negatively related (P = 0.07) with total zooplankton density (Table 1; Fig. 5). Bigheaded carp presence was negatively related to crustacean zooplankton (P < 0.01), total cladoceran (P = 0.03), and Chydoridae (P < 0.01) density, but there was little evidence increasing bigheaded carp CPUE was related to densities of these taxa (P > 0.33; Table 1; Fig. 5, 6). Although bigheaded carp presence was negatively associated with total copepod (P = 0.02) and cyclopoid copepod (P = 0.01) density, increasing

bigheaded carp CPUE was positively related to densities (Table 1; Fig. 5, 7). Rotifer density appeared unrelated to bigheaded carp presence (P = 0.11) but there was evidence suggesting bigheaded carp CPUE was negatively associated with rotifer density (P = 0.05; Table 1; Fig. 6). Finally, there was little evidence to suggest densities of the remaining taxa and taxa groups (*Bosmina*, *Ceriodaphnia*, *Daphnia*, Sididae, calanoid copepods, copepod nauplii, and ostracods) were associated with the presence or CPUE of bigheaded carp in the UMR (P > 0.10; Table 1; Figs. 6, 7).

Taxa and directional (positive versus negative) associations between zooplankton biomass and both bigheaded carp presence and CPUE in the UMR were similar to relationships observed with zooplankton density (Figs. 5, 6 and 7). Bigheaded carp presence was negatively associated with crustacean zooplankton biomass (P < 0.01) but bigheaded carp CPUE was positively associated with biomass (P < 0.01; Table 1; Fig. 5). Similar to density, total cladoceran and Chydoridae biomass were negatively related to bigheaded carp presence (P < 0.01) whereas there was no relationship between bigheaded carp CPUE and biomass of these taxa (P > 0.40; Table 1; Fig. 5, 6). Furthermore, relationships of total copepods (P = 0.04) and cyclopoid copepods (P = 0.03) biomass were negatively associated with bigheaded carp presence and positively associated with bigheaded carp CPUE (P = 0.01 and P = 0.01, respectively; Table 1; Fig. 5,

Table 1 Parameters from ordinary least-squares regression models $(\ln[Y]=\beta_0+\beta_1\ln[1+X_1]+\beta_2X_2)$ used to investigate zooplankton density and biomass (Y) in 2016, 2017, and 2018 at pools 14, 16, 18, 19, and 20 in the Upper Mississippi River with varying abundances of bigheaded carp (X_1) and a dummy variable (X_2) indicating the presence/absence of bigheaded carp in electrofishing surveys ($X_2=0$ if no bigheaded carp were captured, and $X_2=1$ if any bigheaded carp were captured)

