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Competition among river planktivores: are native planktivores still fewer and skinnier in response to the Silver Carp invasion?

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Abstract Planktivorous Silver Carp *Hypophthalmichthys molitrix* and Bighead Carp *H. nobilis* have successfully invaded much of the Upper Mississippi River System and its tributaries during the last 30 years. During the initial years of the invasion, concurrent declines in the body condition and the catch per unit effort (CPUE) of planktivorous Gizzard Shad *Dorosoma cepedianum* and Bigmouth Buffalo *Ictiobus cyprinellus* were attributed to competition with Asian carp. Using an additional seven years of data (2007–2013), we assessed whether Silver Carp have continued to exert adverse pressure on the condition, CPUE, and biomass of native planktivores or whether there is evidence of a potential rebound in the populations of native planktivores. The extended data set reaffirms the body condition and the CPUE of Bigmouth Buffalo remain significantly reduced. However, unlike previous analyses, we also observed significant reductions in the CPUE of Gizzard Shad. Additionally, new results show that the CPUE and biomass of Bigmouth Buffalo were more inversely related to Silver Carp CPUE and biomass relative to the CPUE and biomass of Gizzard Shad. These results reinforce that Silver Carp likely suppress native planktivores and also suggest that diet and other life-history traits may explain some of the subtle differences in species-specific responses. Our results also emphasize that long-term data can be critical to understanding how non-native species can influence native fish population dynamics and how this influence may change over time.

Keywords Asian carp · Illinois River · LTRM · Silver Carp · Gizzard Shad · Bigmouth Buffalo · Body condition

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Introduction

Silver Carp *Hypophthalmichthys molitrix* (Valenciennes) and Bighead Carp *H. nobilis* (Richardson), collectively referred to here as Asian carp, have successfully invaded much of the Upper Mississippi River System (UMRS) during the last 30 years (Irons et al. 2009). The Illinois River, a major tributary of the Mississippi River, harbors possibly the highest known wild densities of Asian carp (Sass et al. 2010). These planktivorous fishes have been documented to have a wide range of impacts (e.g., altering nutrient dynamics, trophic cascades, competition with planktivores) across their introduced ranges (Kolar et al. 2005; Irons et al. 2007; Irons et al. 2009; Solomon et al. 2016). Studies suggest Asian carp can be more efficient than native planktivores at filtering feeding particles (Starostka and Applegate 1970; Drenner 1977; Jennings 1988; Irons et al. 2009). Since the establishment of Asian carp within the La Grange Reach of the Illinois River, both cladoceran and copepod abundance has declined while rotifers have increased (Sass et al. 2014). One of the main questions about the establishment and population expansion of non-natives is the magnitude of competition non-natives may exert on native fishes. However, species responses and population dynamics can change unpredictably during rapid expansions, meaning early patterns and trends may not persist over time (Moyle and Light 1996; Gurevitch and Padilla 2004; Strayer et al. 2014). Thus the rapid spread and continued persistence of Asian carp on a native planktivore assemblage provides an opportunity to assess how natives respond and how their response may change over time.

After the establishment of Asian carp within the La Grange Reach of the Illinois River in 2000, Irons et al. (2007) observed significant declines in the body condition of Gizzard Shad *Dorosoma cepedianum* (Lesueur) and the body condition and catch per unit effort (CPUE) of Bigmouth Buffalo *Ictiobus cyprinellus* (Valenciennes). However, since the initial establishment, the population of Asian carp (particularly Silver Carp, found in much higher densities in the La Grange Reach than Bighead Carp; LTRM 2017) has continued to increase (Fig. 1). Therefore, our objective was to extend the evaluation of potential effects of Silver Carp on two native planktivores, Gizzard Shad and Bigmouth Buffalo, as done by Irons et al. (2007), by including new data from 2007 to 2013. More specifically, we investigated whether: 1) native planktivores' body condition and CPUE has changed by extending the previous data set and 2) adding the new aspect of assessing the relationships between the CPUE and biomass of native planktivores and Silver Carp.

