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COMPETITIVE INTERACTIONS AND COMMUNITY INFLUENCES AMONG INVASIVE
AND NATIVE FISHES AT DIFFERENT SPATIAL SCALES

BY

KIRSTEN A. NELSON

THESIS

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Master's Committee:

David H. Wahl, PhD
Gregory G. Sass, PhD
Associate Professor Angela D. Kent
Professor Carla Cáceres

ABSTRACT

Bighead carp (*Hypophthalmichthys nobilis*) are invasive, filter-feeding planktivores that established in the Mississippi River Basin following their unintentional introduction in the early 1970s. Their subsequent expansion has generated much concern about their potential to compete with native fishes due to their ability to efficiently remove zooplankton from the water column. Despite the reliance of fishes on zooplankton at various life stages, few studies have tested for potential influences of bighead carp on native filter-feeding planktivores, and no studies have addressed interactions between bighead carp and facultative planktivores.

The goal of my thesis was to test for competitive interactions and community influences between bighead carp and facultative planktivores at different spatial scales. I conducted three competition experiments involving bighead carp, bluegill (*Lepomis macrochirus*), and common carp (*Cyprinus carpio*). In the first experiment, I used a response surface design to independently vary the densities of bighead carp and bluegill in mesocosms. This design allowed for the investigation of inter- and intra-specific competitive interactions for both species, as well as the influences of the fishes on zooplankton, macroinvertebrates, and environmental variables. My results suggested that bluegill growth was density dependent, and bighead carp benefited from the presence of bluegill, which was likely due to shifts in nutrient cycling. To test whether the same influences occurred at a larger spatial scale, inter- and intra-specific competition was examined for bluegill with bighead carp in 0.4-hectare experimental ponds. With increased environmental complexity and niche opportunities, my results from the pond experiment differed from the mesocosm experiment, as bluegill were found to benefit from bighead carp presence. Plausible explanations for my results include increases in macroinvertebrate density or biomass via sediment enrichment from bighead carp excretions,

changes in macroinvertebrate composition, and/or differences in bluegill foraging behavior. My results suggest that differences in species foraging behavior can modify communities in unexpected ways through changes in energetic pathways. Competition and facilitation between species is possible due to these modifications regardless of species origin. I also investigated competitive interactions between two invasive species, common carp and bighead carp, using a response surface design in mesocosms. My experiment suggested that intra-specific competition had a greater influence on both species, suggesting coexistence is likely. In all experiments, bighead carp had strong negative influence on zooplankton densities, which supports concerns that this invasive species has the potential to reduce an important food resource and modify aquatic communities.

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In loving memory of Debra M. Nelson

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CHAPTER 1: GENERAL INTRODUCTION

Bighead carp

The establishment of bighead carp (*Hypophthalmichthys nobilis*) in North America has the potential to have ecosystem-wide effects. Bighead and silver carp (*H. molitrix*) were imported to the U.S. in 1973 by a commercial fish producer (Kolar et al. 2007). Both species were then transported widely around the Midwest by various state, federal, and private agencies to research their usefulness in aquaculture and sewage treatment (Kelly 2011). Soon after their introduction, bighead and silver carp escaped into the Mississippi River. The carps' populations have grown exponentially in the productive Mississippi River Basin, and their steady movement northward has generated great concern that they will invade the Laurentian Great Lakes (Chick and Pegg 2001, Mandrak and Cudmore 2010, Patel et al. 2010, Sass et al. 2010, Rasmussen et al. 2011, Sass et al. 2014). Bighead and silver carp are filter-feeding planktivores that filter zooplankton and phytoplankton from the water column using specialized gill rakers (Burke et al. 1986, Kolar et al. 2007). Their large size and constant consumption of plankton has been found to suppress plankton densities, potentially reducing this important food source to inadequate densities for other fishes (Chick and Pegg 2001, Radke and Kahl 2002, Irons et al. 2007, Sampson et al. 2009, Sass et al. 2014).

Although there is some empirical evidence to suggest that bighead and silver carp are negatively affecting the Mississippi River Basin ecosystem (e.g. Sass et al. 2014), very few studies have tested for potential competitive interactions with native fishes. Most tests of competition concerning bighead and/or silver carp have focused on their potential effect on paddlefish (*Polyodon spathula*), bigmouth buffalo (*Ictiobus cyprinellus*), and gizzard shad (*Dorosoma cepedianum*), all non-sport, filter-feeding planktivores native to the Mississippi River Basin. Schrank et al. (2003) examined the effect of age-0 bighead carp on age-0 paddlefish in a

mesocosm experiment and found that relative growth of paddlefish declined in the presence of bighead carp. Sampson et al. (2009) reached a slightly different conclusion when comparing dietary overlap among silver and bighead carp and paddlefish, bigmouth buffalo, and gizzard shad. Silver and bighead carp had the greatest dietary overlap with gizzard shad, followed by bigmouth buffalo, and were dissimilar to paddlefish (Sampson et al. 2009). Contrasts in these findings may have been due to differences in environmental conditions, the zooplankton communities, and size of the fishes. Irons et al. (2007) analyzed long-term data before and after bighead and silver carp establishment in one reach of the Illinois River to test for potential competitive interactions with gizzard shad and bigmouth buffalo. Irons et al. (2007) found reduced body condition of both native species following the establishment of the invasives. Overall, these studies suggest that bighead carp in the Mississippi River Basin could have detrimental effects on native fishes; however, no studies to date have tested for competitive interactions between bighead carp and facultative planktivores, fishes that rely on zooplankton for only part of their life cycle.

Competition and facilitation

Competition among species has been intensively studied in ecology and influences the distribution, abundance, and resource use of all organisms (Connell 1983, Mittelbach 2012). Generally, individuals experience greater competitive interactions from within-species interactions, or intra-specific competition, than from between-species interactions, or inter-specific competition, due to greater overlap in resource and habitat use (Platell et al. 2006, Mittelbach 2012). The relative strength of intra-specific competition over inter-specific competition allows numerous species to coexist, as theory maintains that complete competitors will result in competitive exclusion (Hardin 1960, Schoener 1982). Ecological differentiation is

necessary for coexistence, and resource partitioning, through modifying diet or habitat use, can occur between two species with resource use overlap to reduce the intensity of inter-specific competition (Schoener 1982, Holbrook and Schmitt 1989, Genner et al. 1999, Liso et al. 2013).

Many studies involving competition and invasive species have tested for the detrimental effects of an invasive on an invaded ecosystem and native taxa (Baxter et al. 2007, Herborg et al. 2007, Hayden et al. 2013, Jackson and Britton 2013). Invasive species are often so successful because of their ability to exploit resources more efficiently than the native taxa present, which can cause changes in community composition, reduced reproductive success, or competitive exclusion (Shea and Chesson 2002, Simberloff 2011). However, competition is not the only interaction possible involving invasive species. Although understudied, facilitation is another possible outcome of community interactions, regardless of species origin (Bruno et al. 2003, Rodriguez 2006, Griffen et al. 2008). Any species modifying its environment (e.g. modifies nutrient cycling) may benefit other taxa, even as other species are negatively influenced (Altieri et al. 2010).

Facilitative interactions involving invasive species have often been studied between two or more invasive species (Simberloff 2006). Ever since Simberloff and Von Holle (1999) proposed the existence of an “invasional meltdown”, which is defined as synergistic interactions among invaders causing an acceleration of negative effects on native ecosystems, research concerning invasive species has investigated this phenomenon (Ricciardi 2001, Adams et al. 2003, Griffen and Byers 2009, Johnson et al. 2009, Matsuzaki et al. 2009c). After the accumulation of several years of data, the “invasional meltdown” hypothesis was revisited by Simberloff, who concluded that an actual “invasional meltdown: was not, to date, supported in the data (Simberloff 2006): however, the result of those studies had found situations where two

invasive species had facilitated each other to the detriment of their invaded ecosystem (e.g. Morales and Aizen 2002, Adams et al. 2003, Grosholz 2005). Investigations considering facilitation involving invasive species have neglected to consider instances where invasive species facilitated native species (Rodriguez 2006). Invasive ecosystem engineers, or organisms that significantly modify their environment, can benefit natives through increasing habitat complexity, modifying nutrient cycling, providing a limiting resource, or ameliorating predation or competition (Rodriguez 2006). Examples of facilitation of natives by an invasive species in aquatic ecosystems include tidal habitats being modified by invasive algae and kelp, which increased habitat complexity and facilitated native snails and other species (Thomsen 2010, Guidone et al. 2014). Zebra mussels (*Dreissena polymorpha*), an invasive mussel in the Laurentian Great Lakes, have been found to facilitate adult yellow perch (*Perca flavescens*) due to modifying benthic macroinvertebrate densities and community structure via sediment enrichment and increased habitat heterogeneity (Thayer et al. 1997).

Facilitation of an invasive species can also occur from a native species. Success of an invasive legume (*Melilotus officinalis*) was found to be facilitated by native grasses due to reductions in the intensity of environmental stressors (Smith et al. 2004). Additionally, a native Hawaiian limpet (*Siphonaria normalis*) facilitated an invasive barnacle (*Chthamalus proteus*) by removing algae from rocky surfaces, easing the ability of the invasive species to colonize new habitat (Zabin and Altieri 2007). Once the invasive barnacle was established, the native limpet was less likely to be able to colonize (Zabin and Altieri 2007). A South American study found that a native cordgrass (*Spartina densiflora*), considered an ecosystem engineer due to its ability to colonize rocky shorelines, facilitated an invasive barnacle (*Balanus glandula*) by helping

retain the barnacle and assisting with colonization (Cruz Sueiro et al. 2013). Studies such as these highlight the complex relationships that can develop between invasive and native species.

Overall, facilitation appears to be an understudied phenomenon of species interactions (Bruno et al. 2003). Facultative interactions can occur between many organisms regardless of their evolutionary history and may occur when a species can help alleviate environmental variables such as thermal stress or substrate instability (Rodriguez 2006, Altieri et al. 2010, Cruz Sueiro et al. 2013). The interplay of competition and facilitation among invasive and native species emphasizes the diverse array of possible ecosystem interactions and highlights the necessity of investigating the role invasive species play in novel ecosystems.

Invasive species ecology

Due to intentional and unintentional anthropogenic introductions, invasive species are a driving force of global ecosystem change. Although complete understanding of ecosystem alteration is often unknown, invasive species have increased extinction rates, altered fire regimes, contributed to biotic homogenization, and altered nutrient cycling (Mack et al. 2000, Olden et al. 2006, Elvidge and Ricciardi 2007). Community influences through predation (Sepulveda et al. 2013), competition (Baxter et al. 2007), and shifts in stable states (Parkos et al. 2003) by invasive species have caused drastic changes in some ecosystems. The success of invasive species is often attributed to superior competitive abilities compared to native species, phenotypic plasticity, niche construction, and niche separation (Perkins and Nowak 2013). Freshwater ecosystems are particularly vulnerable to the influences of invasive species due to their high biodiversity and high endemism between basins (Strayer and Dudgeon 2010). This has led to a higher proportion of more detrimental invaders in aquatic systems when compared to terrestrial systems (Ricciardi and Kipp 2008) resulting in homogenization of North American

aquatic fauna (Rahel 2000b, Ricciardi 2001, Olden et al. 2006, Elvidge and Ricciardi 2007). Aquatic invasive species are introduced in a myriad of ways, including ballast water release, aquaculture, bait, sport, and the pet industry (Kolar and Lodge 2002). Once established, aquatic invasive species may compete for limiting resources (Baxter et al. 2007), predate on native taxa (Sepulveda et al. 2013), alter nutrient cycling (Matsuzaki et al. 2009a), hybridize (Boyer et al. 2008, Lamer et al. 2010), or spread disease (Gozlan et al. 2009).

The role of species diversity and invasion success is not fully understood. As invasive species and their influences on invaded ecosystems began to garner attention, it was hypothesized that the establishment and spread of invasive species could be prevented or reduced through increased species diversity or 'biotic resistance' due to reduced niche space (Elton 1958). Although some small scale studies found support for the idea of biotic resistance (Tilman 1997, Carey and Wahl 2010b, Kimbro et al. 2013), at larger scales, it was found that more diverse communities often host more invasive species, suggesting biotic acceptance (Fridley et al. 2007). The contrasting results at different spatial scales were described as an invasion paradox (Fridley et al. 2007) and is thought to be influenced by a multitude of factors that vary across temporal and spatial scales, such as climate, vegetation structure, disturbance, resource availability, propagule pressure, and associated ecosystem processes (Stohlgren et al. 2006b). Additionally, competition and predation are thought to be the driving influences between invasive and native species; however, facilitation is also being found to play an important role (Bruno et al. 2003, Rodriguez 2006). Simultaneous anthropogenic alterations, such as habitat loss and pollution, can also make actual invasive effects difficult to elucidate (Gurevitch and Padilla 2004, Ricciardi 2007). Ultimately, it appears that while increased species richness can be

preventative to invasive species at a microhabitat scale, successful establishment is more likely due to favorable environmental variables (Ricciardi 2001, Shea and Chesson 2002, Alpert 2006).

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CHAPTER 2: COMPETITIVE INTERACTIONS AND COMMUNITY INFLUENCES OF INVASIVE BIGHEAD CARP AND NATIVE BLUEGILL IN MESOCOSMS¹

ABSTRACT

Non-native species introductions are a global phenomenon, and aquatic communities are particularly vulnerable to direct and indirect modifications to ecosystem processes caused by these invaders. Invasive bighead carp (*Hypophthalmichthys nobilis*) are established in the Mississippi River Basin, yet few studies have tested for their effects on native fishes. Previous studies have suggested negative effects on obligate planktivorous fishes. Here, we considered the potential influences of bighead carp on the growth of bluegill (*Lepomis macrochirus*), a native facultative planktivore. We tested for inter- and intra-specific competition, changes in invertebrate densities, and environmental variables using a response surface design in a replicated mesocosm experiment. Bluegill growth was negatively influenced by inter- and intra-specific competition; however, bighead carp were facilitated by the presence of bluegill. Bighead carp also caused large reductions in macrozooplankton densities and suppressed rotifer populations, whereas rotifer densities increased in bluegill-only mesocosms. Our results suggest that an invasive species can be indirectly facilitated by a native species via community modifications due to differences in foraging ecology.

INTRODUCTION

The introduction, establishment, and spread of non-native species in novel environments is an anthropogenically driven source of global ecosystem modification, and aquatic ecosystems are particularly vulnerable to these alterations by non-native species due to their insular nature (Mack et al. 2000, Ricciardi 2007, Ricciardi and Kipp 2008, Strayer and Dudgeon 2010). Once established, non-native species often exploit resources more efficiently than native species,

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causing changes in resource abundances and nutrient cycling (Shea and Chesson 2002, Chumchal et al. 2005, Paolucci et al. 2013). These alterations by invasive species can have consequences for the population dynamics of native species (Feiner et al. 2013). For example, invasive planktivorous fishes have been shown to shift plankton communities to smaller individuals, not only altering plankton community dynamics, but also reducing the amount of suitable prey for other planktivorous fishes (Brooks and Dodson 1965, DeVries and Stein 1992, Chick and Pegg 2001). Because most fishes are planktivorous during larval stages, changes in plankton communities and biomass as a result of invasive planktivorous fishes have implications for all fishes, regardless of later ontogenetic foraging shifts (Cushing 1990, Chick and Pegg 2001, Fiksen and Jorgensen 2011).

Invasive bighead carp (*Hypophthalmichthys nobilis*) consume zooplankton, phytoplankton, and occasionally detritus (Opuszynski 1981, Burke et al. 1986, Lieberman 1996, Schrank et al. 2001, Kolar and Lodge 2002). Due to their rapid growth rates and filter-feeding capabilities, bighead carp have been intentionally introduced to 74 countries and territories globally, mostly for aquaculture and biological control of phytoplankton (Kolar et al. 2007). Since their simultaneous introduction to the Midwestern United States with silver carp (*Hypophthalmichthys molitrix*) in the 1970s, bighead carp escaped confinement, successfully established in the Mississippi River Basin, and population growth has been increasing (Kelly 2011, McClelland et al. 2012). As planktivores, bighead carp have the potential to compete with most native fishes at the larval stages and native obligate planktivores into adulthood (Chick and Pegg 2001).

Tests for the effects of bighead carp on native North American fishes have thus far focused exclusively on filter-feeding planktivores. A manipulative competition experiment

found that the relative growth of bighead carp was negative due to intra-specific competition and positive for inter-specific competition with paddlefish (*Polyodon spathula*) (Schrank et al. 2003). Paddlefish showed negative growth with inter- and intra-specific competition; however, the decline was greater with inter-specific competition. Schrank et al. (2003) concluded that bighead carp may have filtered plankton more efficiently than paddlefish and depleted food resources. Two additional field studies examined diet overlap among bighead carp, silver carp, paddlefish, bigmouth buffalo (*Ictiobus cyprinellus*), and gizzard shad (*Dorosoma cepedianum*) as well as changes in body condition of bigmouth buffalo and gizzard shad pre- and post-carp invasion (Irons et al. 2007, Sampson et al. 2009). Bighead and silver carp were implicated in reducing body condition of bigmouth buffalo and gizzard shad, and diet studies revealed that bighead and silver carp consumed plankton sizes that overlapped most with gizzard shad, followed by bigmouth buffalo, and then paddlefish (Irons et al. 2007, Sampson et al. 2009). These three studies have provided insight into the influences of bighead and silver carp on native obligate planktivores, but none has tested for effects on a native facultative planktivore.

Bluegill (*Lepomis macrochirus*) are a popular sportfish native to the Mississippi River Basin (Rypel 2011). Larval bluegill are zooplanktivorous and undergo an ontogenetic diet shift to macroinvertebrates; however, adults have been found to shift back to reliance on large zooplankters (Mittelbach 1981, Mittelbach and Osenberg 1993). Overall, bluegill are considered omnivorous and rely upon zooplankton and macroinvertebrate prey (Spotte 2007), indicating potential for diet overlap with bighead carp. In large rivers, floodplain lakes are an important habitat for adult and age-0 bluegill (Shoup and Wahl 2009). Bluegill have been shown to grow larger and have better body condition in floodplain lakes, yet still depend on riverine habitats to survive following seasonal flood pulses, when floodplain lake desiccation occurs (Rypel et al.

2012). Larval and juvenile bighead carp utilize floodplain lakes, as well as other off-channel, vegetated waters as nursery areas (Kolar et al. 2007). Adult bighead carp inhabit large rivers, selecting for channel borders and low velocity habitats such as behind wing dikes (Kolar et al. 2007, Degrandchamp et al. 2008). Potential diet overlap and the use of similar habitats by both species suggest competitive interactions are plausible.