Variable	Taxon	Intercept	Bigheaded carp CPUE β_1 (90% CI)	$P(\beta_1)$	Bigheaded carp Presence β_2 (90% CI)	$P(\beta_2)$
Density (#/L)	Total zooplankton	4.50	− 0.15 (− 0.28, − 0.01)	0.072*	0.62 (0.04, 1.20)	0.083*
	Crustacean zooplankton	0.77	0.04 (− 0.03, 0.10)	0.34	− 0.65 (− 0.93, − 0.37)	0.0015**
	Cladocerans	0.24	− 0.06 (− 0.18, 0.07)	0.41	− 0.74 (− 1.29, − 0.20)	0.031**
	Bosmina	− 1.03	− 0.03 (− 0.22, 0.16)	0.76	− 0.11 (− 0.94, 0.72)	0.82
	Ceriodaphnia	0.06	− 0.002 (− 0.01, 0.01)	0.63	− 0.03 (− 0.07, 0.002)	0.11
	Chydoridae	− 0.57	− 0.05 (− 0.26, 0.16)	0.65	− 1.81 (− 2.73, − 0.89)	0.0044**
	Daphnia	− 2.60	− 0.10 (− 0.32, 0.11)	0.42	0.01 (− 0.95, 0.97)	0.98
	Sididae	− 2.81	− 0.21 (− 0.50, 0.08)	0.21	− 0.89 (− 2.15, 0.37)	0.23
	Copepods	− 0.14	0.12 (0.03, 0.21)	0.033**	− 0.63 (− 1.03, − 0.24)	0.015**
	Cyclopoid	− 0.15	0.12 (0.03, 0.21)	0.030**	− 0.65 (− 1.04, − 0.27)	0.011**
	Calanoid	0.01	0.006 (− 0.001, 0.01)	0.16	0.003 (− 0.03, 0.03)	0.87
	Copepod nauplii	1.47	0.06 (− 0.07, 0.19)	0.43	− 0.58 (− 1.16, 0.01)	0.104
	Ostracods	2.17	− 0.25 (− 0.62, 0.13)	0.27	1.44 (− 0.20, 3.08)	0.14
	Rotifers	4.26	− 0.14 (− 0.25, − 0.02)	0.051*	0.48 (− 0.01, 0.96)	0.11
Biomass (µg/l)	Total zooplankton	2.70	− 0.03 (− 0.13, 0.07)	0.55	0.14 (− 0.30, 0.57)	0.58
	Crustacean zooplankton	1.62	0.16 (0.07, 0.25)	0.0072**	− 0.70 (− 1.09, − 0.31)	0.0078**
	Cladocerans	0.62	− 0.04 (− 0.16, − 0.08)	0.55	− 0.76 (− 1.26, − 0.25)	0.022**
	Bosmina	− 0.93	− 0.07 (− 0.27, 0.14)	0.57	− 0.17 (− 1.06, 0.72)	0.74
	Ceriodaphnia	0.05	0.0004 (− 0.01, 0.01)	0.94	− 0.03 (− 0.07, 0.01)	0.15
	Chydoridae	− 0.38	− 0.09 (− 0.29, 0.10)	0.41	− 1.76 (− 2.62, − 0.89)	0.0034**
	Daphnia	− 1.19	− 0.04 (− 0.24, 0.16)	0.73	− 0.06 (− 0.93, 0.81)	0.90
	Sididae	1.77	− 0.14 (− 0.42, 0.14)	0.38	− 1.08 (− 2.30, 0.14)	0.14
	Copepods	1.12	0.22 (0.11, 0.34)	0.0049**	− 0.66 (− 1.16, − 0.16)	0.038**
	Cyclopoid	1.10	0.22 (0.11, 0.34)	0.0048**	− 0.70 (− 1.20, − 0.20)	0.029**
	Calanoid	0.05	0.04 (0.002, 0.07)	0.083*	0.02 (− 0.14, 0.14	0.82
	Copepod nauplii	− 0.71	0.03 (− 0.10, 0.17)	0.66	− 0.57 (− 1.14, 0.01)	0.105
	Ostracods	3.39	− 0.36 (− 0.82, 0.10)	0.19	2.17 (0.16, 4.17)	0.078*
	Rotifers	2.22	− 0.14 (− 0.26, − 0.01)	0.078*	0.48 (− 0.07, 1.04)	0.15

Total zooplankton biomass does not include ostracods. * indicates $0.10 > P$-value > 0.05. ** indicates P-value < 0.05

7). However, some evidence suggested a positive relationship between calanoid copepod biomass and bigheaded carp CPUE ($P=0.08$) where little evidence existed for a relationship between bigheaded carp CPUE on calanoid copepod density ($P=0.16$; Table 1; Fig. 6). There was also some evidence to suggest bigheaded carp presence was positively related to ostracod biomass ($P=0.08$), but there was no evidence for a relationship between bigheaded carp CPUE and ostracod biomass ($P>0.19$; Table 1; Fig. 6). Similar to density, rotifer biomass showed no relationship with bigheaded carp presence whereas there was some evidence bigheaded carp CPUE was negatively related to rotifer biomass ($P=0.08$; Fig. 6). Little evidence was available to support a relationship between biomass of total zooplankton *Bosmina*, *Ceriodaphnia*, *Daphnia*, Sididae, and copepod nauplii and bigheaded carp presence or CPUE ($P>0.10$; Table 1; Fig. 5, 6 and 7).