Materials and methods

Long-term fish monitoring programs

Two long-term fish monitoring programs were used to evaluate the potential effects of Silver Carp on native planktivores; the Long Term Survey and Assessment of Large River Fishes in Illinois (LTEF) and the Long Term Resource Monitoring element (LTRM) of the Upper Mississippi River Restoration (UMRR) Program and are approved by the Institutional Animal Care and Use Committee (Permits #16152 and #17018, respectively). The LTEF, supported by the Federal Aid in Sportfish Restoration Program (F-101-R), conducts standardized fish monitoring at six fixed side-channel sites annually (21 August to 7 October) within the La Grange Reach. Fishes are collected via 1-h AC boat electrofishing and total length (L_T) and weight (W) are recorded for all fishes collected. Additional details can be found in Koel and Sparks (2002). The U.S. Army Corps of Engineers' UMRR LTRM element is implemented by the U.S. Geological Survey's Upper Midwest Environment Sciences Center in cooperation with the five UMRS states (Illinois, Iowa, Minnesota, Missouri, and Wisconsin). The LTRM element conducts standardized fish monitoring along five pools of the UMRS and the La Grange Reach of the Illinois River. Approximately 280 stratified random sites (implemented in 1993) are sampled annually (15 June to 31 October) within the La Grange Reach among all major habitat strata (e.g., main channel border, side channel border, and connected backwaters). Fishes are collected with multiple gears (e.g., pulsed-DC boat electrofishing, fyke nets, and hoop nets) and L_T is recorded for all fishes and W is recorded for select fishes collected between 15 September and 31 October. Additional details can be found in Ratcliff et al. (2014).

Body condition and CPUE

Following a similar methodology to Irons et al. (2007), body condition (indexed as relative weight; W_r) of Gizzard Shad and Bigmouth Buffalo was evaluated with a Mann-Whitney U test before and after the establishment of Silver Carp using 2000 as the year of establishment. The year 2000 was defined as the year of establishment following Irons et al. (2007) and is supported by Chick and Pegg (2001) and by McClelland et al. (2012). Body condition was estimated based on species-specific L_T and W relationships developed for the La Grange Reach using data prior to the establishment of Silver Carp to serve as a baseline standard weight (W_S) equation before the arrival of Silver Carp. From the developed standards, W_r was calculated as $W_r = W \cdot W_S^{-1} * 100$. To estimate the changes in W_r, LTEF data collected between 1983 and 2013 for all records where both L_T and W were measured were used. LTRM data for W_r estimates were omitted because the LTRM protocol did not collect weight data