The objectives of our study were to test for inter- and intra-specific competitive interactions bighead carp and bluegill growth, as well as to examine the influence of these fishes on the invertebrate communities. We expected greater reductions in growth at high fish densities than at low densities, as well as stronger effects of intra-specific competition than inter-specific competition among bighead carp. Although conspecifics often have greater competitive interactions due to niche overlap, a hallmark of highly successful invasive species is their ability to exploit a shared resource more efficiently than native species (Shea and Chesson 2002, Forrester et al. 2006, Asquith and Vonesh 2012, Mittelbach 2012). We also expected bluegill and bighead carp to alter the zooplankton community by reducing densities; however, we hypothesized that bighead carp would have a larger effect because of their ability to exploit a wider range of plankton sizes than bluegill (Kolar et al. 2007).

MATERIALS AND METHODS

Experimental design

We evaluated competitive interactions between age-0 bighead carp and age-1 bluegill in replicated experimental food webs in mesocosms (1325-L polyethylene tanks) at the Sam Parr Biological Station (SPBS), Kinmundy, Illinois, USA. Mesocosms were placed under cover to prevent direct sunlight at two locations at SPBS and filled with water mixed from Forbes Lake, Kinmundy, Illinois, USA and a pond located at SPBS. Water was filtered through a 64 μm mesh net to prevent larval fish introduction and plankton were allowed to colonize. Macrozooplankton

from a number of local lakes were collected with a 64 μm mesh zooplankton sampler, introduced to the mesocosms after two weeks, and allowed to populate for four weeks before fish were introduced. During this four-week period, the mesocosms were homogenized by periodically exchanging water. We placed two white tiles (116.6 cm^2) at the bottom of each mesocosm to quantify colonization of sessile, benthic macroinvertebrates.

We used a response surface experimental design to test for intra- and inter-specific competition between bluegill and bighead carp. The densities of the two species were varied independently, allowing inferences to be made about intra- and inter-specific competition (Inouye 2001, Asquith and Vonesh 2012). We randomly assigned eight treatments with five replicates to 40 mesocosms. The first treatment was a fishless control to monitor temporal changes in taxa densities and environmental variables (Treatment 1). Four of the treatments were single species with low (5 fish/mesocosm) and high (10 fish/mesocosm) densities of bluegill (Treatment 2, 3) or bighead carp (Treatment 4, 5). The final three treatments combined both species: low-density bluegill and low-density bighead carp (10 fish/mesocosm, Treatment 6); high-density bluegill and low-density bighead carp (15 fish/mesocosm, Treatment 7); and low-density bluegill and high-density bighead carp (15 fish/mesocosm, Treatment 8). Total fish biomass was held constant within low and high-density treatments (initial fish biomass among treatments: $F_{6,43}=1.93$; $P=0.10$). Bluegill were collected from natural lakes and ponds near the SPBS, and bighead carp were obtained from Osage Catfisheries, Inc., Missouri, USA. Both species ranged in total length from 50 -100 mm and individual fish biomass ranged from 3 - 11 g. Bluegill density was within the range of natural systems and previous food web studies (Hackney 1979, Johnson et al. 1988, Carey and Wahl 2010b), and bighead carp density was

matched to those of the bluegill. During the first week, any fish mortalities were replaced with a similarly sized fish.

Data collection

Limnological sampling (i.e. temperature, dissolved oxygen, total phosphorus, chlorophyll *a*, turbidity, light intensity, plankton density) was conducted immediately prior to fish introduction and then on a weekly basis until the end of the 29 day experiment. Temperature (°C) and dissolved oxygen (mg/L) were measured from the center of each mesocosm with a model 55 YSI meter. Water column samples were collected (2 x 45 mL samples) to quantify total phosphorus and frozen within one hour of collection until they could be processed in the laboratory by oxidizing with persulfate, adding a molybdate reagent, and measuring absorbance in a spectrophotometer (ug / L; Wahl et al. 2011). Water column chlorophyll *a* was obtained by filtering 100 mL of water onto glass fiber filters (0.7 µm pore size [Millipore, Billerica, Massachusetts, USA]), extracting chlorophyll *a* in 90% acetone for 24 hours, and then measuring fluorescence using a fluorometer (Turner Design, model TD700, Sunnyvale, California, USA)(Carey and Wahl 2011b). Turbidity was measured in nephelometric units (NTU) with an electronic turbidimeter from a water sample taken throughout the water column (Wahl et al. 2011). Light intensity was measured in lux at the center of each mesocosm at mid-depth in the water column using an underwater photometer (Protomatic, Dexter, Michigan, USA). Zooplankton were sampled with a 70 mm diameter x 0.4 m long (1.5 L) vertical tube sampler and preserved in a 10% buffered formalin and rose Bengal solution with baking soda to preserve rotifer identification characteristics (DeVries and Stein 1992, Chick et al. 2010). On each sampling date, three tube samples (1.5 L each) were collected from random locations within the mesocosm, combined, and filtered through a 20 µm mesh net (Chick et al. 2010). On the final

sample date, final fish length and weight (nearest mm, 0.1 g) were recorded. Fifteen tube samples were taken from each mesocosm to ensure accurate population estimates with low zooplankton densities. We collected sessile, benthic invertebrates at the beginning and end of the experiment. One tile was removed from the bottom of the mesocosm on each sample date and any sessile macroinvertebrates were washed into a sample jar. Ethanol with rose Bengal was added to preserve the samples. Five macrozooplankton samples, one rotifer sample, three total phosphorus samples, and three chlorophyll *a* samples were misplaced or mishandled over the duration of the experiment and were not included in the final analyses.

In the laboratory, macrozooplankton and rotifers were separated by filtration of samples through 55 μm and 20 μm mesh nets. Macroinvertebrates and macrozooplankton in the 55 μm samples were enumerated and identified under a dissecting microscope to the lowest possible taxonomic level (Carey and Wahl 2010b). In the 20 μm samples, up to 400 rotifers were identified under a compound microscope to the lowest possible taxonomic level.

Statistical analyses

Initial measurements of all response variables were tested for treatment differences using a one-way analysis of variance (ANOVA) to ensure similarity at the beginning of the experiment. We then used multiple linear regression models to test for treatment effects on average change in total fish length and weight per day, as well as change in benthic taxa density, benthic taxa richness, and abundant individual benthic taxa (Forrester et al. 2006, Asquith and Vonesh 2012). Due to repeated sampling through time, macrozooplankton and rotifer density and richness measurements were averaged by mesocosm and examined using multiple linear regression models. The independent variables in the regression models were bluegill density, bighead carp density, and their interaction. Since mesocosms were housed at two locations at

SPBS, location was used as a block and treated as a random variable. Separate models were constructed for each response variable. Parameter estimates were obtained using the SOLUTION statement in PROC MIXED (SAS[®]). This model tested the null hypothesis that the regression coefficients (β) had a slope equal to zero ($H_0: \beta=0$) for each response variable. Errors were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Brown and Forsythe's Test for Homogeneity of Variance). Statistical significance was determined at the $\alpha = 0.05$ level. If residuals failed to meet the assumptions of ANOVA, a \log_e transformation was applied.

To supplement the regression analyses in determining whether inter- or intra-specific competition had a greater effect on bluegill and bighead carp, we calculated an index of competitive effects (Hu and Tessier 1995, Caceres 1998) for two response variables (change in fish length and biomass). Low and high-density single-species treatments were incorporated (intra-specific interactions; bluegill, Treatment 2, 3; bighead carp, Treatment 4, 5) as well as the low bluegill and low bighead carp treatment (inter-specific interactions; Treatment 6). Mixed-species treatments with the greatest total fish density (15 fish; Treatment 7, 8) were not included due to a limiting number of fish density combinations. The competition index (CI) was calculated as:

Equation 1.
$$CI = \frac{(\bar{Y}_c - \bar{Y}_e)}{\bar{Y}_c}$$

where \bar{Y}_c is the mean of the response variable from a single-species low-density treatment (5 fish) and \bar{Y}_e is the mean of the response variable from either a single-species or mixed-species high-density treatment (10 fish). The relative strength of inter- to intra-specific competition was estimated by calculating the ratio of their CI. A ratio of one indicates that the two species had an equivalent per capita influence on the focal species. Ratios > 1 indicate that inter-specific

competition had a greater effect on the focal species, whereas ratios < 1 indicate that intra-specific competition had a greater effect (Hu and Tessier 1995).

Differences in total macrozooplankton density and richness, total rotifer density and richness, taxa-specific densities, water temperature, dissolved oxygen, turbidity, light intensity, chlorophyll *a*, and phosphorus among treatments were tested with repeated-measures ANOVA with a Kenward Roger correction (SAS[®], PROC MIXED). The CLASS statement included Treatment and Time, and Block was treated as a random variable. The full ANOVA model contained the terms Treatment, Time, and Treatment x Time. This model tested two null hypotheses for each response variable regarding differences in mean values among treatments or changes in response variables over time. The first null hypothesis was no difference in response variables across treatments, and the second null hypothesis was no change in the response variables over time. Residual errors were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Brown and Forsythe's Test for Homogeneity of Variance) to meet the assumptions of ANOVA. A \log_e transformation was applied to response variables if initial residuals failed to meet the assumptions of ANOVA. Serial correlation among sampling dates due to repeated measurements was accounted for by fitting several covariance structures to the data (SAS[®], PROC MIXED) and selecting the best fitting model based on the corrected Akaike's information criterion (AICC; Littell et al. 2000). Statistical significance was determined at the $\alpha = 0.05$ level. Specific comparisons among treatment groups were investigated using CONTRAST statements. To reduce the probability of committing a Type I error, post-hoc CONTRAST statement comparisons were subject to a Bonferroni correction based on the number of treatment group comparisons.

RESULTS

Fish effects

We held initial fish biomass constant between species and across treatments ($F_{6,43}=1.93$; $P=0.10$), but initial fish length varied ($F_{6,43}=6.0$; $P=0.001$) due to species-specific morphologies as bluegill are deeper-bodied than bighead carp. Bluegill growth decreased as conspecific and heterospecific densities increased (Figure 1 a, b). The competition index indicated that intra-specific competition had a greater influence on bluegill change in length and biomass (Table 1); however, not all treatments were included in the comparisons. Regression parameters indicated that per capita effect of adding bighead carp and bluegill had a significant negative influence on the change in bluegill length and weight (Table 2; Figure 1 a, b), suggesting inter- and intra-specific competition negatively influenced bluegill growth. The interaction terms of the regression models for change in length and biomass were positive and significant (Table 2; Figure 1 a, b). Responses in bluegill biomass and length varied with bighead carp densities (Table 2; Figure 1 a, b). When bighead carp were absent, there was a strong negative intra-specific influence on bluegill growth (Change in length, $F_{1,19}=18.37$, $P=0.0004$; Change in biomass, $F_{1,19}=32.89$, $P<0.0001$) following Bonferroni correction ($P\leq 0.0125$). When bighead carp density was increased, the intra-specific interaction was lost (Change in length, $F_{1,19}=0.97$, $P=0.34$; Change in biomass, $F_{1,19}=2.62$, $P=0.12$).

Bighead carp growth was facilitated by the presence of bluegill (Table 2; Figure 1 c, d). The interaction terms of both regression models were not significant and slope parameter estimates indicated that increasing bluegill density had a significant positive influence on per capita bighead carp growth (Table 2). The competition index suggested that intra-specific competition had a greater negative influence on change in bighead carp length and biomass

(Table 1); however, the slope estimates indicated increasing bighead carp density did not have a strong influence (Table 2).

Limnological sampling

There were no significant differences in temperature, dissolved oxygen, turbidity, or light intensity among treatments (Table 5). Time was significant for all four variables and the interaction between treatment and time were not significant (Table 5). For chlorophyll *a* concentration, time (Time; $F_{4,28.1}=15.07$; $P<0.0001$) but not treatment (Treatment; $F_{7,32}=1.14$; $P=0.36$), was significant; however, an interaction was present between treatment and time (Treatment*Time; $F_{28,57.2}= 2.01$; $P=0.01$). Treatments containing fish had significantly higher chlorophyll *a* concentrations than the fishless control (Figure 6). Initial chlorophyll *a* concentrations did not vary among treatments ($F_{7, 30.9} = 0.89$; $P=0.53$) and, with a Bonferroni correction ($P\leq 0.017$), there were no differences through time among bluegill only, bighead carp only, and mixed species treatments ($F_{2, 32} = 0.24$; $P=0.79$; Figure 6). Additive effects were also not significant (Increasing BHC with BLG constant; $F_{2, 32} = 0.12$; $P=0.89$; Increasing BLG with BHC constant; $F_{2, 32} = 0.04$; $P= 0.96$). Initial phosphorus concentrations were similar among treatments ($F_{7, 72.1} = 0.91$; $P=0.50$). Phosphorus concentration varied over time (Time; $F_{4, 123} = 4.83$; $P= 0.001$), but not by treatment or the interaction between treatment and time (Treatment; $F_{7, 36.9} = 1.05$; $P= 0.41$; Treatment*Time; $F_{28,122} = 0.86$; $P= 0.67$; Figure 6). With a Bonferroni correction ($P\leq 0.0125$), treatments containing fish were not significantly different from the fishless control ($F_{1, 36.8} = 0.05$; $P= 0.82$); however, bighead carp only treatments were significantly lower than bluegill only and mixed species treatments ($F_{1,36.9}= 41.48$; $P<0.0001$; Figure 6). Additive effects were not significant (Increasing BHC with BLG constant; $F_{2, 37.1} = 0.73$; $P=0.49$; Increasing BLG with BHC held constant; $F_{2, 37.1} = 0.70$; $P= 0.51$).

Macrozooplankton

The most abundant macrozooplankton taxa were cyclopoid copepods, copepod nauplii, *Bosmina* spp., Chydoridae, *Ceriodaphnia* spp., and Ostracoda (>96% of total macrozooplankton density; Table 3). Other macrozooplankton included *Daphnia* spp., Sididae, *Leptodora* spp., *Simocephalus* spp., and *Scapholeberis* spp. of the Order Cladocera, as well as Calanoida and Harpacticoid of the Subclass Copepoda. Macrozooplankton densities across treatments were similar before fish were added (Treatment; $F_{7,28} = 0.62$; $P = 0.73$). Macrozooplankton density varied through time, treatment, and the interaction between time and treatment (Time; $F_{4,123} = 80.48$; $P < 0.0001$; Treatment; $F_{7,31} = 8.83$; $P < 0.0001$; Treatment*Time; $F_{28,123} = 5.06$; $P < 0.0001$; Figure 2). Following a Bonferroni correction ($P \leq 0.0083$), bluegill only treatments had significantly greater macrozooplankton densities than bighead carp only treatments (BLG vs BHC; $F_{1,31.1} = 15.54$; $P = 0.0004$) and mix species treatments (BLG vs MIX; $F_{1,31.2} = 34.35$; $P < 0.0001$), but similar densities to the control (BLG vs CONTROL; $F_{1,30.8} = 0.31$; $P = 0.58$; Figure 2). The bighead carp only treatments were similar to the mixed species treatments (BHC vs MIX; $F_{1,30.9} = 2.40$; $P = 0.13$), but treatments containing bighead carp had significantly lower macrozooplankton densities than the control (BHC vs CONTROL; $F_{1,30.6} = 14.36$; $P = 0.0007$; MIX vs CONTROL; $F_{1,30.6} = 27.52$; $P < 0.0001$; Figure 2). Regression parameters indicated that the per capita influence of bluegill and bighead carp were not significant; however, bighead carp had 2.5 times more negative influence on macrozooplankton than bluegill (Table 4).

Cladoceran density varied with time (Time; $F_{4,118} = 33.88$; $P < 0.0001$) and treatment (Treatment; $F_{7,40.7} = 8.14$; $P < 0.0001$), but the interaction term was not significant (Treatment*Time; $F_{28,120} = 1.49$; $P = 0.07$; Figure 3). Following a Bonferroni correction ($P \leq 0.0083$), cladocerans in bluegill treatments were similar to the control, but were significantly

higher than all other treatments (BLG vs CONTROL; $F_{1, 40.2} = 0.64$; $P=0.43$; BLG vs BHC, MIX; $F_{1,41.1}=32.34$; $P<0.0001$; Figure 3). Cladoceran densities in bighead carp treatments were significantly lower than the control (BHC vs CONTROL; $F_{1,40}=23.46$; $P<0.0001$), but not from mixed species treatments (BHC vs MIX; $F_{1, 40.6}=0.08$; $P=0.78$; Figure 3). As bighead carp were added, there was a significant decrease in cladoceran density (Increasing BHC with BLG constant; $F_{2, 41.2} = 15.49$; $P<0.0001$); however, adding bluegill while keeping bighead carp density constant did not have a similar effect (Increasing BLG with BHC constant; $F_{2, 40.7}=0.42$; $P=0.66$).

Copepod density varied by time (Time; $F_{4, 119} = 85.14$; $P<0.0001$), treatment (Treatment; $F_{7, 34.8} = 9.11$; $P<0.0001$), and their interaction (Treatment*Time; $F_{28, 119} = 4.62$; $P<0.0001$; Figure 3). Following a Bonferroni correction ($P\leq 0.0083$), bluegill only treatments were significantly higher than treatments with bighead carp (BLG vs BHC, MIX; $F_{1, 35} = 32.16$; $P<0.0001$), but not the control (BLG vs CONTROL; $F_{1, 34.6} = 0.28$; $P=0.60$; Figure 3). Bighead carp only treatments were significantly lower than the control (BHC vs CONTROL; $F_{1, 34.5} = 10.76$; $P=0.002$) and similar to the mixed species treatments (BHC vs MIX; $F_{1, 34.8} = 6.5$; $P=0.015$; Figure 3). Increasing bighead carp density decreased copepod density; however, increasing bluegill density did not have a significant influence (Increasing BHC with BLG constant; $F_{2, 35.1} = 18.55$; $P<0.0001$; Increasing BLG with BHC constant; $F_{2,34.9} = 4.07$; $P= 0.03$).

Macrozooplankton richness was similar across treatments before the fish were introduced ($F_{7, 153} = 1.14$; $P=0.34$). Macrozooplankton richness varied by treatment (Treatment; $F_{7, 31} = 4.33$; $P= 0.002$) and over time (Time; $F_{4, 124} = 23.58$; $P<0.0001$); however, their interaction was not significant (Treatment*Time; $F_{28,124} = 1.39$; $P=0.12$; Figure 2). Following a Bonferroni correction ($P\leq 0.0125$), the fishless control had a significantly greater number of

macrozooplankton taxa throughout the duration of the experiment than treatments containing bighead carp ($F_{1,29,9}=14.97$; $P=0.0005$), but were similar to bluegill only treatments ($F_{1,30,4}=0.48$; $P=0.49$). Bluegill only treatments also had a significantly greater number of macrozooplankton taxa than any treatment containing bighead carp ($F_{1,31,6}=15.87$; $P=0.0004$). The bighead carp only and mixed species treatments had a similar lower number of taxa ($F_{1,30,9}=0.21$; $P=0.65$). Regression parameter estimates indicated that bluegill did not significantly influence macrozooplankton richness, whereas bighead carp had a significant negative influence (Table 4). The per capita effect of adding bighead carp caused macrozooplankton richness to decline 3.4 times more rapidly than the addition of bluegill (Table 4).