Fig. 5 Density (left) and biomass (right; mean ± SE) of zooplankton taxa groups plotted against relative abundance of bigheaded carp (mean CPUE ± SE) sampled from the Upper Mississippi River in 2016, 2017, and 2018
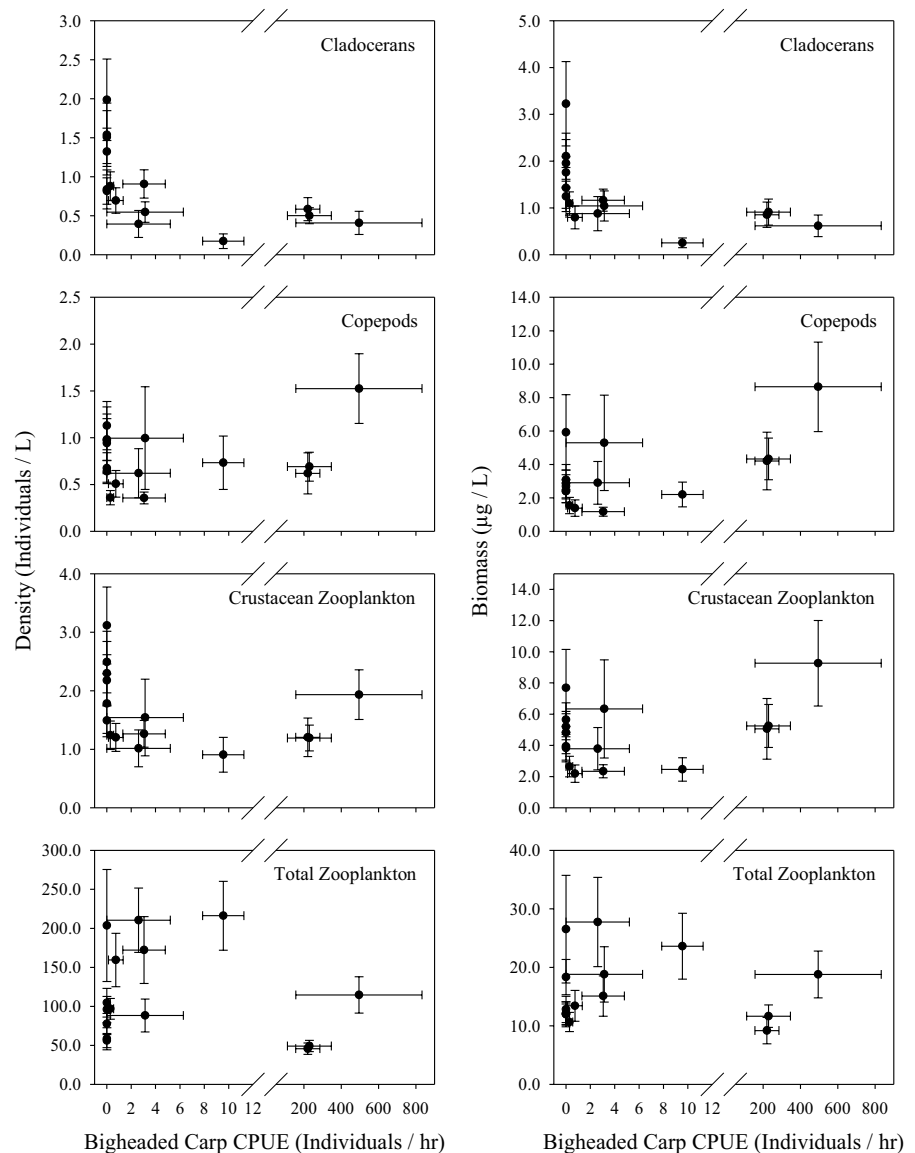