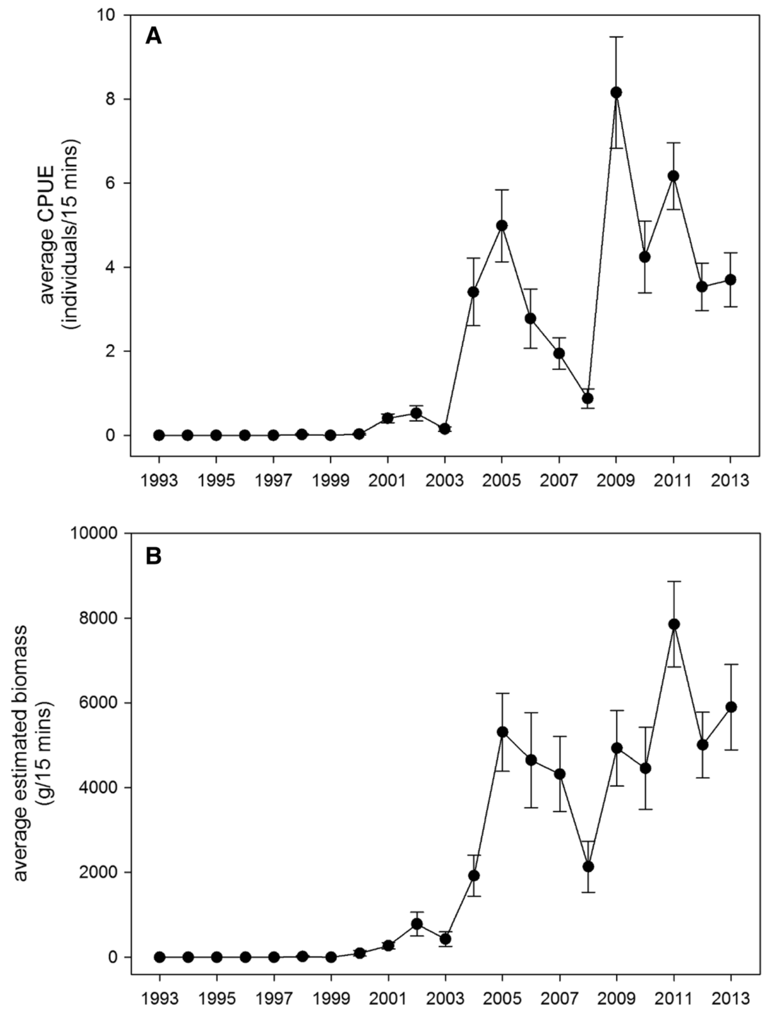

Fig. 1 **a** Average annual catch per unit effort (fish per 15 min day electrofishing; CPUE) and **b** average annual estimated biomass (g per 15 min day electrofishing; with S.E.) of Silver Carp in the La Grange Reach of the Illinois River. Data represent individuals >300 mm collected during 1993–2013 from LTRM DC electrofishing surveys among all river strata

for Gizzard Shad and Bigmouth Buffalo for most of the years prior to the establishment of Silver Carp. After W_r estimates were calculated, outliers were removed for both species using modified z-scores before calculating annual means. Any datum with a modified z-score of $|> 3.5|$ was considered an outlier and excluded from the analysis (Iglewicz and Hoagin 1993). Although the removal of outliers is unnecessary for the statistical test used, measurement errors (i.e. length and weight) can occur and thus influence the interpretation of the results (Bunch et al. 2013; Phelps et al. 2013). After calculating individual W_r, we identified several lengths and weights that were clearly recorded in error, therefore, elected to remove outliers using the modified z-score approach.

A Mann-Whitney test was used to compare changes in the CPUE (number of individuals per 15 min of day electrofishing) of Gizzard Shad and Bigmouth Buffalo from the pre-establishment (1993–1999) period to those from the post-establishment (2000–2013) period. While LTEF data are better suited for developing W_r estimates, two features of the LTRM protocol make it better suited for analyzing CPUE. First, LTEF has a limited spatial coverage in the La Grange Reach, only collecting annual data at six fixed side-channel sites, whereas LTRM is based on a stratified, random sampling design (i.e. multiple habitat strata) with a larger spatial coverage (~ 108 random sites sampled annually; reduced effort during four years due to the onset of stratified random sampling and budgetary restrictions) in the La Grange Reach. Second, LTRM uses pulsed-DC electrofishing, which generally captures more individuals than the AC electrofishing used by LTEF (McClelland et al. 2013).

Relationships in CPUE and biomass between native planktivores and Silver Carp

As mentioned previously, Silver Carp are found in much higher densities in the La Grange Reach relative to Bighead Carp (LTRM 2017), therefore Silver Carp CPUE and biomass (expressed as number of individuals and grams per 15 min of day electrofishing, respectively) were treated as the primary predictor variables. Simple linear regression was used to test for relationships between the average annual CPUE and biomass of native planktivores and those of Silver Carp. All pairwise comparisons for Gizzard Shad and Bigmouth Buffalo to Silver Carp were analyzed (i.e. CPUE to CPUE, biomass to biomass, CPUE to biomass). No transformations to the data were made and the assumptions of simple linear regression were tested for each pairwise comparison. Minor deviations were observed for normality of the error distribution (Gizzard Shad CPUE ~ Silver Carp biomass and Gizzard Shad CPUE ~ Silver Carp CPUE) and for statistical independence of the errors (Gizzard Shad biomass ~ Silver Carp biomass and Gizzard Shad biomass ~ Silver Carp CPUE). The average annual CPUE for each species was indexed using LTRM daytime electrofishing data from all habitat strata from 1993 to 2013. The average annual biomass for each species was estimated from species-specific allometric growth models developed by LTRM specific for the Upper Mississippi River fishes (O'Hara et al. 2007). Both CPUE and biomass are pool-wide averages that include fishes collected from all three LTRM habitat strata between 1993 and 2013 (Ratcliff et al. 2014). Additionally, all Silver Carp <300 mm were excluded as catch rates of young-of-year (YOY) can be highly variable and can artificially inflate CPUE estimates (e.g. catches of individuals <300 mm in 2008 were ~99% of total catch), and to a lesser degree, biomass estimates.