Rotifers

Initial rotifer densities were similar among treatments ($F_{7, 125} = 1.04$; $P=0.40$). Treatment had a significant effect on rotifer density (Treatment; $F_{7,33,7}=2.84$; $P=0.02$). Time and the interaction between treatment and time were not significant (Time; $F_{4, 64,9} = 1.98$; $P=0.11$; Treatment*Time; $F_{28, 89,5} = 1.06$; $P=0.40$). Following a Bonferroni correction ($P\leq 0.0083$), bluegill only treatments were similar to the control ($F_{1, 33,4} = 1.65$; $P=0.21$), but had significantly more rotifers than treatments that contained bighead carp ($F_{1,33,6} = 16.44$, $P=0.0003$). Bighead carp only and mixed species treatments were similar to each other ($F_{1, 34,2} = 0.11$; $P= 0.75$), as well as the control ($F_{1,33,5}= 2.76$; $P= 0.11$). Increasing heterospecific densities did not have a significant influence (Increasing BHC with BLG constant; $F_{2, 33,4} = 4.66$; $P=0.02$; Increasing BLG with BHC constant; $F_{2,33,4} = 0.81$; $P= 0.46$). Regression parameter estimates indicated that per capita bluegill and bighead carp densities did not have a significant influence on total rotifer density (Table 4).

Initial rotifer richness was similar across treatments ($F_{7, 152} = 1.17$; $P=0.32$). The rotifer community included the genera *Anuraeopsis*, *Brachionus*, *Cephalodella*, *Colurella*, *Conochilus*, *Euchlanis*, *Filinia*, *Flosculariaceae*, *Hexarthra*, *Keratella*, *Lepadella*, *Lecane*, *Monommata*, *Monostyla*, *Notommatidae*, *Philodina*, *Platytias*, *Polyarthra*, *Squatinella*, *Synchaeta*, *Testudinella*, and *Trichocerca*. Rotifer richness was significant through time (Time; $F_{4, 121} = 3.01$; $P=0.02$), but not by treatment or the interaction between time and treatment (Treatment; $F_{7, 51.7} = 0.95$; $P=0.48$; Treatment*Time; $F_{28, 127}=0.92$; $P=0.59$; Figure 4). Following a Bonferroni correction ($P\leq 0.01$), treatments were not significantly different from the control (CONTROL vs ALL; $F_{1, 54.2} = 3.56$; $P=0.06$; Figure 4) or from each other (BLG vs BHC; $F_{1, 52.2} = 0.14$; $P=0.71$; BLG vs MIX; $F_{1, 51.3} = 1.67$; $P=0.20$; Figure 4). Increasing fish density did not have an effect on rotifer species richness (Increasing BLG with BHC constant; $F_{2, 51.3} = 0.09$; $P=0.91$; Increasing BHC with BLG constant; $F_{2, 51.3} = 0.07$; $P= 0.93$). Regression parameter estimates for rotifer richness were not significant for bluegill and bighead carp per capita effects (Table 4).

Benthic taxa density

The three most common taxa in the benthic samples were chironomids (Family: Chironomidae; Order: Diptera), ostracods (Class: Ostracoda), and chydorids (Family: Chydoridae) (>88% of total benthic taxa density). Other benthic taxa included Anisoptera larvae (Order: Odonata), Coleoptera larvae (Order), Diptera pupae (Order), Ephemeroptera larvae (Order), Gastropoda (Class), Nematoda (Phylum), and Trichoptera larvae (Order). Regression parameters indicated that bighead carp had a per capita positive influence on total benthic taxa density, but not richness (Table 4). Bluegill did not have a significant effect on either (Table 4). Bighead carp density had a positive influence on total benthic taxa density compared to bluegill, as regression parameters indicated benthic taxa density was 25 times greater with bighead carp

present than with bluegill (Table 4). Among the most abundant taxa, chydorid density (Treatment; $F_{7,32} = 0.70$; $P=0.67$) and ostracod density (Treatment; $F_{7,31} = 1.21$; $P=0.33$) were not significantly different among treatments (Table 4). In contrast, chironomid density was significantly different among treatments (Treatment; $F_{7,32} = 3.82$; $P=0.004$; Figure 5). Regression parameter estimates showed that bighead carp had a significant positive influence on chironomid density, and that the per capita influence of adding bighead carp caused a fourfold increase in chironomid density compared to the per capita effects of bluegill (Table 4; Figure 5). The change in chironomid density was similar in all other treatments (BLG vs CONTROL; $F_{1,32} = 0.00$; $P= 0.98$; BLG vs MIX; $F_{1,32} = 0.72$; $P= 0.40$; Figure 5) following a Bonferroni correction ($P\leq 0.025$). Change in chironomid length was not significant among treatments ($F_{7,32} = 0.90$; $P= 0.52$).

DISCUSSION

Nonnative species are often cited for contributing to declines in growth of native species (Ruetz et al. 2003, Britton et al. 2007, Irons et al. 2007, Johnson et al. 2009, Wolfe et al. 2009), that can be attributed to their ability to exploit resources more efficiently (Shea and Chesson 2002, Simberloff 2011, Simberloff et al. 2013). From competition theory, stable coexistence is possible when intra-specific competition is stronger than inter-specific competition (Mittelbach 2012). Our competition index suggested that when bighead carp were present in low densities, intra-specific competition had a greater influence than inter-specific competition on bluegill. Per capita influences of bluegill and bighead carp had significant negative influences on bluegill growth, but the significant interaction indicated that the effect of one species was influenced by the density of the other. At low fish densities, the per capita influence of both species was likely negative as limited food resources were consumed. As fish densities increased, we suspect food

resources were so efficiently exploited that additional fish appeared to have little effect. Compared to the generalist pump-filter feeding of bighead carp, bluegill rely on visual acuity, individually selecting prey for consumption (Kolar et al. 2007, Spotte 2007). The rapid suppression of zooplankton by bighead carp removed an important food resource, which ultimately had a negative inter-specific influence on bluegill growth. Previous studies have found reduced bluegill growth in the presence of zooplanktivorous fishes, likely due to partial diet overlap and exploitative competition (DeVries and Stein 1992, Welker et al. 1994, Stein et al. 1995). Our results support those findings. Bluegill are omnivorous and likely exploited other food resources such as benthic and terrestrial macroinvertebrates (Spotte 2007), which likely contributed to the strength of intra-specific competition.

There has been much recent focus on invasive species facilitation by other nonnatives (e.g. “Invasional Meltdown”) (Simberloff and Von Holle 1999, Simberloff 2006), but fewer studies have found facilitation of an invader by a native species (but see Altieri et al. 2010, Thompson and Schiel 2012, Cruz Sueiro et al. 2013). We found that increasing bluegill density had a positive effect on bighead carp growth, whereas intra-specific competition among bighead carp had no significant effect. Macrozooplankton were rapidly exploited in all treatments, including the low-density bighead carp treatment (Treatment 4), and density-dependence may not have been observed because all bighead carp were food limited. A plausible mechanism driving bluegill facilitation of bighead carp is modification of nutrient flow. Phosphorus concentrations with bluegill present were significantly greater than when only bighead carp were present, suggesting bluegill were consuming not only large zooplankters, but also macroinvertebrates. Excretion by bluegill would redirect phosphorus from benthic and terrestrial macroinvertebrates to the pelagic area, where water-column phosphorus would be available for

assimilation (Carpenter et al. 1992, Schindler and Scheuerell 2002, Glaholt and Vanni 2005). These pathways could have indirectly benefited bighead carp by increasing zooplankton and rotifer densities. The transfer of nutrients from terrestrial and benthic habitats to pelagic areas by omnivorous fishes is thought to have strong effects on plankton community dynamics (Brabrand et al. 1990, Schindler and Scheuerell 2002, Parkos et al. 2003). Although the total amount of nutrients excreted by fishes is only about a tenth of what is excreted by zooplankton (Brabrand et al. 1990) and orders of magnitude lower than that recycled by bacteria (Brabrand et al. 1990), these nutrients constitute a ‘new’ introduction (Schindler and Scheuerell 2002), which can greatly alter community productivity and plankton populations (Brabrand et al. 1990, Vanni et al. 1997a, Vanni and Layne 1997b). Chlorophyll *a* levels in bluegill only treatments did not reflect the higher phosphorus concentrations. However, previous studies have found that zooplankton grazing can decouple these relationships, causing chlorophyll *a* to be suppressed while phosphorus concentrations remain high (Mazumder and Lean 1994, Kufel 2001). Nutrient cycling can also occur in a matter of hours or days (Goldman 1984, Ramin et al. 2012), and the transfer of energy may have occurred more rapidly than our weekly sampling could detect.

A common theory in invasion ecology is the concept of biotic resistance, where more diverse communities will inhibit non-native establishment and spread (Elton 1958, Carey and Wahl 2010b, Kimbro et al. 2013). Greater species diversity is thought to increasingly sequester resources, making them unavailable for a newly introduced species (Elton 1958, Alpert 2006). Results from studies of biotic resistance have been mixed with evidence of an ‘invasion paradox’, where small-scale studies found increasing diversity resisted invasive species, but larger-scale studies found greater densities of non-native species positively correlated to community diversity (Fridley et al. 2007). The contrasting results at different scales may be

influenced by a multitude of factors that vary across temporal and spatial scales, such as climate, vegetation structure, disturbance, resource availability, propagule pressure, and associated ecosystem processes (Stohlgren et al. 2006b, Carey et al. 2010). The concept of biotic acceptance, where natural systems tend to accommodate the establishment and coexistence of nonnative species regardless of native species diversity, maintains that the success or failure of a nonnative species may largely be due to whether or not abiotic conditions are suitable (Moyle and Light 1996, Stohlgren et al. 2006a, Stohlgren et al. 2006b). Further, species that alter nutrient cycling or create structure that is more favorable to an invader are going to indirectly facilitate the invasion (Shea and Chesson 2002, Altieri et al. 2010, Thompson and Schiel 2012). Our results support the biotic acceptance hypothesis, as bluegill appeared to alter nutrient cycling through omnivorous foraging, indirectly favoring bighead carp by increasing plankton densities.

Bighead carp shifted energy resources to the benthos as these treatments had significantly higher chironomid midge density than any other treatment, including the control. Previous studies have also found that silver carp had a positive influence on benthos biomass, especially chironomids (Opuszynski 1980a). Silver carp have been shown to consume suspended organic matter, and up to 80% of the food consumed is excreted and settles to the bottom (Leventer and Teltsch 1990). Bighead and silver carp have been found to increase nutrient levels in bottom sediments (Starling 1993, Kolar et al. 2007), while decreasing phosphorus in pelagic areas (Ruan 2005). Although bighead carp increased chironomid midge density, these changes did not appear to benefit bluegill in the mixed species treatments. Adult chironomids may have been consumed by bluegill before egg laying occurred, negating benefits.

Bluegill and bighead carp experienced weight and length loss during the experiment in some treatments. Similarly, a mesocosm experiment examining competitive effects between

bighead carp and paddlefish observed negative growth in intra-specific competition treatments (Schrank et al. 2003). Plankton availability has been found to be a limiting factor for bighead carp growth (Cooke et al. 2009). Although loss in biomass is not unusual in mesocosm experiments (Micucci et al. 2003, Schrank et al. 2003, Carey and Wahl 2010b), reduced length is less typical. Temporary losses in body length have been found in vertebrates subjected to harsh conditions, anorectic stress, and low food availability (Wikelski and Thom 2000, Huusko et al. 2011). In our experiment, fish were subjected to a stressful, food-limited situation in some treatments.

Through filter-feeding and rapid biomass accumulation, bighead carp are extremely efficient at reducing plankton populations (Cooke et al. 2009). We found that macrozooplankton densities were greatly reduced and rotifer densities suppressed by bighead carp. The opportunistic feeding habits of bighead carp allow them to consume a variety of plankton sizes, even when plankton densities are low, as well as detritus and phytoplankton (Opuszynski 1981, Kolar et al. 2007, Sampson et al. 2009, Siddiquee et al. 2012). Particles that are smaller than the gill raker width can become captured by a mucus coating on the gill rakers, allowing the particles to aggregate until large enough to pass to the esophagus (Kolar et al. 2007). All treatments, including the control, experienced a decline in macrozooplankton densities after the first week of the experiment. By the third week, some zooplankton taxa (Cydoridae, *Bosmina* spp.) were increasing in the bluegill only and control treatments, whereas any treatments containing bighead carp had consistently low macrozooplankton densities. Rotifer densities increased in bluegill-only treatments, which may have been influenced by competitive release as large zooplankters were removed as well as positive bottom-up effects via nutrient transport from benthic and terrestrial sources (Williams and Moss 2003, Glaholt and Vanni 2005). Fish can influence

plankton dynamics through complex pathways including direct consumption, nutrient excretion, and modifying the rate at which plankton receive nutrients (Vanni and Layne 1997b). Due to the facilitation of bighead carp by bluegill presence, it is plausible that a bottom-up influence on plankton by bluegill played an important role. Although rotifer densities in treatments with bighead carp were similar to the control, bighead carp appear to have exploited a portion of the rotifer community and kept densities suppressed.

The potential effects of bighead carp on other species native to the Mississippi River Basin are understudied. Previous studies have focused on obligate planktivores (Schrack et al. 2003, Irons et al. 2007, Sampson et al. 2009), whereas our experiment is the first to examine interactions with a facultative planktivore. We provide evidence that bighead carp had a negative influence on bluegill growth; however, the outcome of competitive interactions depended on bluegill and bighead carp densities. At lower densities, intra-specific competition had a stronger influence than inter-specific competition on bluegill, suggesting coexistence of the two species is likely. However, inter-specific competition could become more important as bighead carp densities increase within the Mississippi River Basin. Although inter- and intra-specific competition influenced bluegill, the potential still exists for greater negative inter-specific influences by bighead carp on bluegill through high abundance. Density-dependent reduced growth with increasing competition for food resources has been observed in bluegill (Mittelbach 1988, Osenberg et al. 1988, DeVries and Stein 1992, Nibbelink and Carpenter 1998, Partridge and DeVries 1999), and growth has been positively correlated to macrozooplankton densities (Welker et al. 1994). Insufficient zooplankton densities or size structure can reduce bluegill growth, leaving them susceptible to predation (Werner and Gilliam 1984, Osenberg et al. 1988, Breck 1993). If bighead carp shift the zooplankton community to smaller individuals, they

reduce a valuable food resource for bluegill as well as other native Mississippi River Basin species.

Interestingly, we found that the presence of bluegill facilitated bighead carp growth, which appeared to be driven by bottom-up effects of altered nutrient cycling caused by bluegill omnivory (Vanni and Layne 1997b, Glaholt and Vanni 2005). Facilitation plays an important, but often unrecognized, role in natural systems (Bruno et al. 2003, Altieri et al. 2010). Using commercially desirable fishes for synergistic interactions is common in aquaculture; however, these facultative interactions are only recently gaining attention in invasion ecology (Opuszynski 1981, Opuszynski and Shireman 1993, Griffen et al. 2008, Altieri et al. 2010). Our results support the possibility of biotic acceptance that has implications for understanding and avoiding the potential establishment of bighead carp in novel habitats.

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TABLES AND FIGURES

Table 1. Competition Indices (CI) for change in length and biomass of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). Low and high single-species treatments (intra-specific interactions; bluegill, Treatment 2, 3; bighead carp, Treatment 4, 5) and the low bluegill and low bighead carp treatment (inter-specific interactions; Treatment 6) were included. Values were calculated as the ratio of CI inter-specific values (CI inter) to CI intra-specific values (CI intra). Ratios greater than one indicated that inter-specific competition had a greater effect on the focal species, ratios of less than one indicated that intra-specific competition had a greater effect, and a ratio of one indicates that the two species had an equivalent per capita effect. See text for details on calculating the CI (Hu and Tessier 1995, Caceres 1998).

	Bluegill			Bighead carp		
	CI Intra	CI Inter	Ratio	CI Intra	CI Inter	Ratio
Change in Biomass	1.78	1.05	0.59	-0.57	0.66	-1.15
Change in Length	1.34	1.01	0.75	-2.98	11.93	-4.00

Table 2. Regression models testing effects of conspecific and heterospecific density, and their interaction, on changes in length and biomass of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). Displayed are model r^2 values, regression coefficients (β), and P-values for an associated significance test ($H_0: \beta=0$) for each term in the model.

	<u>Intercept</u>		<u>Conspecific density</u>			<u>Heterospecific Density</u>			<u>Interaction</u>		
			β		P	β		P	β		P
Bluegill Responses											
Change in Length (mm/ day)	0.146	(±0.036)	-0.017	(±0.004)	0.0002	-0.025	(±0.005)	0.0002	0.003	(±0.001)	0.008
Change in Biomass (g/ day)	0.05	(±0.008)	-0.006	(±0.001)	<0.0001	-0.009	(±0.002)	<0.0001	0.001	(±0.0002)	0.001
Bighead Carp Responses											
Change in Length (mm/ day)	0.012	(±0.053)	-0.003	(±0.007)	0.70	0.024	(±0.010)	0.02	-0.003	(±0.002)	0.08
Change in Biomass (g/ day)	-0.008	(±0.014)	-0.001	(±0.002)	0.64	0.006	(±0.003)	0.04	-0.001	(±0.0004)	0.14

Table 3. Repeated measures ANOVA examining effects of treatment, time, and their interaction on the most abundant zooplankton taxa. Taxa were considered abundant if their density·L⁻¹ was ≥ 5% of the total number of zooplankton. Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), F-statistics, and P-values are presented for each analysis. A Kenward-Rodger correction was used to obtain degrees of freedom. A log_e transformation was applied to the taxa to meet the assumptions of ANOVA.