Discussion

Results of our study provide insight into the zooplankton community in the UMR within the context of the progressing bigheaded carp invasion. The ecological ramifications of invasive bigheaded carp can be diverse in their nature and severity (Cooke, 2016) and cascading effects of these invasive planktivores may not be immediately noticeable (Crooks, 2005; Chick et al., 2020). It is useful and important to monitor the dynamics of at-risk taxa in response to invasive species (Wilcove et al., 1998; Cooke, 2016)

despite inherent difficulties in quantifying those effects (Moyle & Light, 1996). Our data provide an improved understanding of the differential responses of zooplankton taxa to invasive planktivores and have established reference zooplankton community data at sites with varying abundances of bigheaded carp. Consistent with our hypothesis and findings of other studies (e.g., Sass et al., 2014; DeBoer et al., 2018; Chara-Serna & Casper, 2021), zooplankton communities differed relative to bigheaded carp presence and generally shifted away from cladoceran taxa in the presence of carp. Bigheaded carp presence and

Fig. 6 Density (left) and biomass (right; mean ± SE) of individual cladoceran taxa plotted against relative abundance of bigheaded carp (mean CPUE ± SE) sampled from the Upper Mississippi River in 2016, 2017, and 2018
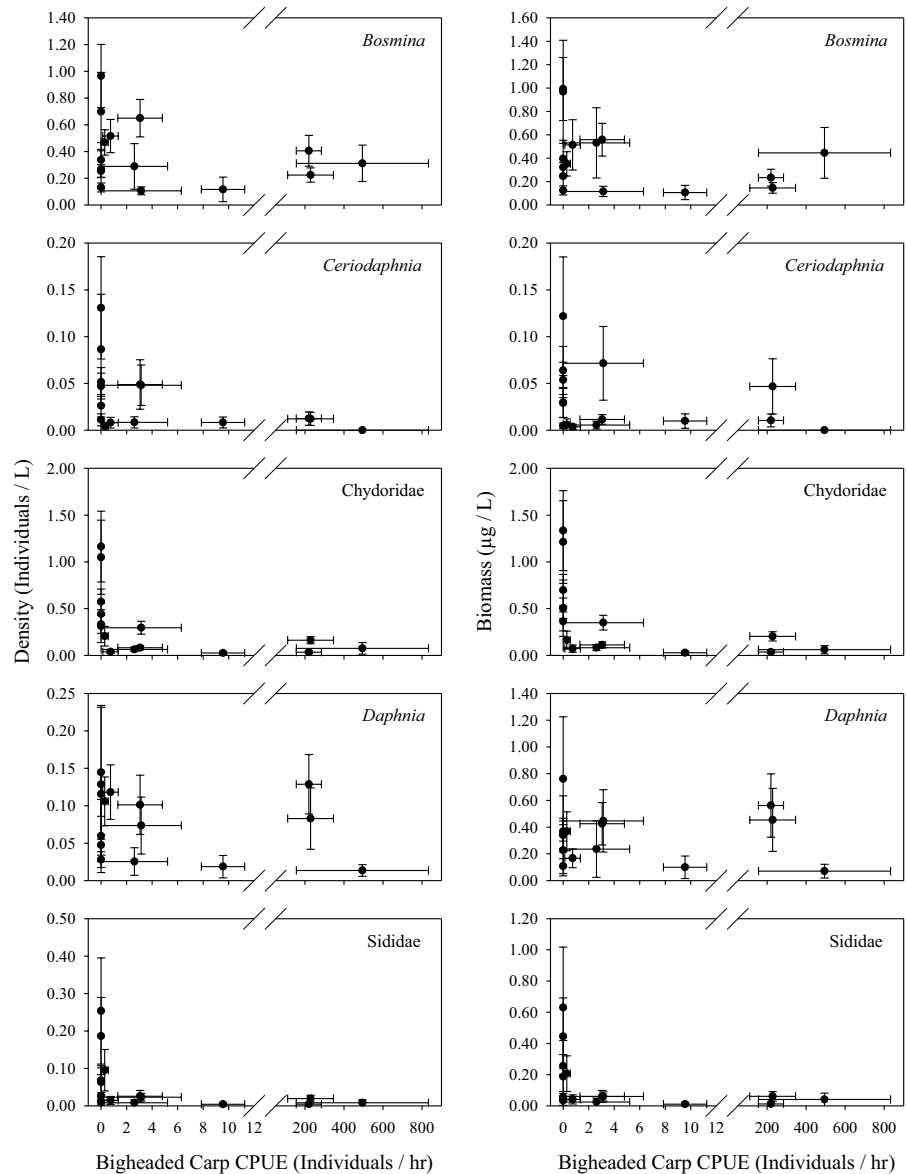

relative abundance was associated with zooplankton density and biomass for two taxa; however, the magnitude of the effect of bigheaded carp presence tended to affect model parameters to a greater extent and significantly influence more taxa than bigheaded carp relative abundance. Consequently, detectable effects of bigheaded carp on zooplankton might occur quickly following invasion regardless of abundance and efforts to control bigheaded carp abundance may do little to increase zooplankton densities.