Results

Body condition and CPUE

The body condition of Gizzard Shad and Bigmouth Buffalo were significantly lower after the establishment of Asian carp in 2000 (Mann-Whitney U = 80,568, $p < 0.001$; U = 7039, $p < 0.001$, respectively; Fig. 2). Average body condition decreased from 104.4 (±17.8 S.D. and ±1.0 S.E.) during pre-establishment years to 96.5 (±17.2 S.D. and ±0.6 S.E.) during post-establishment years for Gizzard Shad and decreased from 103.4 (±8.2 S.D. and ±0.5 S.E.) to 96.7 (±8.1 S.D. and ±0.8 S.E.) for Bigmouth Buffalo. However, general trends over time indicate the body condition of Bigmouth Buffalo has slightly increased after 2005 relative to previous years (Fig. 2). In terms of CPUE, both Gizzard Shad and Bigmouth Buffalo had significantly lower CPUEs during post-establishment years (Mann Whitney U = 403,174, $p < 0.001$ and U = 405,002, $p < 0.001$, respectively; Fig. 2). Average CPUE decreased from 170.3 (±975.0 S.D. and ±38.5 S.E.) individuals during pre-establishment years to 88.0 (±230.9 S.D. and ±6.1 S.E.) during post-establishment for Gizzard Shad and decreased from 4.3 (±10.8 S.D. and ±0.4 S.E.) individuals to 2.7 (±8.1 S.D. and ±0.2 S.E.) for Bigmouth Buffalo. Median CPUE also decreased from 33 to 22 individuals between establishment periods for Gizzard Shad. Due to the large proportion of samples in which no Bigmouth Buffalo were collected, no differences were observed in median CPUE (i.e. 0 individuals) between establishment periods. Over time, the CPUE of Bigmouth Buffalo has remained low (most notably since 2007), while Gizzard Shad exhibited periods of increased CPUE in several years post-establishment of Silver Carp.

Relationships in CPUE and biomass between native planktivores and Silver Carp

Linear regressions indicated that Gizzard Shad CPUE and biomass were negatively related to both Silver Carp CPUE and biomass, however, only Silver Carp CPUE significantly described Gizzard Shad biomass ($p = 0.02$; Table 1). Bigmouth Buffalo CPUE and biomass were negatively related to both Silver Carp CPUE and biomass, with Silver Carp biomass being the better predictor based on r^2 and AIC values (Table 1). When average annual CPUE or biomass of Bigmouth Buffalo was plotted as a function of Silver Carp biomass, both CPUE and biomass of Bigmouth Bufffalo remained low, with low variability, as Silver Carp biomass increased (Fig. 3). This same pattern was not observed for Gizzard Shad CPUE and biomass when plotted against Silver Carp CPUE or biomass (Appendix 1).