Zooplankton		NDF	DDF	F	P
Copepoda					
	Cyclopoid	7	30.9	4.12	0.003
	Treatment	4	124	8.84	<0.0001
	Time	28	124	3.5	<0.0001
	Treatment x Time				
	nauplii	7	30.8	8.6	<0.0001
	Treatment	4	124	103.76	<0.0001
	Time	28	124	6.42	<0.0001
	Treatment x Time				
Cladocera					
	Bosminidae				
	Treatment	7	30.8	2.93	0.02
	Time	4	124	2.61	0.04
	Treatment x Time	28	124	1.12	0.33
	Ceriodaphnia				
	Treatment	7	31	5.19	0.0005
	Time	4	125	32.77	<0.0001
	Treatment x Time	28	125	2.14	0.002
	Chydoridae				
	Treatment	7	30.8	1.69	0.15
	Time	4	124	25.98	<0.0001
	Treatment x Time	28	124	1.19	0.25
Ostracoda					
	Treatment	7	30.8	8.84	<0.0001
	Time	4	126	6.48	<0.0001
	Treatment x Time	28	126	2.51	0.0003

Table 4. Regression models testing effects of per capita bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*) density, and their interaction, on the average change in macrozooplankton and rotifer density and richness over the duration of the experiment, as well as the difference (end sample date - beginning sample date) of the total sessile benthic taxa density and richness. The differences in density of the three most common benthic taxa (Family: Chydoridae; Family: Chironomidae; Class: Ostracoda) were examined separately. Displayed are model r^2 values, regression coefficients (β) and P -values for an associated significance test ($H_0: \beta=0$) for each term in the model.

	r^2	Intercept		Bluegill density			Bighead Carp Density			Interaction		
				β	P	β	P	β	P			
Zooplankton Responses												
Density (# / L)	0.13	4.91	(±0.60)	-0.04	(±0.05)	0.46	-0.10	(±0.05)	0.06	0.0003	(±0.01)	0.97
Richness (# / sample)	0.34	6.15	(±0.54)	-0.05	(±0.05)	0.32	-0.17	(±0.05)	0.001	0.002	(±0.01)	0.85
Rotifer Responses												
Density (# / L)	0.32	5.65	(±0.37)	0.05	(±0.06)	0.36	-0.11	(±0.06)	0.08	-0.01	(±0.01)	0.23
Richness (# / sample)	0.09	9.27	(±0.42)	0.03	(±0.06)	0.68	0.06	(±0.06)	0.32	0.005	(±0.01)	0.72
Benthic taxa												
Total taxa (# / cm ²)	0.15	0.83	(±0.16)	0.002	(±0.03)	0.93	0.05	(±0.03)	0.05	-0.005	(±0.005)	0.34
Richness (# / sample)	0.15	0.60	(±0.53)	-0.120	(±0.08)	0.16	0.06	(±0.08)	0.48	0.004	(±0.017)	0.82
Chydorid (# / cm ²)	0.05	0.15	(±0.33)	0.03	(±0.05)	0.61	0.03	(±0.03)	0.53	0.003	(±0.01)	0.80
Chironomid (# / cm ²)	0.38	0.13	(±0.20)	-0.02	(±0.03)	0.53	0.08	(±0.05)	0.02	-0.02	(±0.006)	0.01
Ostracod (# / cm ²)	0.10	-0.01	(±0.19)	0.007	(±0.02)	0.76	0.03	(±0.02)	0.24	0.001	(±0.004)	0.75

Table 5. Repeated measures ANOVA with a Kenward Rodger correction examining the effects of treatment on temperature (°C), dissolved oxygen (mg L⁻¹), turbidity (NTU), and light intensity (lux) through time. Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), F-statistics, and p-values are presented for each analysis.

Response	Effect	NDF	DDF	F	P
Temperature	Treatment	7	32	0.85	0.55
	Time	3	30	2364.5	<0.0001
	Treatment x Time	21	52.3	1.02	0.46
Dissolved oxygen	Treatment	7	32	0.86	0.55
	Time	3	30	49.5	<0.0001
	Treatment x Time	21	52.3	0.75	0.77
Turbidity	Treatment	7	31.8	0.74	0.64
	Time	3	30	7.8	0.0005
	Treatment x Time	21	52.3	1.79	0.05
Light intensity	Treatment	7	28.3	0.37	0.91
	Time	3	56.1	46.6	<0.0001
	Treatment x Time	21	70.7	0.49	0.97

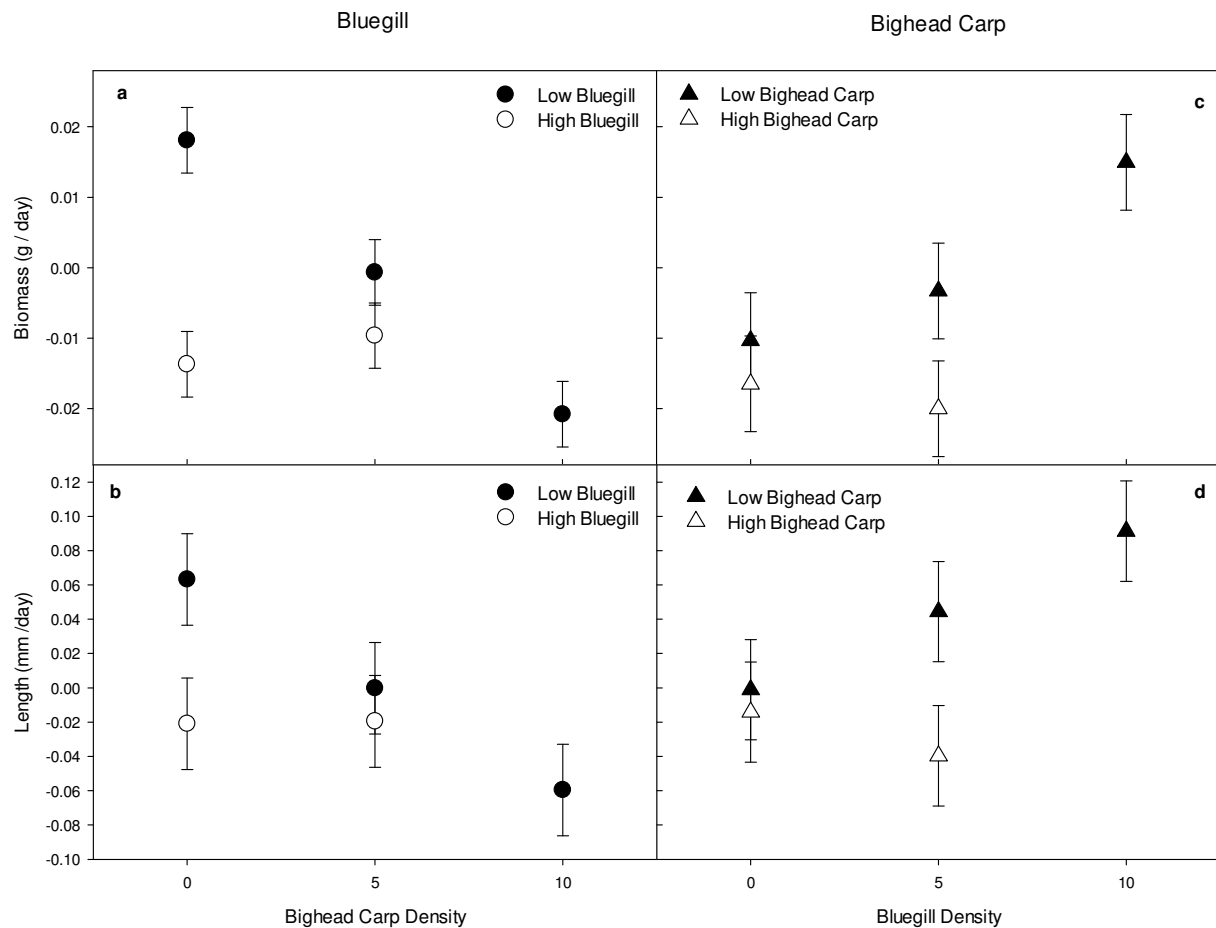


Figure 1. Mean change in biomass (top panels) and length (bottom panels) per day of bluegill (*Lepomis macrochirus*) (circles; a, b) and bighead carp (*Hypophthalmichthys nobilis*) (triangles; c, d) across heterospecific density levels of zero, five, and ten fish. ‘Low’ refers to a fish density of five and ‘high’ refers to a fish density of ten. The average change in total length and total biomass per mesocosm for each species was divided by the duration of the experiment. Error bars represent ± 1 standard error about the mean.

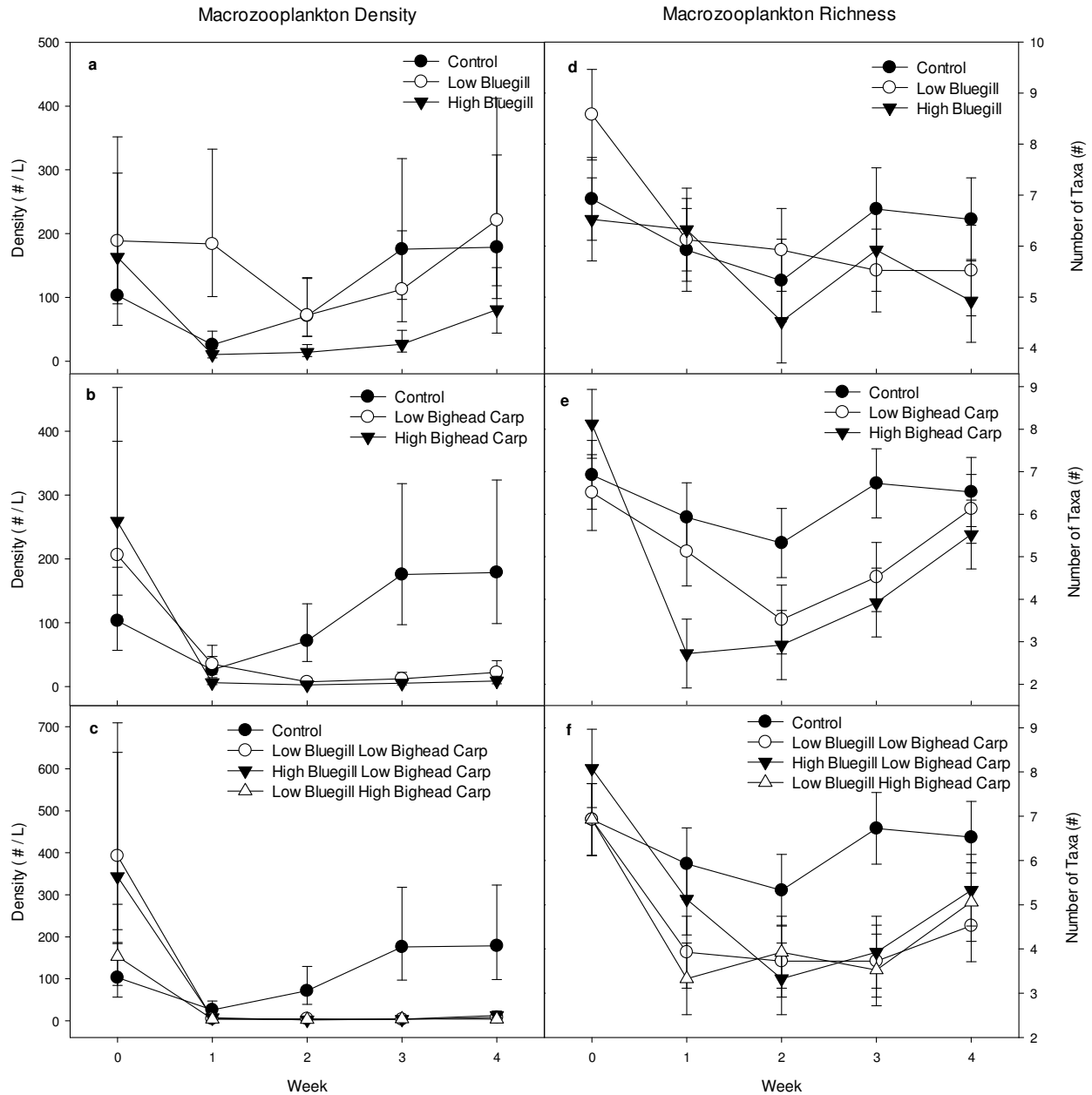


Figure 2. Weekly mean total zooplankton density (number of organisms $\cdot L^{-1}$; a,b,c) and richness (total number of taxa; d,e,f) from the mesocosm experiment including bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). “Control” refers to the fishless control, “low” refers to a fish density of five, and “high” refers to a fish density of ten. Mean values for macrozooplankton density and richness were calculated with LSMEANS in a repeated measures ANOVA with a Kenwood Rodgers correction. Macrozooplankton density was transformed with natural log and mean values were back transformed. Error bars represent ± 1 standard error about the mean.

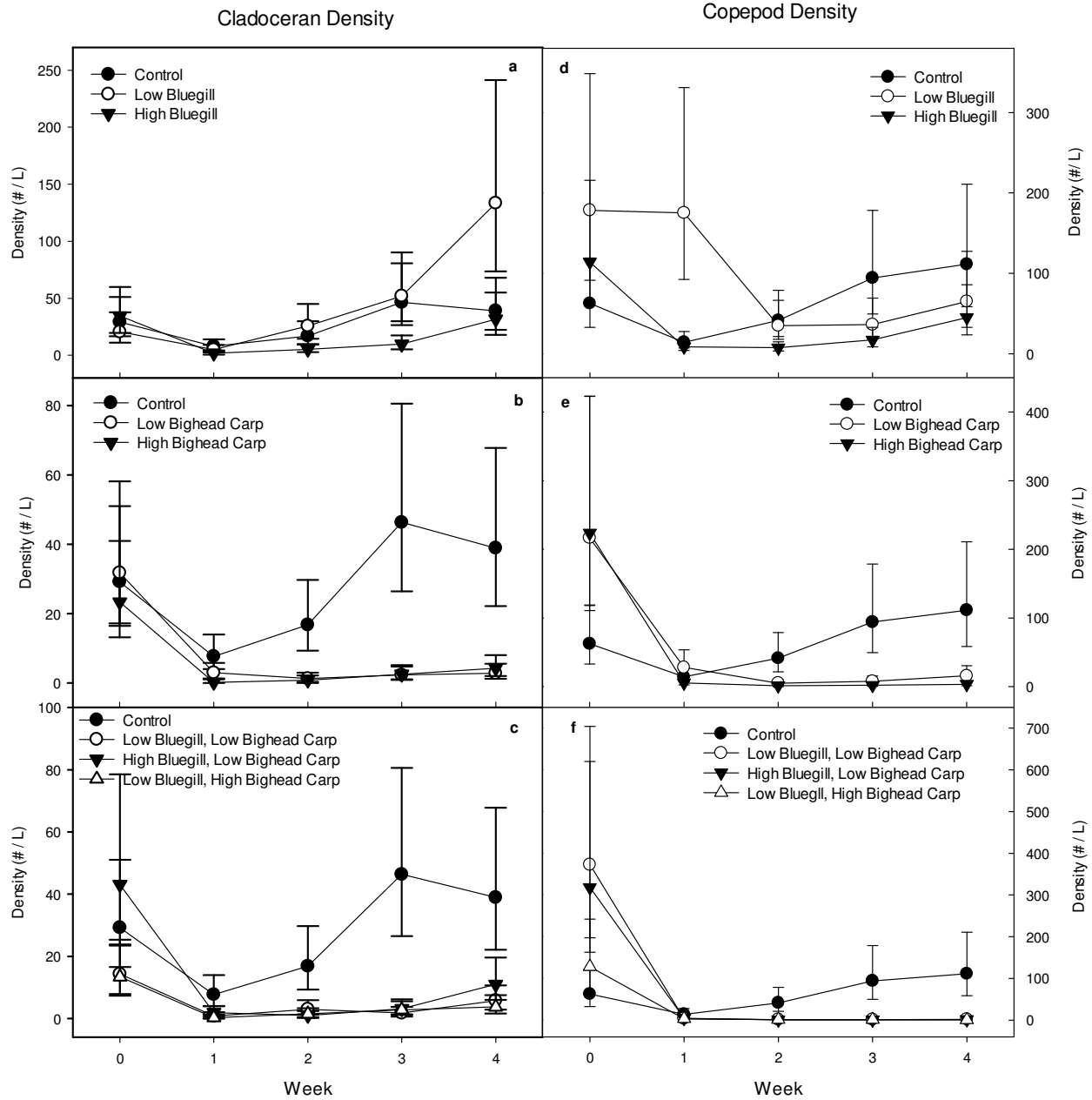


Figure 3. Weekly mean cladoceran (a,b,c) and copepod (d,e,f) densities from mesocosm experiment with bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). “Control” refers to the fishless control, “low” refers to a fish density of five and “high” refers to a fish density of ten. Mean values for Cladoceran and Copepod density were calculated with LSMEANS in a repeated measures ANOVA with a Kenwood Rodgers correction. Densities were transformed with natural log to meet the assumptions of ANOVA and mean values were backtransformed. Error bars represent ± 1 standard error about the mean.