Low densities of crustacean zooplankton taxa in the UMR are concerning, as native fish recruitment may be limited below minimum zooplankton thresholds (Werner & Blaxter, 1980; Bunnell et al., 2003; Dettmers et al., 2003) and densities in the UMR were typically low (< 5 individuals/l) regardless of bigheaded carp presence. Although declines in crustacean zooplankton associated with the presence of bigheaded carp were statistically significant in our study and consistent with our hypotheses, a change from ~ 3 individuals/l to ~ 1.5 individual/l may not be biologically significant for larval fish or native planktivores given typical minimum thresholds of zooplankton density (Werner & Blaxter, 1980). Similar

Fig. 7 Density (left) and biomass (right; mean ± SE) of adult copepods, copepod nauplii, ostracods, and rotifers plotted against relative abundance of bigheaded carp (mean CPUE ± SE) sampled from the Upper Mississippi River in 2016, 2017, and 2018
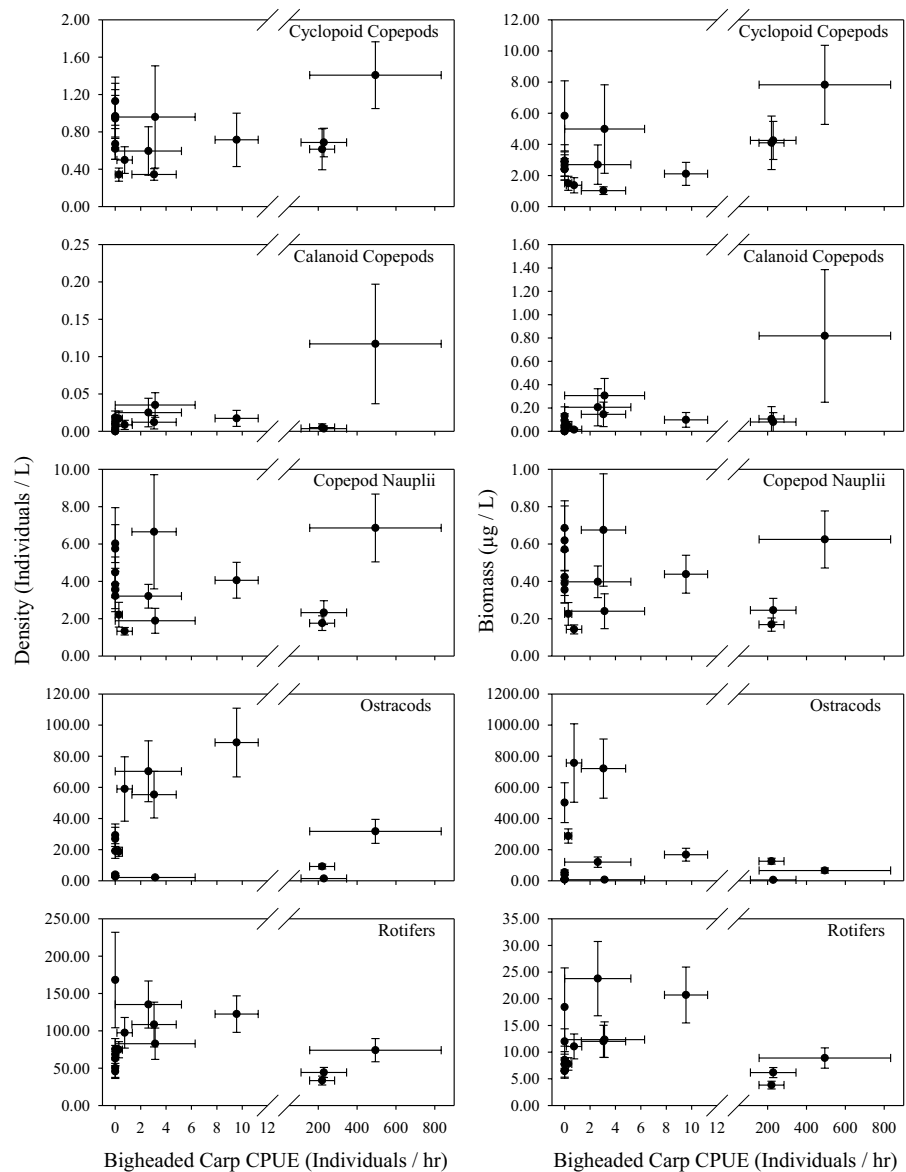
to our study, low densities (≤ 5 individuals/l) of copepods and cladocerans were also observed across two reaches of the Illinois River by Sass et al. (2014) and post-invasion of bigheaded carp by DeBoer et al. (2018). We found similar reductions in cladoceran density due to bigheaded carp; however, Sass et al. (2014) found an overall decrease in copepod density as a result of bigheaded carp presence. We found a similar negative effect of bigheaded carp presence but also found copepod densities increased significantly with bigheaded carp relative abundance. To our knowledge, this is the first instance a positive