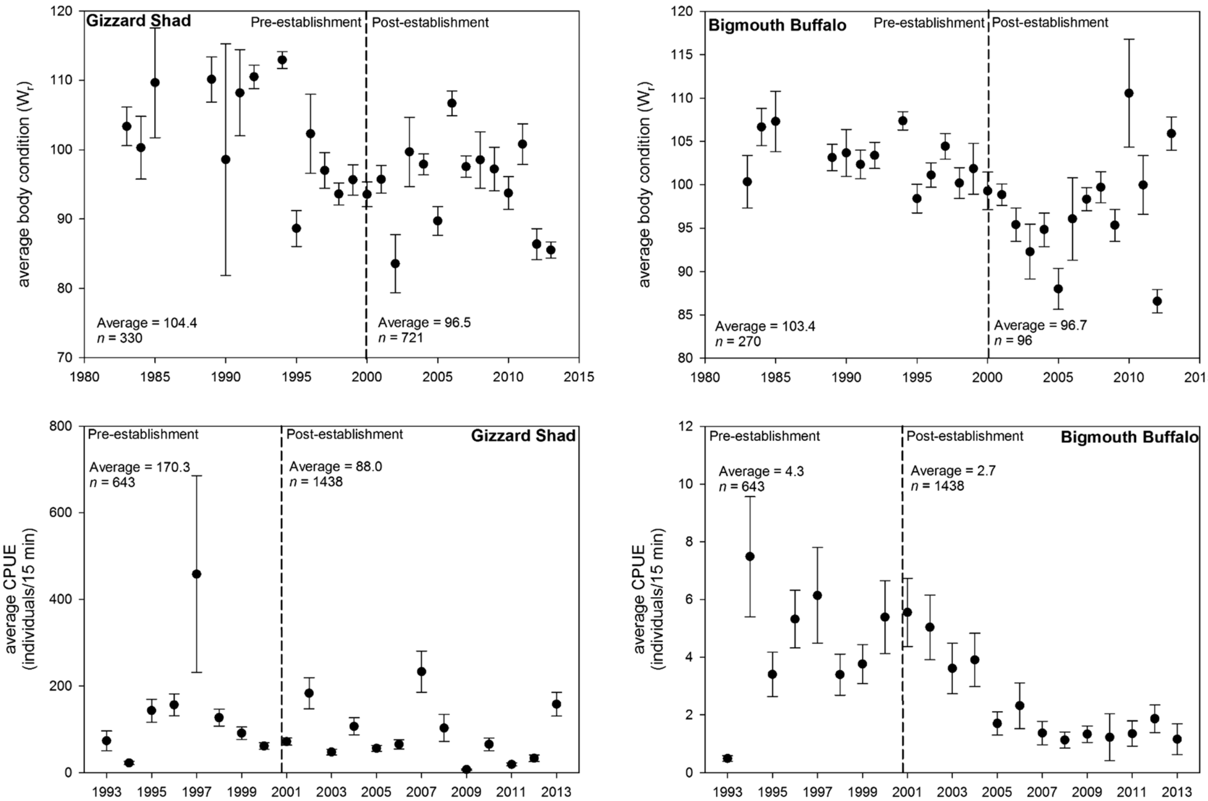

Fig. 2 Average ± S.E. body condition and average catch per unit effort (fish per 15 min day electrofishing; CPUE) of Gizzard Shad and Bigmouth Buffalo. Average body condition from LTEF AC electrofishing monitoring during pre- (1983–1999) and post-Silver Carp establishment (2000–2013) and average CPUE from LTRM DC electrofishing monitoring during pre- (1993–1999) and post-Silver Carp establishment (2000–2013). Dashed line represent the year of Silver Carp establishment (Irons et al. 2007)

Discussion

Understanding which factors are driving population dynamics, and under what environmental circumstances, is important in predicting species responses and food web dynamics over extended periods. Unfortunately, there are negative pressures on fish assemblages from threats such as the introduction of non-native species even as we document recoveries in fish assemblages in response to factors such as improvements in water quality (McClelland et al. 2012; Parker et al. 2016). For examples, Quist and Hubert (2005) determined native

Table 1 Results from simple linear regression models of the average annual catch per unit effort (fish per 15 min day electrofishing; CPUE) and biomass (g per 15 min day electrofishing) of native planktivores in relation to the average annual CPUE and biomass of Silver Carp

Response variable	Predictor variable	Slope	Standardized coefficient	Intercept	r^2	p	AIC
Gizzard Shad CPUE	Silver Carp biomass	−0.01	−0.28	133.5	0.08	0.22	255.9
	Silver Carp CPUE	−15.11	−0.37	138.3	0.14	0.10	254.5
Gizzard Shad biomass	Silver Carp biomass	−0.05	0.37	1074.1	0.14	0.10	309.8
	Silver Carp CPUE	−76.65	−0.51	1103.0	0.26	0.02	306.7
Bigmouth Buffalo CPUE	Silver Carp biomass	0.00	−0.69	4.4	0.47	< 0.001	80.6
	Silver Carp CPUE	−0.49	−0.59	4.1	0.35	< 0.01	85.0
Bigmouth Buffalo biomass	Silver Carp biomass	−0.56	−0.64	4943.7	0.41	< 0.01	377.7
	Silver Carp CPUE	−535.44	−0.58	4703.1	0.33	< 0.01	380.4