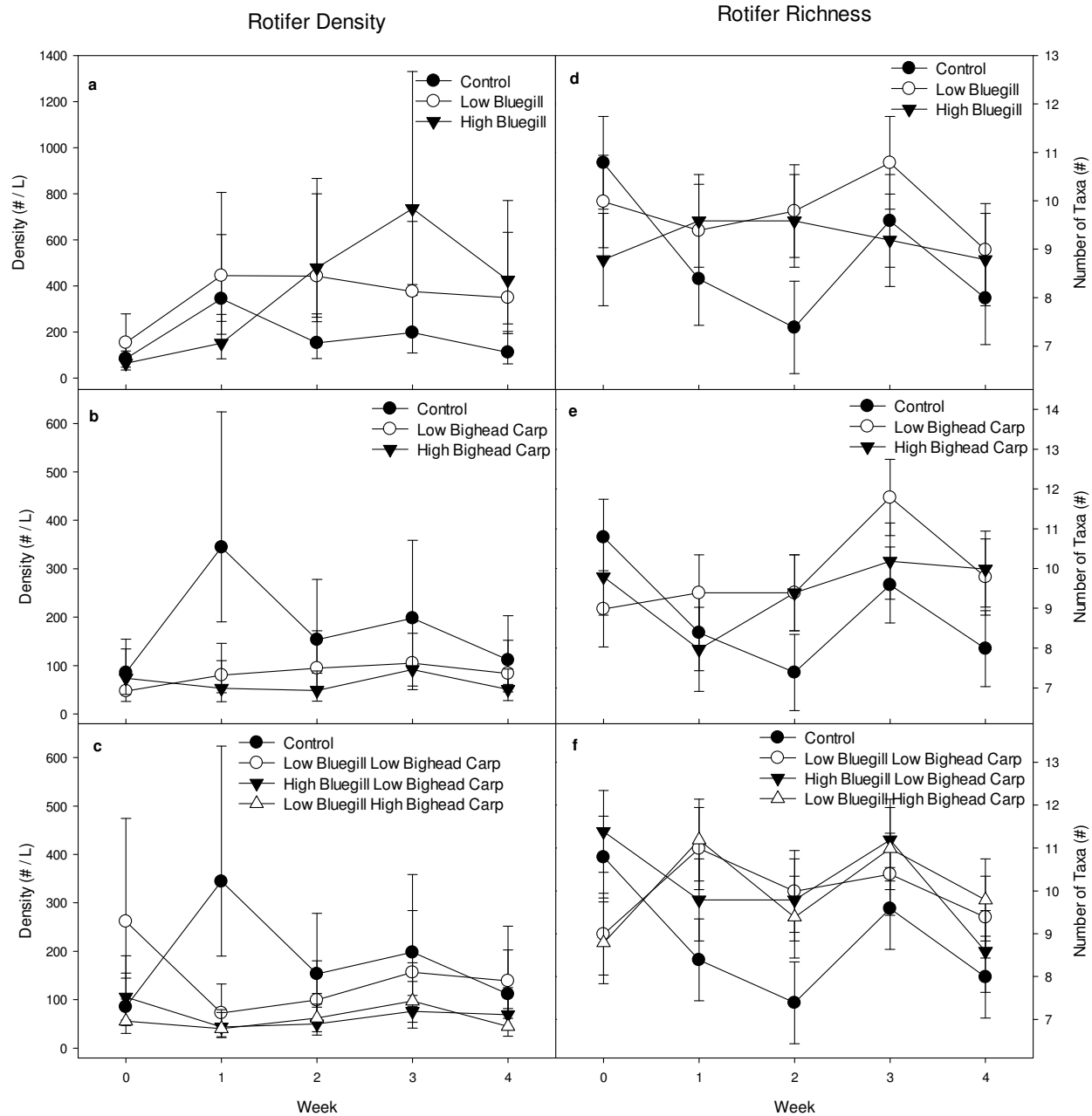


Figure 4. Weekly mean rotifer density (number of organisms \cdot L $^{-1}$; a, b, c) and richness (total number of taxa; d, e, f) from the mesocosm experiment with bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). “Control” refers to the fishless control, “low” refers to a fish density of five and “high” refers to a fish density of ten. Mean values for rotifer density and richness were calculated with LSMEANS in a repeated measures ANOVA with a Kenwood Rodgers correction. Density was log $_e$ transformed. Error bars represent \pm 1 standard error about the mean.

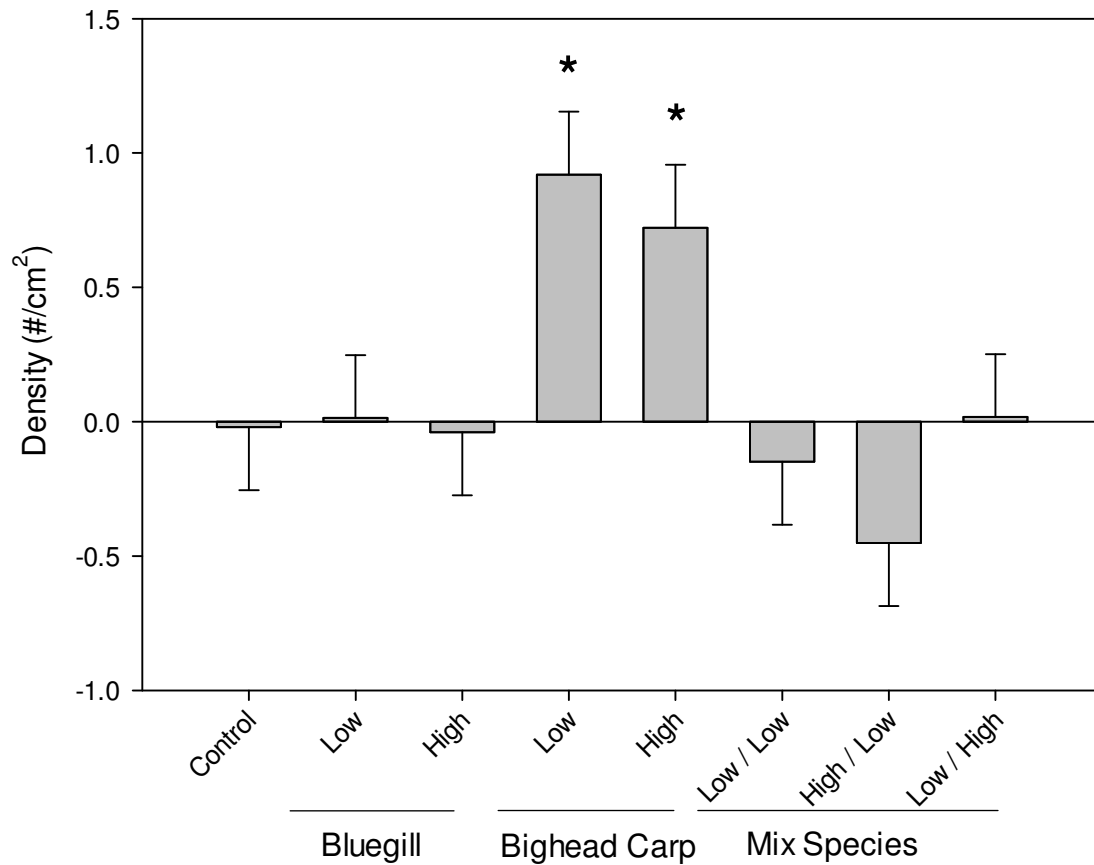


Figure 5. Mean change in chironomid density ($\#/cm^2$) by treatment. “Control” refers to the fishless control, “low” refers to a fish density of five, and “high” refers to a fish density of ten. For “Mixed Species”, treatments are combinations of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). “Low / Low” refers to low densities of bluegill and bighead carp (Treatment 6; total fish / mesocosm = 10), “High / Low” refers to high bluegill and low bighead carp density (Treatment 7; total fish / mesocosm = 15), and “Low / High” refers to low bluegill and high bighead carp (Treatment 8; total fish / mesocosm = 15). Error bars represent ± 1 standard error about the mean. Asterisks indicate significantly different treatments ($P < 0.05$).

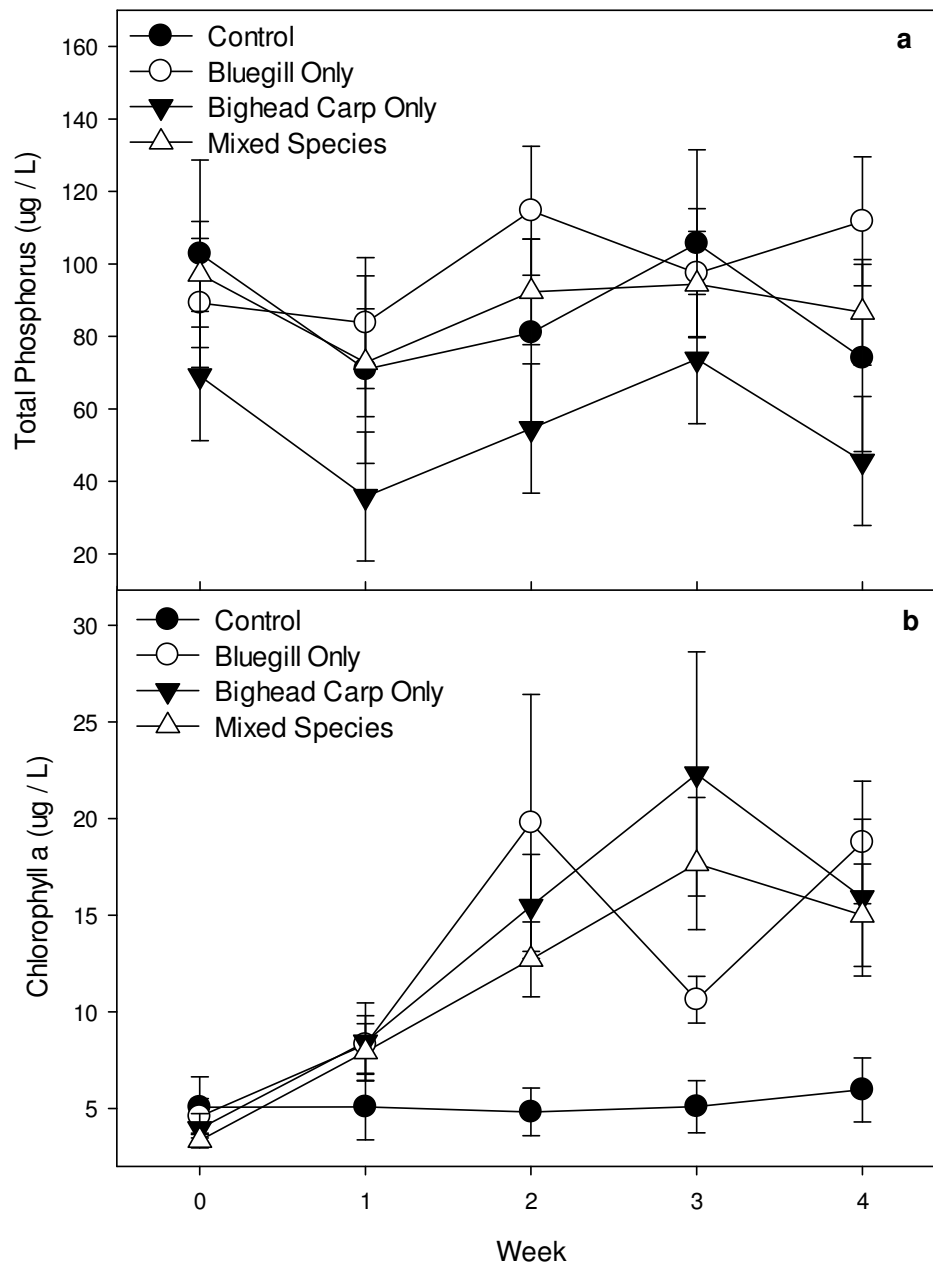


Figure 6. Average total water column phosphorus ($\mu\text{g}\cdot\text{L}^{-1}$; a) and average chlorophyll *a* ($\mu\text{g}\cdot\text{L}^{-1}$; b) by week in mesocosms. The eight treatments were combined into four groups: the fishless control (“Control”; Treatment 1), low and high bluegill (*Lepomis macrochirus*) only treatments (“Bluegill Only”; Treatment 2, 3), low and high bighead carp (*Hypophthalmichthys nobilis*) only treatments (“Bighead Carp Only”; Treatment 4, 5), and mixed species treatments (“Mixed Species”; low bluegill low bighead carp, Treatment 6; high bluegill low bighead carp, Treatment 7; low bluegill high bighead carp, Treatment 8). “Low” refers to a fish density of five and “high” refers to a fish density of ten. Error bars represent ± 1 standard error about the mean.

CHAPTER 3: COMPETITIVE INTERACTIONS AND COMMUNITY INFLUENCES
OF INVASIVE BIGHEAD CARP AND COMMON CARP IN MESOCOSMS

ABSTRACT

Invasive species are a driving force of global ecosystem change and competitive interactions with native species are likely. Tests for competitive interactions between invasive species have been less studied. We tested for competitive interactions between two invasive species, common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*). Common carp and bighead carp prey upon zooplankton as juveniles, creating the potential for competitive interactions before common carp undergo an ontogenetic diet shift to benthic macroinvertebrates around 100 mm. In a replicated mesocosm experiment using a response surface design, we manipulated densities (low density = 5 fish, high density = 10 fish) of juvenile common and bighead carp to test for the per capita effects of inter- and intra-specific competition, as well as influences on zooplankton, macroinvertebrates, and environmental variables. Increasing common carp density reduced common carp length and weight 2.4 and 1.5 times more than increasing bighead carp, respectively. Increasing bighead carp density reduced bighead carp length and weight 1.6 and 2 times more than increasing common carp density, respectively, which indicated that intra-specific competition had a greater influence. Both species significantly reduced macrozooplankton densities. Bighead carp appeared to use rotifers as a food source, whereas common carp presence led to increased rotifer densities. The presence of common carp had a negative influence on benthic taxa richness. Our results suggest that common carp and bighead carp appear to partition food resources during scarcity.

INTRODUCTION

Invasive species are a driving force of global ecosystem change (Moyle and Light 1996, Vitousek et al. 1996, Rahel 2000a, Gozlan et al. 2010, Geist 2011). In aquatic systems, invasive species have been found to alter nutrient cycles (Fischer et al. 2013), increase disease (Gozlan et al. 2009), increase predation on native fishes (Budy et al. 2013), and compete for limiting food resources (Baxter et al. 2007). Consumption of food resources by invasive fishes has implications for fish populations (Feiner et al. 2013), especially if the competition is occurring at larval and juvenile life stages as limited food resources at these stages may influence fish growth, survival, and recruitment (Graeb et al. 2004, Martino and Houde 2010, 2012).

Many studies have focused on competitive interactions between exotic and native species (Parkos et al. 2003, Baxter et al. 2007, Feiner et al. 2013, Kakareko et al. 2013). Dietary overlap leading to competition between invasive and native fishes has been implicated in causing negative influences on larval and juvenile native fishes (Mercado-Silva et al. 2007, Feiner et al. 2013). Interactions among sympatric invasive species have often tested for inter-specific facilitation leading to more non-native establishment potential (e.g. "invasion meltdown"; Simberloff and Von Holle 1999, Adams et al. 2003, Simberloff 2006). However, few studies have tested for competitive interactions between nonnative taxa despite the possibility that competitive interactions may occur between any two species that share a common resource, regardless of species origin (Coghlan et al. 2007). Competitive interactions may reduce fitness and lessen influences of invasive species on invaded communities (Shea and Chesson 2002, Griffen et al. 2008), and such interactions may be most likely at the more vulnerable larval and juvenile life stages.

Invasive bighead carp (*Hypophthalmichthys nobilis*) have generated much interest in recent years since their simultaneous escape and establishment into the Mississippi River Basin in the early 1970s (Chick and Pegg 2001, Kelly 2011). Bighead carp preferentially consume zooplankton; however, they are capable of consuming phytoplankton and detritus, especially in times of zooplankton scarcity (Opuszynski 1981, Burke et al. 1986, Lieberman 1996, Schrank et al. 2001, Kolar and Lodge 2002, Sampson et al. 2009). Food selectivity is thought to be assisted by a mucous coating on their specialized gill rakers, enabling capture of smaller particles (Opuszynski et al. 1991, Kolar et al. 2007). Due to their opportunistic feeding habits and ability to reduce macrozooplankton concentrations (Nelson et al. 2014), much concern has arisen about possible influences on growth, survival, and recruitment of native fishes (Chick and Pegg 2001). Decreased body condition of native filter-feeding zooplanktivores and zooplankton community shifts has been observed; however, how the long-term implications of these findings on the entire ecosystem have yet to be elucidated (Schrank et al. 2003, Irons et al. 2007, Sass et al. 2014).

Common carp (*Cyprinus carpio*) are a widely introduced aquatic species and are invasive in North America and in many places around the world (McCrimmon 1968). Common carp can contribute to regime shifts in aquatic ecosystems, where a previously clear water body transitions to a turbid condition due to benthic foraging activity (Matsuzaki et al. 2007, Scheffer and Jeppesen 2007, Fischer et al. 2013). Exploitation of benthic resources by adult common carp has been linked to increased turbidity, increased nutrient suspension, destabilized substrate, and decreased macrophyte cover, which leads to overall environmental degradation (Parkos et al. 2003, Weber and Brown 2009, Wahl et al. 2011, Fischer et al. 2013). Like many fishes, juvenile common carp prey upon zooplankton until about 100 mm in length before undergoing an ontogenetic diet shift to benthic macroinvertebrates (Britton et al. 2007, Weber and Brown

2009). Common carp recruitment is often variable; however, biotic and abiotic influences during their first year are thought to strongly influence recruitment (Bajer and Sorensen 2010, Weber and Brown 2013a). Larval and juvenile common carp have been found to use main channel and emergent vegetation habitats (Nannini et al. 2012, Weber and Brown 2012). As bighead carp have spread throughout the Mississippi River Basin, potential for competitive interactions between common carp and bighead carp during juvenile stages has grown (Irons et al. 2011, McClelland et al. 2012) due to increased habitat overlap. Larval and juvenile bighead carp inhabit backwater lakes and off-channel, vegetated waters (Kolar et al. 2007), whereas adult bighead carp tend to use slack water habitats adjacent to the main channel (Kolar et al. 2007, Degrandchamp et al. 2008). Competition for limiting food resources during the juvenile stage can delay ontogenetic shifts, slow growth, and increased predation risk for juveniles (Kaspersson et al. 2012, Heermann and Borcharding 2013).

Using a replicated mesocosm experiment, we sought to quantify the per capita influence of inter- and intra-specific competition among juvenile common and bighead carp as well as their influences on the aquatic community. We hypothesized that inter-specific competition would have a greater influence on common carp than intra-specific competition due to efficient zooplankton removal by the filter feeding behavior of bighead carp. We also predicted intra- and inter-specific competition would have a negative influence on bighead carp growth due to limiting food resources and expected zooplankton densities to decline and become limiting due to predation by both species.

MATERIALS AND METHODS

Experimental design

Competitive interactions between age-0 bighead carp and age-0 common carp were tested for in replicated experimental mesocosms (1325-L polyethylene tanks) at the Sam Parr

Biological Station (SPBS), Kinmundy, Illinois, USA. Mesocosms were placed under cover to prevent direct sunlight and filled with water mixed from Forbes Lake, Kinmundy, Illinois, USA and a pond located at SPBS. Water was filtered through a 64- μm mesh net to prevent larval fish introduction. Phyto- and zooplankton were allowed to colonize and populate the mesocosms for four weeks prior to fish introduction. During this four-week period, the mesocosms were homogenized by periodically exchanging water. Two white tiles (116.6 cm^2) were also placed at the bottom of each mesocosm to quantify colonization of sessile, benthic macroinvertebrates.

To support/fail to support our hypotheses about inter- and intra-specific competition, a response surface experimental design was used to test for competition between common and bighead carp. Response surface experimental designs vary the densities of the two species independently, allowing inferences to be made about the per capita influence of intra- and inter-specific competition (Inouye 2001, Young 2004, Asquith and Vonesh 2012). Forty-five mesocosms were divided into nine treatments with five replicates. Treatments were randomly assigned to mesocosms and were housed at two separate locations at SPBS (two full replicates under one structure and three full replicates under a second structure). The first treatment was a fishless control to monitor ambient changes of invertebrate densities and environmental parameters through time (Treatment 1). Four treatments were single species with low (5 fish / mesocosm) and high (10 fish / mesocosm) densities of common (Treatment 2, 3) or bighead carp (Treatment 4, 5) to test for intra-specific competition. The final four treatments combined both species: low density common carp and low density bighead carp (10 fish / mesocosm; Treatment 6); high density common carp with low density bighead carp (15 fish / mesocosm; Treatment 7); low density common carp with high density bighead carp (15 fish / mesocosm; Treatment 8); and high density common carp with high density bighead carp (20 fish / mesocosm; Treatment 9).