relationship between bigheaded carp relative abundance and copepods has been reported, potentially indicating copepods may be less susceptible to predation by bigheaded carp (Drenner et al., 1978), are taking advantage of competitive release by declining populations of other taxa (e.g., Neill 1975), or are regulated by factors other than bigheaded carp in the UMR. However, the observed increasing relationship between copepods and bigheaded carp is driven by one point (year of data at a site) with high leverage. When removed, there is no evidence of an increasing relationship between copepods and bigheaded carp

($P > 0.10$). We did not find evidence bigheaded carp were related to *Daphnia* density. Large-bodied cladocerans like *Daphnia* frequently decline in the presence of bigheaded carp (Radke & Kahl, 2002; Cooke et al., 2009; Collins & Wahl, 2018). Instead, *Daphnia* densities in the UMR are low (< 0.15 individuals/l) and factors other than bigheaded carp appear to be regulating them in the UMR. Although the overall range of cladoceran and copepod densities for our spatial comparison were similar to spatial comparisons by Sass et al. (2014) in the Illinois River, temporal comparisons of these taxa prior to bigheaded carp invasion in his study revealed original densities of 19.7 individuals/l for cladocerans and 71.2 individuals/l for copepods. These pre-invasion quantities of crustacean zooplankton were much higher than densities found anywhere in our study, including sites where bigheaded carp were not detected. However, we do not believe that pre-invasion densities of zooplankton in our reach of the UMR were similar to the Illinois River, as Pillard & Anderson (1993) reported densities of crustacean zooplankton from UMR Pool 19 that more closely match densities observed with our data. Consequently, differences in abiotic characteristics between the Illinois River and the UMR likely also contribute to differences in zooplankton densities in sites and years where bigheaded carp were absent.

Biotic interactions of invasive fishes with native taxa can constrain recruitment and production of native taxa even under favorable abiotic conditions (Quist & Hubert, 2005; Weber & Brown, 2011; Chick et al., 2020). The Biotic-Abiotic Constraining Hypothesis (BACH; Quist et al. 2003) may explain several relationships between bigheaded carp relative abundance and zooplankton taxa observed here. This hypothesis predicts that at low abundance of a biotic predictor variable (here, bigheaded carp), a biotic response variable (here, zooplankton density or biomass) can be highly variable based on spatiotemporal variation in abiotic conditions. However, when the biotic predictor variable is abundant, the response variable is always suppressed at low abundance. With the exception of *Daphnia*, our NMDS analysis suggested cladoceran taxa (*Bosmina*, *Ceriodaphnia*, Chydoridae, and Sididae) density and biomass were more associated with the absence of bigheaded carp. Linear relationships between density and biomass of these taxa and bigheaded carp abundance were not detected