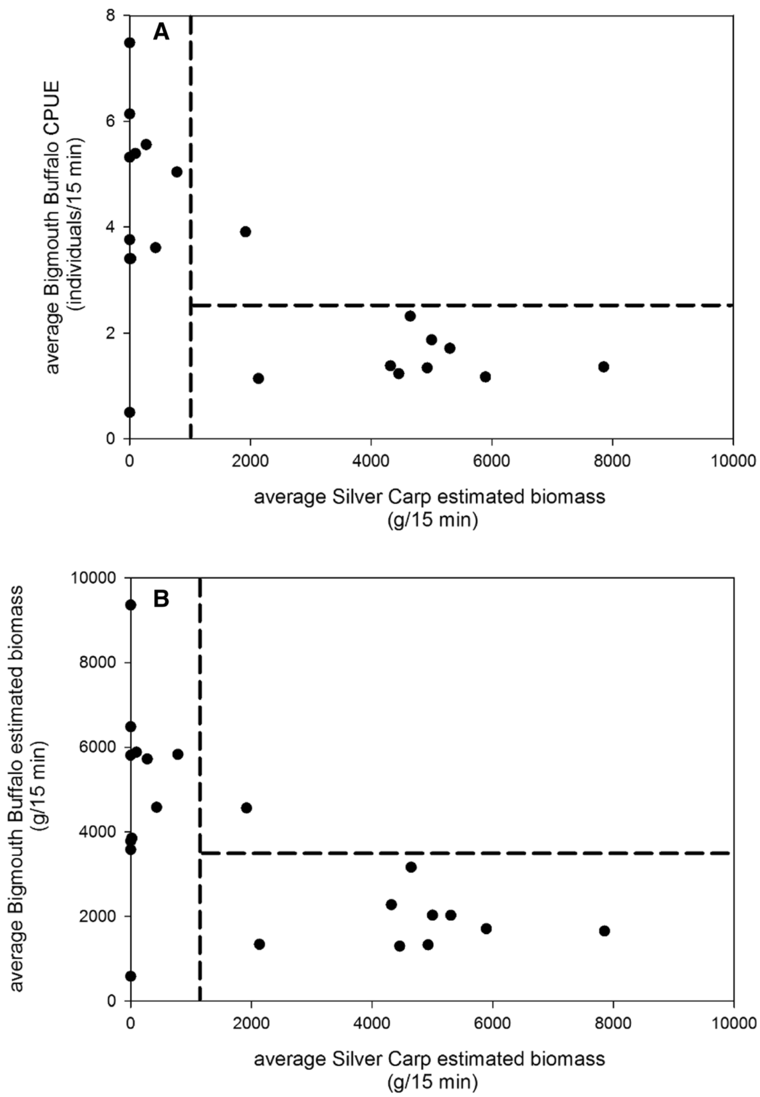

Fig. 3 Relationship between (**a**) average annual Bigmouth Buffalo catch per unit effort (fish per 15 min day electrofishing; CPUE) and average annual Silver Carp biomass (g per 15 min day electrofishing) and (**b**) average annual Bigmouth Buffalo biomass and average annual Silver Carp biomass (g per 15 min day electrofishing) during 1993–2013. Vertical and horizontal dashed lines represent hypothesized abiotic and biotic interactions, respectively (sensu Quist et al. 2003)

Cutthroat Trout *Oncorhynchus clarkii* (Richardson) densities were primarily driven by abiotic factors in streams where Brown Trout *Salmo trutta* (Linnaeus) and Brook Trout *Salvelinus fontinalis* (Mitchill) were introduced, but only when the introduced species were at low densities. Conversely, in streams with high densities of Brown Trout and Brook Trout, Cutthroat Trout densities were consistently lower and less variable likely due to competitive interactions. The authors suggest that biotic interactions among species can have an "overriding" adverse influence even when abiotic conditions are favorable [biotic- abiotic constraining hypothesis; sensu Quist et al. (2003) and results therein]. Taken together, these studies suggest that when non-native species are below a certain density, abiotic factors can regulate population dynamics. However, once densities of non-natives exceed a certain density, biotic interactions can have an adverse influence even when abiotic conditions are favorable. Similarly, we observed the CPUE and biomass of Bigmouth Buffalo were relatively higher and more variable during years of low Silver Carp biomass. However, during years of moderate to high Silver Carp biomass, the CPUE and biomass of Bigmouth Buffalo were consistently lower and less variable relative to other years. As this same relationship was not observed between Gizzard Shad and Silver Carp, Bigmouth Buffalo may be more adversely influenced by Silver Carp relative to Gizzard Shad as all linear regressions between Bigmouth Buffalo and Silver Carp CPUE and biomass were significant; only the relationship between Gizzard Shad biomass and Silver Carp CPUE was significant.