Total fish biomass per mesocosm was held constant, depending on whether the treatment was at low or high densities (target total biomass at low densities: 8 g; target total biomass at high densities: 16 g). Age 0 bighead and common carp were obtained from a commercial hatchery (Osage Catfisheries, Inc., Osage Beach, Missouri, USA). Initial lengths and weights for bighead and common carp were 56.6 ± 6.3 mm and 1.6 ± 0.6 g 50.8 ± 16.0 mm and 1.6 ± 0.4 g, respectively.

Data collection

Limnological sampling was conducted immediately prior to fish introduction and then repeated on a weekly basis. Fish were introduced to the mesocosms, and during the first week, any fish mortalities were replaced with a similarly sized fish (≤ 2 mm difference). Fish mortality beyond the first week of the experiment occurred in one replicate of the low bighead carp and low common carp treatment (Treatment 6), therefore this replicate was removed from all further analyses. Two chlorophyll *a* and one benthic macroinvertebrate sample were also mishandled and not included in further analyses. The experiment ran for 29 days and final fish length and weight (nearest mm, 0.1g) were recorded. Zooplankton were sampled with a 70 mm diameter x 0.4 m long (1.5 L) vertical tube sampler and preserved in a 10% buffered formalin and rose Bengal mixture with baking soda to preserve rotifer identification characteristics (DeVries and Stein 1992, Chick et al. 2010). On each sampling date, three tube samples (1.5 L each) were collected from random locations in the mesocosm, combined, and filtered through a 20 μ m mesh net (Chick et al. 2010). Sessile, benthic invertebrates were collected at the beginning and end of the experiment. At the time of collection, one tile was removed from the bottom of the mesocosm and any macroinvertebrates were washed into a sample jar and preserved using ethanol with rose Bengal. In the laboratory, macroinvertebrates and zooplankton were

enumerated and identified under a dissecting microscope to the lowest possible taxonomic level (Carey and Wahl 2010b). Up to 400 rotifers were identified under a compound microscope to the lowest possible taxonomic level and densities were estimated.

Temperature, dissolved oxygen, total phosphorus, chlorophyll *a*, turbidity, and light intensity were quantified weekly. Temperature (°C) and dissolved oxygen (mg/L) were measured from the center of each mesocosm with a model 55 YSI meter. Total phosphorus (µg/L) samples (2 x 45 mL samples) were collected and frozen within one hour of collection until they could be processed in the laboratory by oxidizing with persulfate, adding a molybdate reagent, and measuring absorbance in a spectrophotometer (Wahl et al. 2011). Chlorophyll *a* (ug/ L) was obtained by filtering 100 mL of water onto glass fiber filters (0.7 µm pore size [Millipore, Billerica, Massachusetts, USA]), extracting chlorophyll *a* in 90% acetone for 24 hours, and then measuring fluorescence using a fluorometer (Turner Design, model TD700, Sunnyvale, California, USA) (Carey and Wahl 2010b). Turbidity was measured in nephelometric units (NTU) with an electronic turbidimeter from a water sample taken throughout the water column (Wahl et al. 2011). Light intensity was measured in foot-candles, a non-SI unit of illuminance, from the center of each mesocosm at mid-depth in the water column using an underwater photometer and then converted to lux, an SI derived unit of illuminance (Protomatic, Dexter, Michigan, USA).

Statistical Analyses

Initial measurements of all response variables were tested for treatment differences using a one-way analysis of variance (ANOVA) to ensure similarity at the beginning of the experiment. Multiple linear mixed models were used to determine parameter estimates for per capita treatment effects on change in fish length and weight, as well as change in benthic

invertebrate density and richness (Forrester et al. 2006, Asquith and Vonesh 2012). Due to repeated sample events, macrozooplankton and rotifer density and richness were averaged by mesocosm and analyzed using multiple linear mixed models to determine parameter estimates for per capita treatment effects. The independent variables in the regression models were common carp density, bighead carp density, and their interaction (Forrester et al. 2006). Growth rates were determined by averaging change in total length ($\text{mm}\cdot\text{day}^{-1}$) and total weight ($\text{g}\cdot\text{day}^{-1}$) per mesocosm divided by the duration of the experiment for both species. Separate models were constructed for each response variable. Parameter estimates were obtained using the SOLUTION statement in PROC MIXED (SAS[®]). This model tested the null hypothesis that the regression coefficients (β) had a slope equal to zero ($H_0: \beta=0$) for each response variable. Errors were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Brown and Forsythe's Test for Homogeneity of Variance). Statistical significance was determined at the $\alpha = 0.05$ level. A \log_e transformation was used when residuals failed to meet the assumptions of ANOVA.

To supplement the regression analyses in testing whether inter- or intra-specific competition had a greater effect on common carp and bighead carp growth, I calculated an index of competitive effects for two response variables (change in fish length and biomass) using a subset of treatment groups (Hu and Tessier 1995, Caceres 1998). Treatments used were low and high-density single-species treatments (Treatments 2, 3, 4, 5) and the low common carp and low bighead carp treatment (Treatment 6). The competition index (CI) was calculated with the following method:

Equation 1.
$$CI = \frac{(\bar{Y}_c - \bar{Y}_e)}{\bar{Y}_c}$$

where \bar{Y}_c is the mean of the response variable from a single-species low density treatment (0.5 x) and \bar{Y}_e is the mean of the response variable from either a single-species or both-species high density treatment (1x for intra-specific competition, mix for inter-specific competition). The relative strength of inter-specific competition to intra-specific competition was estimated by calculating their ratio:

Equation 2.
$$\frac{\text{CI INTERspecific}}{\text{CI INTRAspecific}}$$

A ratio of one indicates that the two species had an equivalent per capita influence on the focal species. Ratios > 1 indicate that inter-specific competition has a greater effect on the focal species, whereas ratios < 1 indicate that intra-specific competition has a greater effect.

Macrozooplankton and rotifer density and richness, along with water temperature, dissolved oxygen, turbidity, light intensity, chlorophyll *a*, and phosphorus concentration were also examined for treatment differences with a repeated-measures ANOVA with a Kenward Roger correction (SAS[®], PROC MIXED; Table 3). The CLASS statement included Treatment, Block, and Time. Since mesocosms were housed at two locations at SPBS, location was used as a block and treated as a random variable. The full ANOVA model contained the terms Treatment, Time, and Treatment and Time. This model tested two null hypotheses for each response variable regarding differences in mean values among treatments or changes in response variables over time. The first null hypothesis was no difference in response variables across treatments and the second null hypothesis was no change in the response variables over time. Residual errors were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Brown and Forsythe's Test for Homogeneity of Variance) to meet the assumptions of ANOVA. A log_e transformation was applied to the response variable if the residuals failed meet the assumptions of ANOVA. Serial correlation among sampling dates due to repeated

measurements was accounted for by fitting several covariance structures to the data (SAS[®], PROC MIXED) and selecting the best fitting model based on the corrected Akaike's information criterion (AICC; Littell et al. 2000). Statistical significance was determined at the $\alpha = 0.05$ level, and the level from $0.05 < \alpha < 0.10$ was considered moderately significant. Specific comparisons among treatment groups were investigated using CONTRAST statements. To reduce the probability of committing a Type I error, CONTRAST statement comparisons were subject to a Bonferroni correction based on the number of treatment group comparisons.

RESULTS

Fish effects

Initial common carp and bighead carp length and weight were similar across treatments (common carp; Initial length; $F_{5,24} = 1.25$; $P = 0.32$; Initial weight; $F_{5,23} = 1.21$; $P = 0.34$; bighead carp; Initial length; $F_{5,23} = 0.77$; $P = 0.58$; Initial weight; $F_{5,24} = 0.6$; $P = 0.70$). Common carp growth was unaffected by increasing bighead carp density, but declined with increasing conspecific density (Figure 7 a, b). On a per capita basis, conspecific density had a significant negative influence on common carp growth, whereas heterospecific density did not (Table 6). Regression slope estimates indicated that increasing common carp density reduced common carp length and weight 2.4 and 1.5 times more than increasing bighead carp density, respectively (Table 6). The ratio of competition indices indicated that intra-specific competition had a greater effect than inter-specific competition on change in length and biomass for common carp (Table 7). Bighead carp growth also declined with increasing conspecific density (Figure 7 c, d). Similar to common carp, the per capita influence of increasing conspecific density had a significant negative influence on bighead carp biomass and a moderately significant effect on bighead carp length (Table 6). The per capita influence of increasing common carp density did

not significantly reduce bighead carp growth (Table 6). Regression slope estimates indicated that increasing bighead carp density reduced bighead carp length and weight 1.6 and 2 times more than increasing common carp density, respectively (Table 6). The ratio of competition indices indicated that intra-specific competition had a greater influence on bighead carp growth (Table 7). For bighead and common carp, the interaction term between conspecific and heterospecific density was not statistically significant.

Environmental Parameters

All environmental variables were similar among mesocosms on the initial sample date (all $P > 0.05$). There were no significant differences of temperature, turbidity, light intensity, chlorophyll *a*, or phosphorus among treatments (Table 8). Dissolved oxygen ($F_{8, 52.5} = 2.39$; $P = 0.03$; Table 8) was greater in the low common carp and low bighead carp treatment; however, all treatments had high dissolved oxygen concentrations $> 7 \text{ mg} \cdot \text{L}^{-1}$. Time was significant for all variables except phosphorus (Table 8). A significant treatment by time interaction was found for chlorophyll *a* ($F_{32, 358} = 2.42$; $P < 0.0001$; Table 8). To evaluate the chlorophyll *a* interaction further, the nine treatments were combined into four groups: the fishless control ($n = 1$), common carp only treatments ($n = 2$), bighead carp only treatments ($n = 2$), and mixed species treatments ($n = 4$). Using these four groups, there was a significant treatment (Treatment; $F_{3, 41} = 2.92$; $P = 0.045$), time (Time; $F_{4, 378} = 38.76$; $P < 0.0001$), and interaction (Treatment*Time; $F_{12, 378} = 1.8$; $P = 0.046$). Chlorophyll *a* concentrations in each treatment group declined over the course of the experiment; the mixed species and common carp treatment groups declined linearly, whereas the bighead carp treatment group was more constant throughout the duration of the experiment (Figure 8). Phosphorus concentrations were also examined by grouping treatments together; however, no treatment effect was observed (Treatment; $F_{3, 40.5} = 1.11$; $P = 0.36$).

Macrozooplankton

Macrozooplankton densities were similar among treatments on the first sample date before fish were added ($F_{8,36} = 1.52$; $P = 0.19$). Total macrozooplankton density varied by treatment (Treatment; $F_{8,35.1} = 12.55$; $P < 0.0001$), time (Time; $F_{4,142} = 109.68$; $P < 0.0001$), and their interaction (Treatment*Time; $F_{32,142} = 3.44$; $P < 0.0001$; Figure 9 a, b, c). With a Bonferroni correction ($P \leq 0.007$), the fishless control had significantly greater zooplankton densities than all other treatments ($F_{1,34.7} = 61.93$; $P < 0.0001$; Figure 9 a, b, c). Whereas macrozooplankton densities declined quickly in all treatments with fish, mixed species treatments were significantly lower than common carp-only or bighead carp-only treatments ($F_{1,35.1} = 29.16$; $P < 0.0001$). Common and bighead carp had a similar influence on zooplankton densities ($F_{1,34.7} = 0.02$; $P = 0.89$). Increasing bighead carp density, while holding common carp density constant, significantly lowered zooplankton density (Low common carp density with bighead carp density increasing; $F_{2,35.9} = 6.8$; $P = 0.003$; High common carp density with bighead carp density increasing; $F_{2,34.7} = 6.13$; $P = 0.005$). Increasing common carp density, while holding bighead carp density constant, significantly lowered zooplankton density at the higher bighead carp density, but not at the lower (Low bighead carp density with common carp density increasing; $F_{2,35.9} = 5$; $P = 0.01$; High bighead carp density with common carp density constant; $F_{2,34.7} = 8.95$; $P = 0.0007$). The most common zooplankton taxa ($\geq 5\%$ total macrozooplankton density) were Copepod cyclopoids, Copepod nauplii, Bosminidae, Ceriodaphnia, and Chydoridae (Table 9). All abundant taxa were significantly influenced by time (Table 9). Copepod cyclopoids and Bosminidae were not significantly influenced by treatment or the interaction between treatment and time, whereas Copepod nauplii and Ceriodaphnia were significantly influenced by both

(Table 9). Chydoridae were moderately influenced by treatment and were not influenced by the interaction between treatment and time (Table 9).

On a per capita basis, increasing common carp and bighead carp density had a negative influence on zooplankton density (Table 10). Regression slope estimates indicated that increasing common carp density reduced zooplankton density 1.3 times faster than increasing bighead carp density (Table 10, across rows). Increasing both species had a moderately negative influence on zooplankton richness (Table 10). Slope estimates indicated that the influence of the two species was about equivalent, with increasing common carp density having a 6% greater influence on richness than the per-capita influence of bighead carp (Table 10). The interaction parameter was not significant for zooplankton density or richness, and was one to two orders of magnitude smaller than the main effects.

Total Cladoceran taxa included Daphnia, Bosminidae, Sididae, Chydoridae, Ceriodaphnia, Simocephalus, and Scapholeberis. Cladoceran densities varied by treatment (Treatment; $F_{8,34.9} = 8.15$; $P < 0.0001$), time (Time; $F_{4,143} = 78.53$; $P < 0.0001$), and their interaction (Treatment*Time; $F_{32,143} = 1.86$; $P = 0.007$). With a Bonferroni correction ($P \leq 0.017$), the fishless control had significantly greater Cladoceran densities than all other treatments ($F_{1,34.2} = 53.48$; $P < 0.0001$; Figure 10 a, b, c). The common carp-only and bighead carp-only treatments were similar ($F_{1,34.1} = 0.06$; $P = 0.81$), but the mixed species treatments had significantly lower Cladoceran densities ($F_{1,35} = 9.44$; $P = 0.004$; Figure 10 a, b, c).

Total Copepoda taxa included Cyclopoida, Calanoida, and immature nauplii. Copepod densities varied by treatment (Treatment; $F_{8,35.1} = 10.7$; $P < 0.0001$), time (Time; $F_{4,143} = 83.27$; $P < 0.0001$), and their interaction (Treatment*Time; $F_{32,143} = 2.7$; $P < 0.0001$). With a Bonferroni correction ($P \leq 0.017$), the fishless control had significantly greater Copepod densities than all

other treatments ($F_{1,34.6} = 48.7$; $P < 0.0001$; Figure 10 d, e, f). The common carp-only and bighead carp-only treatments were similar ($F_{1,34.5} = 0.02$; $P = 0.89$), but the mixed species treatments had significantly lower Copepod densities ($F_{1,35.2} = 28.25$; $P < 0.0001$; Figure 10 d, e, f).

Macrozooplankton richness was similar among treatments at the first sample date before the addition of fish ($F_{8,35} = 0.71$; $P = 0.68$). Both treatment (Treatment; $F_{8,35.7} = 3.44$; $P = 0.005$) and time (Time; $F_{4,142} = 33.78$; $P < 0.0001$) varied significantly; however, no interaction was present (Treatment*Time; $F_{32,142} = 1.26$; $P = 0.18$). With a Bonferroni correction ($P \leq 0.017$), the fishless control had significantly more macrozooplankton taxa through the duration of the experiment ($F_{1,35.3} = 9.96$; $P = 0.003$; Figure 9 d, e, f). The common carp-only and bighead carp-only treatments were similar throughout the duration of the experiment ($F_{1,35.2} = 0.1$; $P = 0.76$; Figure 9 d, e). Mixed species treatments had significantly lower macrozooplankton richness ($F_{1,35.8} = 11.67$; $P = 0.002$; Figure 9 f).

Rotifers

Rotifer density and richness were similar among treatments at the first sample date before fish introduction (Density; $F_{8,35} = 1.59$; $P = 0.16$; Richness; $F_{8,35} = 0.47$; $P = 0.87$). For rotifer density, there was an overall treatment effect (Treatment; $F_{8,53.8} = 2.46$; $P = 0.02$) which varied significantly through time (Time; $F_{4,64.3} = 35.55$; $P < 0.0001$). An interaction was also present between treatment and time (Treatment*Time; $F_{32, 90.4} = 2.23$; $P = 0.002$). With a Bonferroni correction ($P \leq 0.01$), common carp only treatments had greater rotifer densities than any treatment with bighead carp present ($F_{2,53.6} = 6.28$; $P = 0.004$) as well as the fishless control ($F_{1,53.3} = 7.21$; $P = 0.01$). Bighead carp only treatments were similar to the mixed species treatments ($F_{1,53.8} = 4.01$; $P = 0.05$). Treatments containing bighead carp were similar to the

control ($F_{2,53.6} = 2.35$; $P = 0.11$; Figure 11 b, c). Increasing fish density did not have an effect on rotifer populations ($F_{3,53.8} = 0.98$; $P = 0.41$). Regression parameter estimates found that common carp presence had a significant positive influence on rotifer density, whereas bighead carp presence did not have a statistically significant influence (Table 10). Rotifer richness ranged from 6 - 11 taxa per sampling event for the duration of the experiment and was significantly different across time (Time; $F_{4,125} = 7.34$; $P < 0.0001$), but not by treatment or their interaction (Treatment; $F_{8,175} = 0.42$; $P = 0.91$; Treatment*Time; $F_{32,175} = 0.86$; $P = 0.68$). With a Bonferroni correction ($P \leq 0.025$), all treatments were similar to the control ($F_{3,175} = 0.77$; $P = 0.51$) and increasing fish density did not have an effect ($F_{3,175} = 0.13$; $P = 0.94$; Figure 11 d, e, f).

Benthic taxa

The three most common taxa in the benthic samples were chironomids (Family: Chironomidae), ostracods (Class: Ostracoda), and chydorids (Family: Chydoridae). Initial total benthic density trended toward differences before fish were added ($F_{8,35} = 1.97$; $P = 0.08$) and initial richness was similar across all treatments ($F_{8,35} = 0.52$; $P = 0.83$) before fish were added. Benthic density was not influenced by treatment ($F_{8,34} = 1.09$; $P = 0.40$), and regression parameters indicated per capita increases in common carp or bighead carp were not significant (Table 10; Figure 12). The change in benthic richness was influenced by treatment ($F_{8,34} = 2.65$; $P = 0.02$). With a Bonferroni correction ($P \leq 0.017$), the control was significantly higher than all other treatments ($F_{1,34} = 8.65$; $P = 0.006$; Figure 12). The bighead carp only and common carp only treatments had similar benthic richness ($F_{1,34} = 1.87$; $P = 0.18$), but were significantly higher than the mixed species treatments ($F_{1,34} = 5.34$; $P = 0.01$; Figure 12). Regression parameters indicated a per capita increase in common carp density had a significant negative influence on

benthic taxa richness, and increasing common carp density had three times more negative influence on richness than increasing bighead carp density (Table 10, across rows; Figure 12).