but biplots suggested these cladoceran taxa may be constrained once bigheaded carp populations reached catchable abundances via boat electrofishing. Similarly, cladoceran densities in the Illinois River were significantly higher in the upper reaches where Silver Carp were absent than in the lower reaches where Silver Carp were present and the relative scale of their decline (3.3 to 1.9 individuals/l) was comparable to our study (Sass et al., 2014). Because we were unable to assess the temporal influence of abiotic attributes (e.g., temperature, discharge) on zooplankton communities at our sites, we are unable to definitively say abiotic conditions were equally favorable among sites or could explain variability in zooplankton densities when carp abundance was low. However, the close geographic proximity and interconnectedness of our sites suggests environmental conditions were generally similar among pools and the trends in zooplankton in relation to bigheaded carp abundance suggests the BACH hypothesis provides a useful framework for understanding these interactions.

The potential negative relationship observed between bigheaded carp relative abundance and rotifer density and biomass was contrary to our hypothesis, but not unexpected given conflicting reports of rotifer dynamics in response to bigheaded carp in large rivers (Sass et al., 2014; DeBoer et al., 2018). Some of our findings regarding copepod nauplii dynamics contradict prior research and were inconsistent with our hypotheses. Although multivariate analyses grouped copepod nauplii more closely with pools and years where bigheaded carp were absent, we found no significant linear association between copepod nauplii and bigheaded carp presence and abundance. Copepod nauplii are especially vulnerable to bigheaded carp (Dong et al., 1992) and most studies find significant reductions in density and biomass of copepod nauplii (Domaizon & Dévaux, 1999; Collins & Wahl, 2018; DeBoer et al., 2018). Given the increasing relationship of copepod density and biomass with bigheaded carp relative abundance in our study, we speculate reductions in nauplii due to predation could be offset by increased production by adult copepods. Our conclusions regarding rotifers and copepod nauplii are only specific to individuals and taxa large enough to be vulnerable to our gear, as our mesh size was too large to capture all size classes of these taxa (Chick et al., 2010). Although we may not have captured the full range of rotifer and

nauplii sizes or taxa, densities of these groups were higher than any other and we reason we appropriately describe the dynamics of individuals (although potentially not taxa) > 63 μm in the population. Further, any potential biases of larger mesh size used here would be similar among all pools, allowing us to evaluate the relationships between rotifers and bigheaded carp throughout this invasion gradient. If systematic differences in rotifer sizes or taxa existed among pools as a result of other conditions beyond bigheaded carp, it may have biased our results here. However, because of the close proximity of sampling sites and interconnectedness of the pools, systematic variation in rotifer sizes and taxa that coincide with the bigheaded carp abundance gradient are unlikely. Thus, we believe our results provide meaningful relationships between small bodied zooplankton and bigheaded carp in this study but we caution the interpretation of our results and comparison of rotifer densities observed here to other studies using smaller mesh that would capture rotifers more effectively.

When investigating the effects of invasive planktivores, it is important to consider both zooplankton density and biomass, as both metrics inform about zooplankton community dynamics and disparities between them indicate differential size structure within taxa. For example, changes in zooplankton biomass but not density could be indicative of changes in zooplankton size structure. Altered zooplankton size structure can affect higher trophic levels, including growth of larval fish (Mills et al., 1989) and foraging ecology of older fish (Bartell, 1982). Based on disparities in density and biomass observed here, our data suggest altered size structure of crustacean zooplankton, calanoid copepods, and ostracods relative to the gradient of bigheaded carp abundance in the UMR. Given the reliance of fish larvae on adequately sized prey, altered zooplankton size structure and density may play a role in regulating fish survival during early life stages, eventually resulting in declines of adult populations. Accordingly, bigheaded carp have been linked to the decline of several native fish taxa, including both planktivores (Irons et al., 2007) and omnivorous sportfishes (Chick et al., 2020). Although there is evidence of competitive processes driving limited zooplankton resources in large rivers and resulting in declines of native planktivores (Irons et al., 2011; Solomon et al., 2016; Pendleton et al., 2017), mechanisms driving fish declines are