Differences in the life-histories between Gizzard Shad and Bigmouth Buffalo could explain the greater perceived effects on Bigmouth Buffalo. Gizzard Shad are able to filter smaller particles relative to Bigmouth Buffalo (Starostka and Applegate 1970; Drenner 1977), therefore, could have access to a broader size spectrum of food particles relative to Bigmouth Buffalo. Gizzard Shad can also often readily consume detritus when zooplankton may be limiting (Yako et al. 1996; Schaus et al. 2002). Although less data are available, Bigmouth Buffalo mainly consume zooplankton (primarily large zooplankters), and to a lesser degree, algae, diatoms, and detritus (Minckley et al. 1970; Starostka and Applegate 1970; Adámek et al. 2003; COSEWIC 2009). The ability of Gizzard Shad to consume smaller particles and readily incorporate detritus as a diet item may decrease competitive interactions with Asian carp in light of the recent declines in large zooplankton within the Illinois River (Sass et al. 2014). Spatial data regarding the utilization and plasticity of food resources by Bigmouth Buffalo is lacking in the literature, but knowledge of both in relation to varying densities of Silver and Bighead Carp could provide additional information regarding the degree of competitive overlap among these species.

Reproductive information may also explain why Bigmouth Buffalo may be more adversely influenced relative to Gizzard Shad since the establishment of Silver Carp. Bigmouth Buffalo spawn once per season (Johnson 1963; Becker 1983; COSEWIC 2009), whereas, Gizzard Shad can be serial spawners (i.e. capable of spawning multiple times per season; Bodola 1966). Serial spawning can be advantageous for fishes in stochastic environments when spawning success may be limited by factors such as water level fluctuation, food availability, or susceptibility to predation (Lambert and Ware 1984; Weddle and Burr 1991). As water levels on the Illinois River are regulated by locks and dams, the timing, duration, and magnitude of floods greatly differs from the natural hydrograph (Sparks et al. 1998) which can potentially limit species that rely on spring flooding for successful reproduction. Information regarding specific spawning requirements for both species in large rivers is generally lacking; however, the ability of Gizzard Shad to spawn multiple times in a season increases their probability of encountering favorable spawning conditions relative to Bigmouth Buffalo.

In addition to the relationship between native planktivores CPUE and biomass and that of Silver Carp, the seven additional years of continued, standardized, long-term monitoring data indicated that Gizzard Shad and Bigmouth Buffalo exhibit lower average CPUE and body condition compared to years prior to the establishment of Silver Carp. Notably, the CPUE of Gizzard Shad has become significantly lower post-establishment of Silver Carp [CPUE lower than previously reported by Irons et al. (2007)], while the CPUE of Bigmouth Buffalo has remained consistently lower compared to pre-establishment years. Although Gizzard Shad CPUE has declined, the reduction was more variable relative to Bigmouth Buffalo as Gizzard Shad still occasionally exhibited marked year class pulses (i.e. 2002, 2007, 2013). One potential mechanism for a reduction in CPUE may be related to the overall reduction in body condition of both native species. Studies have showed that reduced condition or reduction in food resources can adversely influence fecundity (Benejam et al. 2010; McBride et al. 2015 and references therein), therefore the potential exists to influence recruitment and population dynamics. Willis (1987) observed that the body condition of adult Gizzard Shad was positively related to the relative abundance of YOY Gizzard Shad during the following year. As the average body condition of Gizzard Shad has remained lower post-establishment of Silver Carp, the continued reduction in body condition may partly explain the lower average CPUE that has occurred since Irons et al. (2007). Bigmouth Buffalo average CPUE has remained low since the establishment of Silver Carp, despite a slight increase in the average body condition that has occurred after 2005.