DISCUSSION

We hypothesized that common carp would be influenced more by inter-specific competition than intra-specific competition and expected inter- and intra-specific competition to negatively influence bighead carp. However, our results implied that density dependent intra-specific competition negatively influenced growth for both species, whereas inter-specific interactions had little effect. We suspect the greater strength of intra-specific competition was due to resource partitioning following the efficient exploitation of macrozooplankton resources. Supporting our third hypothesis, bighead and common carp greatly reduced macrozooplankton densities, indicating both species extensively used these resources. Previous studies have documented changes in zooplankton densities due to consumption in the presence of both carp species (Khan et al. 2003, Kolar et al. 2007). Common carp rely upon macrozooplankton until around 100 mm, at which point they undergo an ontogenetic diet shift to benthic macroinvertebrates. However, the timing of the diet shift can be variable (40 - 150 mm; Britton et al. 2007, Weber and Brown 2013b). In contrast, bighead carp are filter-feeding planktivores that are able to consume a wider range of plankton sizes (Burke et al. 1986, Cooke et al. 2009). Although both species had an effect on macrozooplankton, the differences in life history traits between the two species were magnified concerning rotifer densities. Common carp focused on Cladocera and Copepoda (Khan et al. 2003), releasing rotifers from competition and predation (Brooks and Dodson 1965, Richardson et al. 1990, Habdija et al. 2011), causing densities to increase in common carp only treatments. Bighead carp, however, are capable of filtering food particles as small as 17 μm , with a preferred range of 50 - 100 μm (Kolar et al. 2007, Sampson et

al. 2009). Bighead carp primarily prey upon macrozooplankton, but they are opportunistic and will consume rotifers and phytoplankton during times of zooplankton scarcity (Burke et al. 1986, Kolar et al. 2007). Rotifers appeared to be used as a food resource by bighead carp, as densities remained low in the bighead carp only treatments throughout the duration of the experiment. However, the rotifer densities were similar to that of the fishless control, suggesting the effect of bighead carp predation was apparently equivalent to the competitive and predation effects rotifers experience from larger zooplankters.

Benthic taxon were dominated by chironomids (Family: Chironomidae), ostracods (Class: Ostracoda), and chydorids (Family: Chydoridae), with very low densities of several other taxa (e.g. gastropods (Class: Gastropoda) and mayfly larvae (Order: Ephemeroptera)). Although total density of the organisms was not significantly modified by either bighead or common carp, taxa richness was significantly reduced in the presence of common carp. Common carp undergo an ontogenetic shift from zooplankton to benthic macroinvertebrates as juveniles, and the timing and abruptness of this transition can be variable depending on prey resources (Weber and Brown 2013b). Common carp are generalist foragers (Parkos et al. 2003) and have been found to alter benthic community richness, biomass, and density (Wahl et al. 2011, Fischer et al. 2013), although fish age can also influence foraging patterns (Kloskowski 2011). That we found benthic macroinvertebrate richness, but not density, decreased in the presence of age- 0 common carp may have been due to gape limitation, selective foraging, or that the common carp had not fully transitioned to relying on this food source.

Although bighead carp and common carp exploited the shared zooplankton resource, the reduction of rotifer densities by bighead carp and the reduction of benthic richness by common carp suggested resource partitioning by the two carp species. Optimal foraging theory predicts

that as food resources become more limiting, an organism will broaden its diet to include less profitable prey (Emlen 1966, Mittelbach 1983, Hodgson and Kitchell 1987, Mittelbach 2012); however, greater overlap in resource use between two species can increase inter-specific competition (Schoener 1982, Hanson and Leggett 1985, Holbrook and Schmitt 1989). To reduce the intensity of inter-specific competition during times of scarcity, resource-partitioning leading to niche differentiation can allow two species to coexist (Hardin 1960, Schoener 1982, Chargulaf et al. 2011, Fobert et al. 2011, Liso et al. 2013). As preferred prey items are exhausted, each organism will exploit less profitable resources that they are better adapted to use (Holbrook and Schmitt 1989, Chargulaf et al. 2011, Fobert et al. 2011). We assumed resource limitation as the mesocosms showed declines in zooplankton availability. With macrozooplankton resources exhausted, it appears bighead carp used rotifers whereas common carp consumed various benthic invertebrates. Partitioning of food resources reduces the magnitude of inter-specific competition, often allowing intra-specific competition to increase and both species to coexist (Hardin 1960, Mittelbach 2012).

Although juvenile common and bighead carp use zooplankton resources at juvenile life stages, an important consideration is that organisms often have multiphasic life cycles, with individuals occupying distinct niches at different stages in their life history (Bruno et al. 2003, Rius et al. 2014). After their ontogenetic shift to benthic macroinvertebrates, common carp benthic foraging can modify invaded ecosystems by increasing turbidity, decreasing macrophytes, and resuspending nutrients (Parkos et al. 2003, Scheffer and Jeppesen 2007, Matsuzaki et al. 2009b, Fischer et al. 2013). Generally, adult common carp have been shown to increase phytoplankton and rotifer densities with variable influences on macrozooplankton (Richardson et al. 1990, Parkos et al. 2003, Roozen et al. 2007, Matsuzaki et al. 2009a).

Increases in zooplankton through trophic cascades may potentially cause indirect facilitation of bighead carp by adult common carp. These interactions have been suggested previously, as common carp and bighead carp have been used globally for aquaculture where polyculture is aimed to increase overall biomass (Buck et al. 1983). The addition of adult silver and bighead carp has been used to increase biomass in common carp ponds (Opuszynski 1981). Bighead carp grew more rapidly than silver carp, and common carp production was found to decline with the addition of bighead carp (Opuszynski 1981). It was concluded that bighead carp were not good as additional fish in common carp ponds due to diet overlap; however, common carp diets were supplemented by sorghum and total fish biomass was not held constant across treatments, potentially confounding results through density dependent effects (Opuszynski 1981). Most aquaculture studies using bighead and common carp also include silver and grass carp (*Ctenopharyngodon idella*), as well as add external food sources, clouding the inferences that can be made about inter-specific effects and effects on the plankton community (Opuszynski 1981, Buck et al. 1983, Fallahi et al. 2013). Although facilitation may occur at adult life stages, this study is the first to our knowledge to examine bighead and common carp exclusively at the juvenile life stage and demonstrate evidence for resource partitioning.

Intra-specific competition had a stronger influence on common and bighead carp, suggesting coexistence is probable when these two species are in a common environment (Mittelbach 2012). Indeed, coexistence has been well documented in the Mississippi River Basin (Irons et al. 2011, McClelland et al. 2012). Although facilitation as adults is unknown, even competitive interactions between the two species at any sympatric life stage may have detrimental implications for native fishes. Both species have been shown to alter ecosystems, either through changing zooplankton densities and community composition via removal by

bighead carp (Guo et al. 2014, Sass et al. 2014) or increasing turbidity and removing macrophytes via foraging by common carp (Parkos et al. 2003, Fischer et al. 2013). When common and bighead carp exist together, native larval and juvenile fishes may be simultaneously effected by reduced food sources coupled with loss of protective cover (Welker et al. 1994, Collingsworth and Kohler 2010). Low zooplankton densities have been linked to larval fish starvation and slow juvenile growth (Welker et al. 1994, Graeb et al. 2004). Slowed juvenile growth increases predation risk, as does insufficient macrophyte cover (Collingsworth and Kohler 2010, Wahl et al. 2011). The potential influence of these two invasive species on ecosystem processes has serious implications for native fish populations.

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TABLES AND FIGURES

Table 6. Regression models testing for effects of conspecific and heterospecific density, and their interaction, on changes in length and biomass of common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*). Displayed are model r^2 values, regression coefficients (β), and P-values for an associated significance test ($H_0: \beta=0$) for each term in the model.

	r^2	Intercept		Conspecific density		Heterospecific Density		Interaction				
				β	P	β	P	β	P			
Common Carp Responses												
Change in Length (mm/ day)	0.49	0.25	(±0.04)	-0.019	(±0.005)	0.002	-0.008	(±0.007)	0.24	0.001	(±0.0008)	0.51
Change in Biomass (g/ day)	0.35	0.03	(±0.01)	-0.003	(±0.001)	0.007	-0.002	(±0.001)	0.24	0.0001	(±0.0002)	0.41
Bighead Carp Responses												
Change in Length (mm/ day)	0.28	0.24	(±0.07)	-0.018	(±0.009)	0.07	-0.011	(±0.011)	0.33	0.0006	(±0.001)	0.66
Change in Biomass (g/ day)	0.25	0.03	(±0.01)	-0.002	(±0.001)	0.048	-0.001	(±0.001)	0.29	0.0001	(±0.0002)	0.51

Table 7. Competition Indices (CI) for change in length and biomass of common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*). Low and high single-species treatments (intra-specific interactions; common carp, Treatment 2, 3; bighead carp, Treatment 4, 5) and the low common carp and low bighead carp treatment (inter-specific interactions; Treatment 6) were included. Values were calculated as the ratio of CI inter-specific values (CI inter) to CI intra-specific values (CI intra). Ratios > 1 indicated that inter-specific competition had a greater effect on the focal species; ratios < 1 indicated that intra-specific competition had a greater effect, and a ratio of one indicates that the two species had an equivalent per capita effect. See text for details on calculating the CI (Hu and Tessier 1995, Caceres 1998).

	Common Carp			Bighead carp		
	CI Intra	CI Inter	Ratio	CI Intra	CI Inter	Ratio
Change in Biomass	0.93	0.15	0.17	0.69	0.23	0.33
Change in Length	0.58	0.07	0.12	0.52	0.33	0.63

Table 8. Repeated measures ANOVA testing for the effects of treatment on temperature ($^{\circ}\text{C}$), dissolved oxygen (mg L^{-1}), turbidity (NTU), light intensity (lux), water column chlorophyll *a* (ug L^{-1}), and total phosphorus (ug L^{-1}) through time. Nine treatments with five replicates consisted of a fishless control (Treatment 1), low and high fish densities of either common carp (*Cyprinus carpio*;) (Treatments 2, 3) or bighead carp (*Hypophthalmichthys nobilis*) (Treatments 4, 5), and low and high-density combinations with both species (Treatment 6, 7, 8, 9). Low-density refers to a fish density of five and high-density refers to a fish density of ten. One replicate (low common carp, low bighead carp; Treatment 6) was lost due to fish mortality and was removed from analyses. Two chlorophyll *a* samples were mishandled and not included in the analyses. Mesocosms were held in two locations, and location was used as a random block. Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), F-statistics, and P-values are presented for each analysis. A Kenward Roger correction was used to obtain degrees of freedom.

Response	Effect	NDF	DDF	F	P
Temperature	Treatment	8	68.3	0.86	0.56
	Time	4	128	1567.13	<0.0001
	Treatment x Time	32	138	0.54	0.98
Dissolved oxygen	Treatment	8	52.5	2.39	0.03
	Time	4	50.4	70.54	<0.0001
	Treatment x Time	32	95.2	0.53	0.98
Turbidity	Treatment	8	51	0.99	0.45
	Time	4	51.2	27.66	<0.0001
	Treatment x Time	32	96	0.48	0.99
Light intensity	Treatment	8	59.7	0.6	0.77
	Time	4	51.7	4.4	0.004
	Treatment x Time	32	96.5	0.47	0.99
Chlorophyll <i>a</i>	Treatment	8	35.5	1.38	0.24
	Time	4	358	50.6	<0.0001
	Treatment x Time	32	358	2.42	<0.0001
Phosphorus	Treatment	8	34.6	0.76	0.64
	Time	4	143	0.89	0.47
	Treatment x Time	32	142	0.77	0.80

Table 9. Repeated measures ANOVA testing for effects of treatment, time, and their interaction on the most abundant macrozooplankton taxa in the mesocosms. Taxa were considered abundant if their density·L⁻¹ was ≥ 5% of the total number of zooplankton. Nine treatments with five replicates consisted of a fishless control (Treatment 1), low and high fish densities of either common carp (*Cyprinus carpio*) (Treatments 2, 3) or bighead carp (*Hypophthalmichthys nobilis*) (Treatments 4, 5), and low and high-density combinations with both species (Treatment 6, 7, 8, 9). Low-density refers to a fish density of five and high-density refers to a fish density of ten. One treatment (low common carp, low bighead carp; Treatment 6) was lost due to fish mortality and was removed from analyses. The mesocosms were held in two locations and location was used as a random block. Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), F-statistics, and P-values are presented for each analysis. A Kenward-Rodger correction was used to obtain degrees of freedom. A log_e transformation was applied to the taxa to meet the assumptions of ANOVA.

Zooplankton	NDF	DDF	F	P
Copepoda				
Cyclopoid				
Treatment	8	35	1.72	0.13
Time	4	141	54.54	<0.0001
Treatment x Time	32	141	1.35	0.12
nauplii				
Treatment	8	35.1	11.57	<0.0001
Time	4	141	77.71	<0.0001
Treatment x Time	32	141	2.6	<0.0001
Cladocera				
Bosminidae				
Treatment	8	33.9	1.14	0.36
Time	4	140	17.63	<0.0001
Treatment x Time	32	140	0.6	0.95
Ceriodaphnia				
Treatment	8	34.8	10.19	<0.0001
Time	4	140	77.78	<0.0001
Treatment x Time	32	140	1.71	0.02
Chydoridae				
Treatment	8	33.2	2.02	0.07
Time	4	140	17.63	<0.0001
Treatment x Time	32	140	1.27	0.18

Table 10. Regression models testing for the per capita effects of common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*) density, and their interaction, on the average change in macrozooplankton density, macrozooplankton richness, rotifer density, and rotifer richness over the duration of the experiment, as well as the difference (end sample date - beginning sample date) of the total sessile, benthic taxa density and richness. The differences in density of the three most common benthic taxa (Chydoridae; Chironomidae; Ostracoda) were examined separately. Displayed are model r^2 values, regression coefficients (β), and P-values for an associated significance test ($H_0: \beta=0$) for each term in the model.

	r^2	Intercept	Common carp density		Bighead Carp Density		Interaction		
			β	P	β	P	β	P	
Macrozooplankton Responses									
Density (# / L)	0.33	5.55 (\pm 0.25)	-0.107 (\pm 0.035)	0.004	-0.082 (\pm 0.035)	0.025	0.005 (\pm 0.005)	0.33	
Richness (# / sample)	0.33	3.91 (\pm 0.28)	-0.084 (\pm 0.426)	0.056	-0.079 (\pm 0.426)	0.07	-0.001 (\pm 0.007)	0.90	
Rotifer Responses									
Density (# / L)	0.21	4.99 (\pm 0.32)	0.113 (\pm 0.050)	0.03	-0.043 (\pm 0.050)	0.39	-0.007 (\pm 0.008)	0.37	
Richness (# / sample)	0.04	8.72 (\pm 0.35)	-0.019 (\pm 0.051)	0.71	-0.042 (\pm 0.051)	0.42	0.008 (\pm 0.008)	0.30	
Benthic taxa									
Total taxa (# / cm ²)	0.06	-0.99 (\pm 0.91)	0.119 (\pm 0.112)	0.30	0.096 (\pm 0.111)	0.39	-0.026 (\pm 0.017)	0.14	
Richness (# / sample)	0.22	1.04 (\pm 0.58)	-0.191 (\pm 0.090)	0.04	-0.063 (\pm 0.090)	0.48	0.002 (\pm 0.014)	0.89	
Chydoridae (# / cm ²)	0.06	-1.02 (\pm 0.77)	0.147 (\pm 0.096)	0.13	0.081 (\pm 0.095)	0.40	-0.022 (\pm 0.015)	0.14	
Chironomidae (# / cm ²)	0.03	0.03 (\pm 0.05)	0.001 (\pm 0.005)	0.92	-0.002 (\pm 0.005)	0.65	-0.0002 (\pm 0.001)	0.77	
Ostracoda (# / cm ²)	0.10	-0.08 (\pm 0.39)	-0.062 (\pm 0.059)	0.30	0.023 (\pm 0.061)	0.71	-0.002 (\pm 0.009)	0.82	

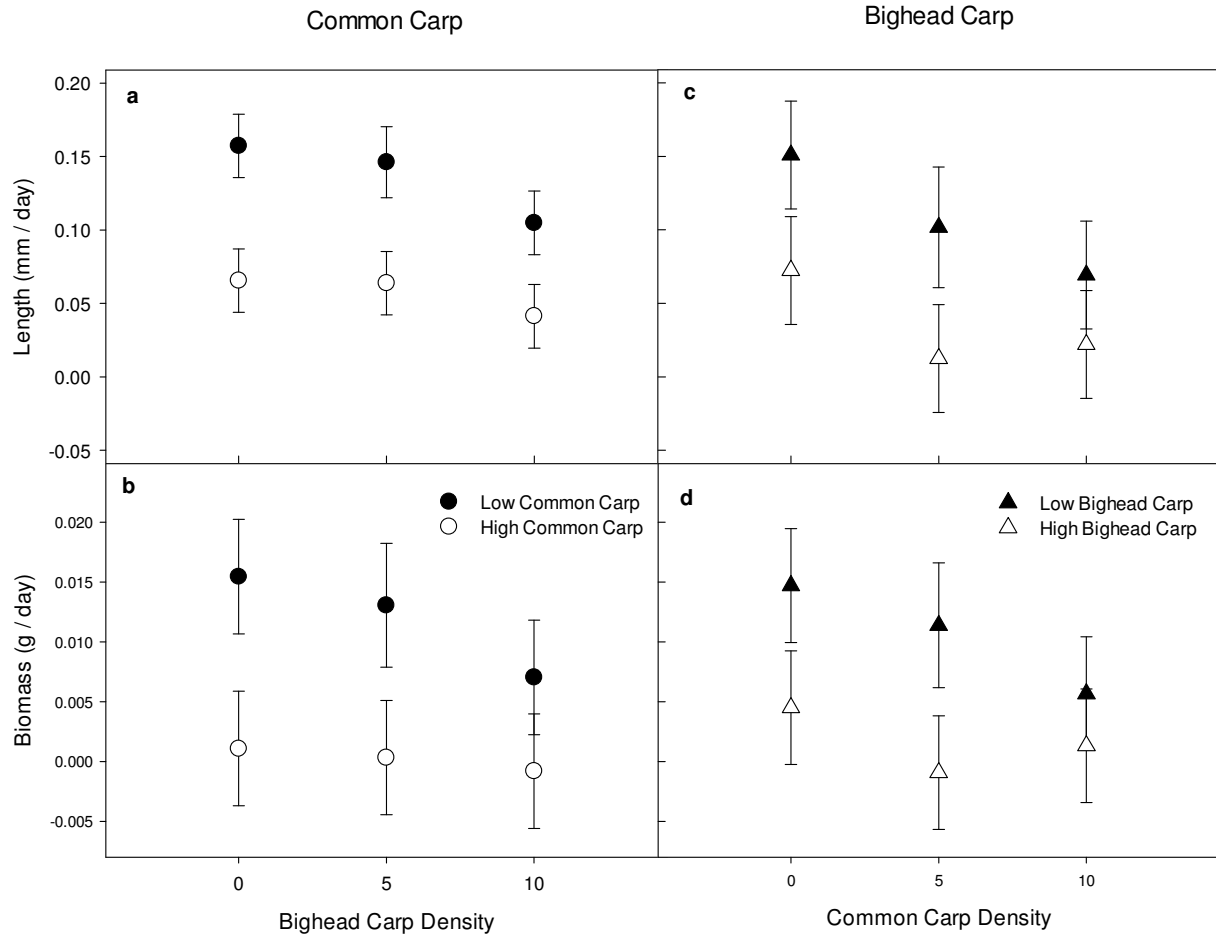


Figure 7. Mean change in length (top panels; a, c) and biomass (bottom panels; b, d) per day of common carp (*Cyprinus carpio*) (circles; a, b) and bighead carp (*Hypophthalmichthys nobilis*) (triangles; c, d) across heterospecific density levels of zero, five, and ten fish. ‘Low’ refers to a fish density of five and ‘high’ refers to a fish density of ten. The average change in total length and total biomass per mesocosm for each species was divided by the duration of the experiment. Error bars represent ± 1 standard error about the mean.