less understood. Growth of fish larvae is affected by prey availability (Welker et al., 1994; Betsill and Van Den Avyle, 1997; Bunnell et al., 2003) and reduced growth of fish larvae can significantly affect fish recruitment (Houde, 1987; Kamimura et al., 2015). The effects of bigheaded carp on zooplankton communities could inhibit foraging and subsequent recruitment of larval fish via competition (Calkins et al., 2012; Chick et al., 2020) and reduced larval growth in the presence of bigheaded carp has been observed for Bluegill (*Lepomis macrochirus* Rafinesque, 1819) in an experimental setting (Fletcher et al., 2019). Fish larvae often rely on rotifers and other small zooplankton as sources of first-food before transitioning to larger crustacean zooplankton (i.e., copepods and cladocerans) as they develop (Siefert, 1972; Dettmers & Stein, 1992). Although the reduced density and biomass of cladocerans in the presence of bigheaded carp may be numerically supplemented by the increase in copepod density and biomass, age-0 fishes [e.g., Yellow Perch *Perca flavescens* (Mitchill, 1814); Mills et al. 1984] prefer large-bodied cladocerans over copepods when they reach 30–35 mm in total length and can experience higher survival when consuming cladocerans compared to other zooplankton prey [e.g., Walleye *Sander vitreus* (Mitchill, 1818); Mayer & Wahl, 1997]. Increasing copepod density and biomass in relation to bigheaded carp relative abundance may increase larval fish food availability, but recruitment of larval fish may be reduced if cladocerans are important for survival.

Differential effects of bigheaded carp presence and relative abundance on some zooplankton taxa may be the result of more complex ecological processes, as there are numerous other biotic and abiotic factors (e.g., native planktivores, river discharge and temperature, nutrient availability, etc.; Kobayashi, 1997; Bonecker et al., 2013) potentially affecting zooplankton density and biomass in large rivers (Pillard & Anderson, 1993; Dickerson et al., 2010). Consequently, multiple years of data may be necessary to disentangle these interwoven relationships. Additionally, annual averages of zooplankton taxa may not be sensitive indicators to planktivory by bigheaded carp compared to data collected on shorter temporal scales. Studies examining both pre- and post-invasion zooplankton data are necessary, or a gradient of bigheaded carp abundances at study sites must be present in order to evaluate their

effects. However, both aforementioned scenarios are challenging and problematic, as they must deal with spatial or temporal variability. Furthermore, assessing bigheaded carp presence and relative abundance at sites can be challenging due to their propensity to leap out of the water rather than be stunned during typical boat electrofishing. The effects of these challenges on bigheaded carp relative abundance data are evidenced in our study by the lack of significant differences between catch rates in the upper four pools (Pools 19, 18, 16, and 14). Accordingly, we do not suggest that our electrofishing surveys provide evidence of true absence of bigheaded carp from a site, but rather that catch rates are relative among the pools assessed here. Catch rates (CPUE) of bigheaded carp below LD19 were two orders of magnitude higher than those in the Illinois River where other studies of zooplankton dynamics have been conducted (Sass et al., 2014; DeBoer et al., 2018); however, electrofishing methodologies between our studies may differ enough to preclude meaningful comparisons. Finally, our zooplankton sampling using a tube sampler for the top 50 cm of water that sampled the entire water column for some locations but only a portion of the water column in other locations. If zooplankton were not mixed homogenously, this sampling technique may not represent zooplankton composition or density lower in the water column at some sites. Regardless of these potential limitations, our analyses indicate bigheaded carp are related to alterations in zooplankton communities in the UMR and prior research has shown Silver Carp biomass to be a better predictor of zooplankton metrics than any other variable (DeBoer et al., 2018). Consequently, in situ studies like ours, Sass et al. (2014) and DeBoer et al. (2018) provide real-world insight into complex zooplankton taxa and community dynamics in the presence of bigheaded carp in lotic systems, as well as highlight the importance of long-term monitoring.

Data availability The datasets generated and analyzed in this study are available from the corresponding author upon reasonable request.

Code availability The code files used for analyses in this study are available from the corresponding author upon reasonable request.

Declarations

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