The overall lower average body condition for both native planktivores indicate potential competitive interactions for planktonic resources may be continuing to occur, or are occurring to a greater degree (based on the significant decline in the CPUE of Gizzard Shad) congruent with the population increase of Silver Carp. As Silver Carp are more able to efficiently filter zooplankton relative to native planktivores (Starostka and Applegate 1970; Drenner 1977; Irons et al. 2009), native planktivores may have fewer resources available (Sass et al. 2014) or resources of lower quality (i.e. less energy to devote to body condition maintenance and/or growth). During periods of low zooplankton availability, Gizzard Shad have been shown to consume more detritus which can contribute to lower growth and condition due to lower nutritional quality of local detrital resources (Mundahl and Wissing 1987). Similarly, growth rates and survival of Gizzard Shad were much higher when feeding extensively on zooplankton compared to lower-quality detritus (Schaus et al. 2002; Kim et al. 2007). However, the relationship between growth and condition of Gizzard Shad and the reliance on detritus can vary based on the nutritional value/availability of food resources, in addition to, the age, size, and relative density of Gizzard Shad (Yako et al. 1996; Schaus et al. 2002; Kim et al. 2007). These additional factors, coupled with high densities of Silver Carp within a large dynamic river, make it difficult to infer causality, yet provide evidence that the availability of zooplankton can influence the body condition and growth of Gizzard Shad. Unfortunately, a paucity of data exists to make inferences on the reduced body condition of Bigmouth Buffalo, yet we speculate if zooplankton is limiting, Bigmouth Buffalo may experience lower growth and condition through similar feeding constraints as Gizzard Shad. However, as the body condition of Bigmouth Buffalo has slightly increased after 2005, the coinciding reduction in Bigmouth Buffalo CPUE (most notably after 2007) may have allowed for increases in overall body condition mediated by a reduction in intra- or interspecific competition (i.e. fewer individuals competing for potential limiting resources). Future studies examining the growth rates of Gizzard Shad and Bigmouth Buffalo in the presence and absence of Silver Carp could greatly aid in determining the magnitude of competition among these species.

While the establishment and population increase of Silver Carp corresponds to a reduction the body condition and CPUE of Gizzard Shad and Bigmouth Buffalo, other factors should be considered that could potentially contribute to or explain these reductions. Alterations in the hydrology from the construction of locks and dams and changing climatic patterns has resulted in increased water level fluctuations (Sparks et al. 1998). For instance, it appears an increase in flooding has occurred within recent decades as six of the ten highest crests on record have occurred since 1993 (NOAA 2017). These floods appear to be more erratic and in greater magnitude and frequency compared to historic data (Sparks et al. 1998) and these fluctuations can have both positive and negative influences on the fish community (Sparks et al. 1998; Koel and Sparks 2002). For example, YOY Gizzard Shad correlated with near average hydrological variables (e.g., maximum/minimum stage, duration of major floods, reversal of surface water elevation), whereas nonnative species (i.e. Common Carp *Cyprinus carpio* (*Linnaeus*) and Goldfish *Carassius auratus (Linnaeus)*) were more abundant during years with above average stage variability (Koel and Sparks 2002). As mentioned previously, fluctuations in water levels may influence native planktivore reproduction, particularly for Bigmouth Buffalo that spawn once per year. With changing climatic patterns, increased flows have been observed in the Mississippi River and runoff is predicted to increase throughout the Midwest (Palmer et al. 2009). Changes in these parameters have also likely altered nutrient and decomposition dynamics, yet a paucity of data exists for the Illinois River to fully investigate how these parameters may be influencing native planktivores.

Overall, Silver Carp are capable of influencing zooplankton and thus suppressing other planktivores (Irons et al. 2007; Sass et al. 2014; this study). Economic effects may also arise, as Bigmouth Buffalo are important commercially and economically (Bowler 2004), while Gizzard Shad are frequently used as bait among anglers (Evermann 1899; Wickliff 1932; Schneidermeyer and Lewis 1956) and are a common prey item for numerous economically important sport fishes (Bauer 2002, Ward et al. 2007, Shoup and Wahl 2009). Furthermore, this study demonstrates that effects of non-natives may become more pronounced as the duration of the invasion increases, as Gizzard Shad CPUE is now lower relative to findings by Irons et al. (2007). Pairwise analyses of native planktivore biomass and CPUE with Silver Carp biomass and CPUE also revealed additional insight into the relationships between these planktivores and provided evidence that Bigmouth Buffalo may be more negatively influenced by Silver Carp relative to Gizzard Shad. Focused research is still needed to identify the specific mechanisms influencing the body condition and CPUE of native planktivores, such as food-web dynamics, growth rates, and life-history traits that may influence species- specific responses to non-native species. In addition, future research should also consider investigating other potential mechanisms (e.g. water level fluctuations, climate change, altered nutrient dynamics) that may contribute to or explain the observed reductions in native planktivore body condition and CPUE. Finally, this assessment of the ecological responses to an invasion clearly shows the value of long-term monitoring to detect more subtle effects that may manifest later in the invasion process or change through time (Dodds et al. 2012; Strayer et al. 2014).

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