Chlorophyll-a Concentrations

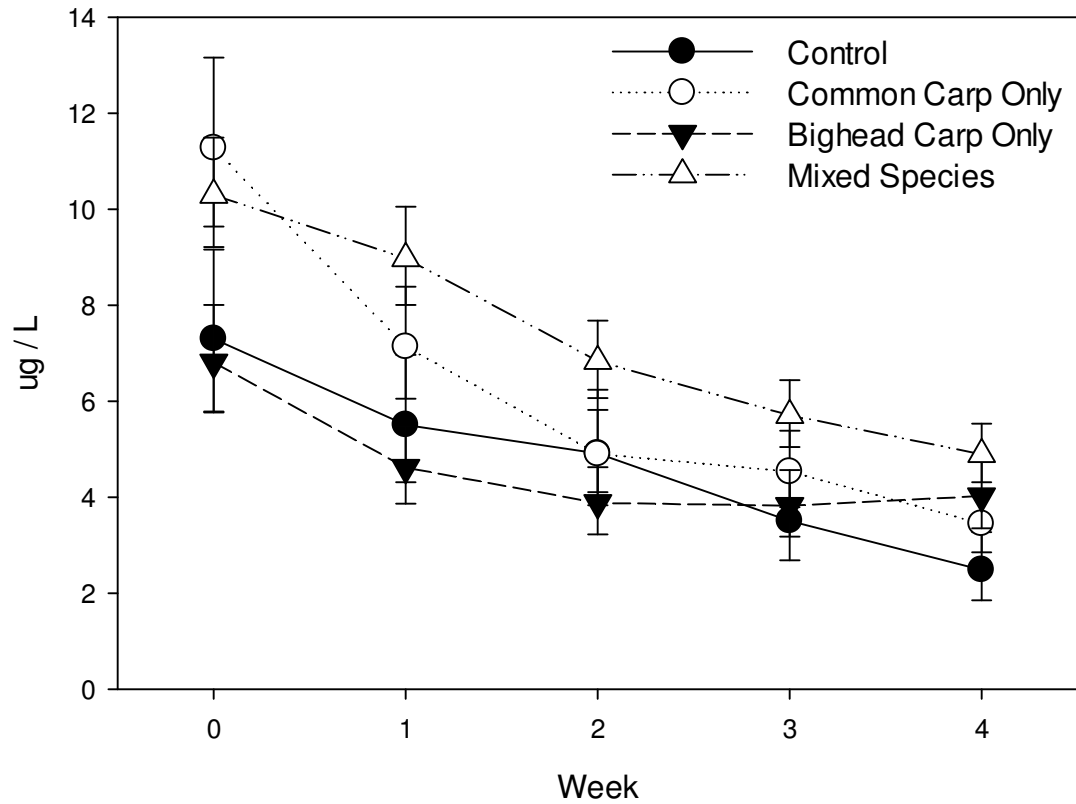


Figure 8. Mean chlorophyll-*a* concentrations ($\mu\text{g}\cdot\text{L}^{-1}$) by week of the experiment. The nine treatments were combined into four groups: the fishless control (“Control”; $n = 1$), common carp only treatments (*Cyprinus carpio*) (“Common Carp Only”; $n = 2$), bighead carp only treatments (*Hypophthalmichthys nobilis*) (“Bighead Carp Only”; $n = 2$), and mixed species treatments (“Mixed Species”; $n = 4$). Error bars represent ± 1 standard error about the mean.

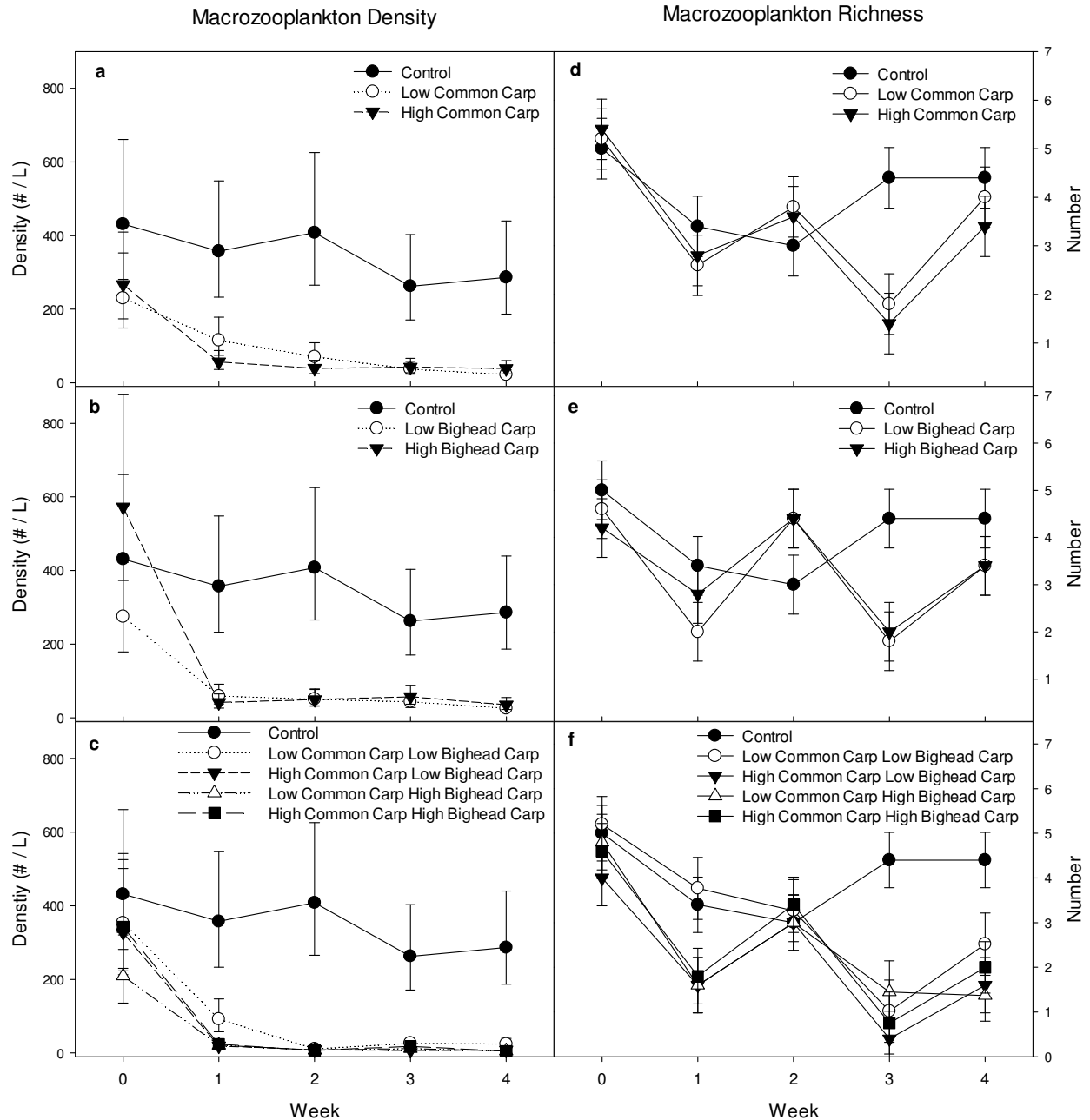


Figure 9. Weekly mean total macrozooplankton density (number of organisms \cdot L⁻¹; panels a, b, c) and richness (total number of organisms identified to lowest taxonomic level; panels d, e, f) collected from water samples filtered through a 55 μ m mesh. Low common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*) treatments had a total of five fish / mesocosm. High common carp and bighead carp treatments had a total of ten fish / mesocosm. For mixed species treatments, ‘low’ refers to a fish density of five and ‘high’ refers to a fish density of ten. Mixed species treatments had a total fish density of ten, fifteen, or twenty depending on the treatment. Error bars represent \pm 1 standard error about the mean.

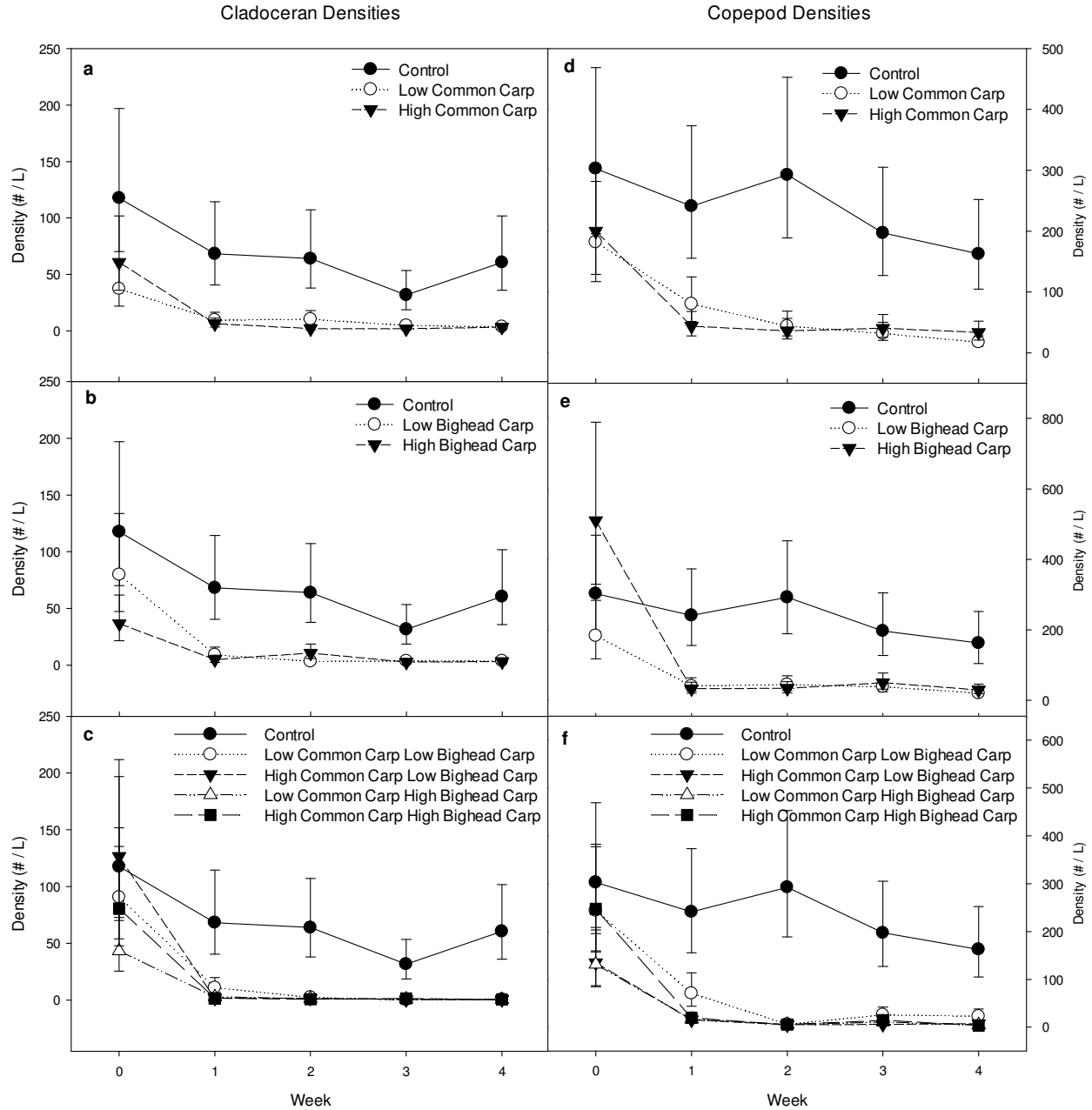


Figure 10. Weekly mean total cladoceran density (number of organisms $\cdot L^{-1}$; panels a, b, c) and copepod density (number of organisms $\cdot L^{-1}$; panels d, e, f) collected from water samples filtered through a 55 μm mesh. Low common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*) treatments had a total of five fish / mesocosm. High common carp and bighead carp treatments had a total of ten fish / mesocosm. For mixed species treatments, ‘low’ refers to a fish density of five and ‘high’ refers to a fish density of ten. Mixed species treatments had a total fish density of ten, fifteen, or twenty depending on the treatment. Error bars represent ± 1 standard error about the mean.

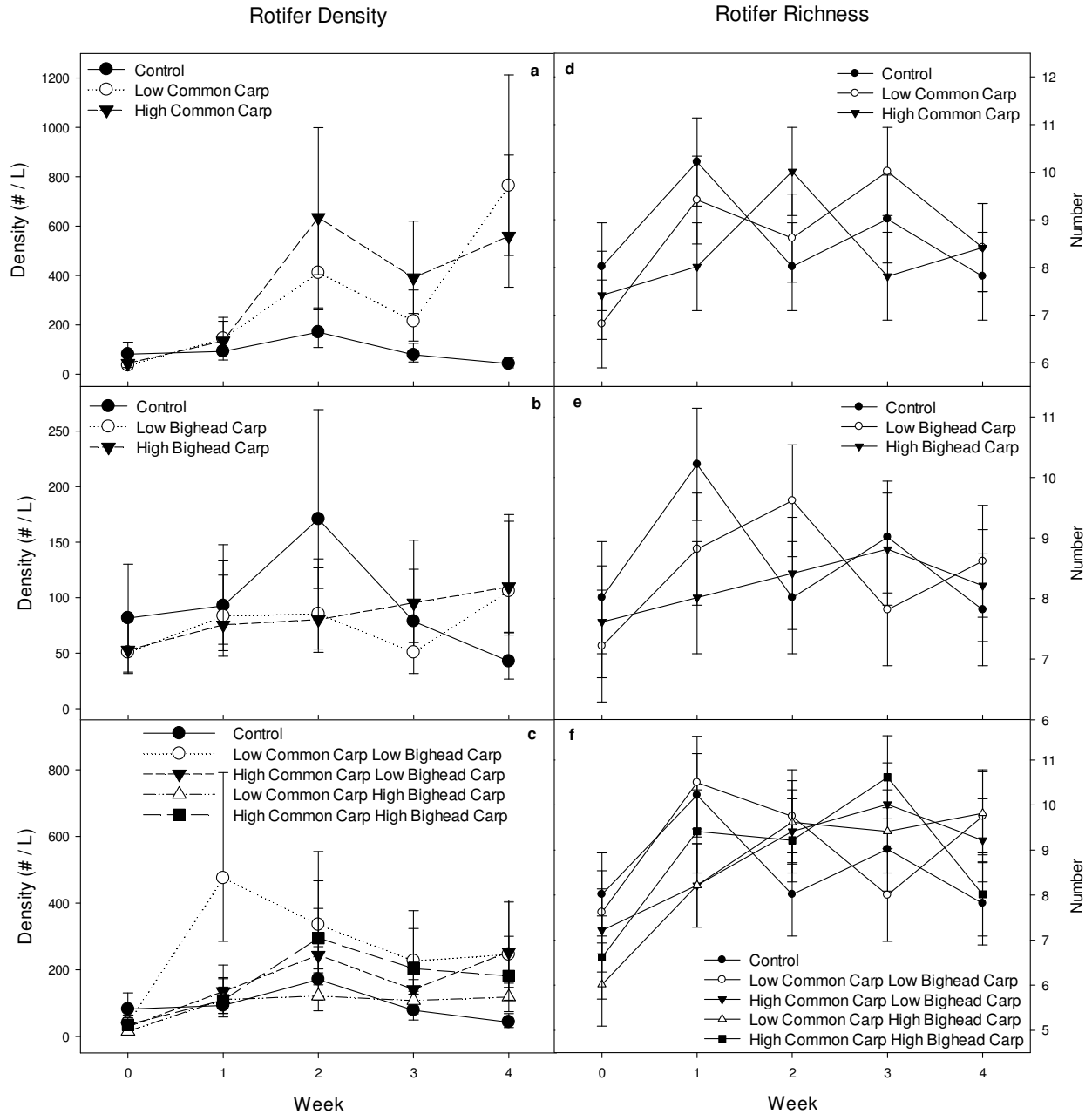


Figure 11. Weekly mean rotifer density (number of organisms $\cdot L^{-1}$; a, b, c) and rotifer richness (number of taxa $\cdot sample^{-1}$; d, e, f) collected from water samples filtered through a 20 μm mesh (Chick et al. 2010). Low common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*) treatments had a total of five fish / mesocosm. High common carp and bighead carp treatments had a total of ten fish / mesocosm. For mixed species treatments, ‘low’ refers to a fish density of five and ‘high’ refers to a fish density of ten. Mixed species treatments had a total fish density of ten, fifteen, or twenty depending on the treatment. Error bars represent ± 1 standard error about the mean.

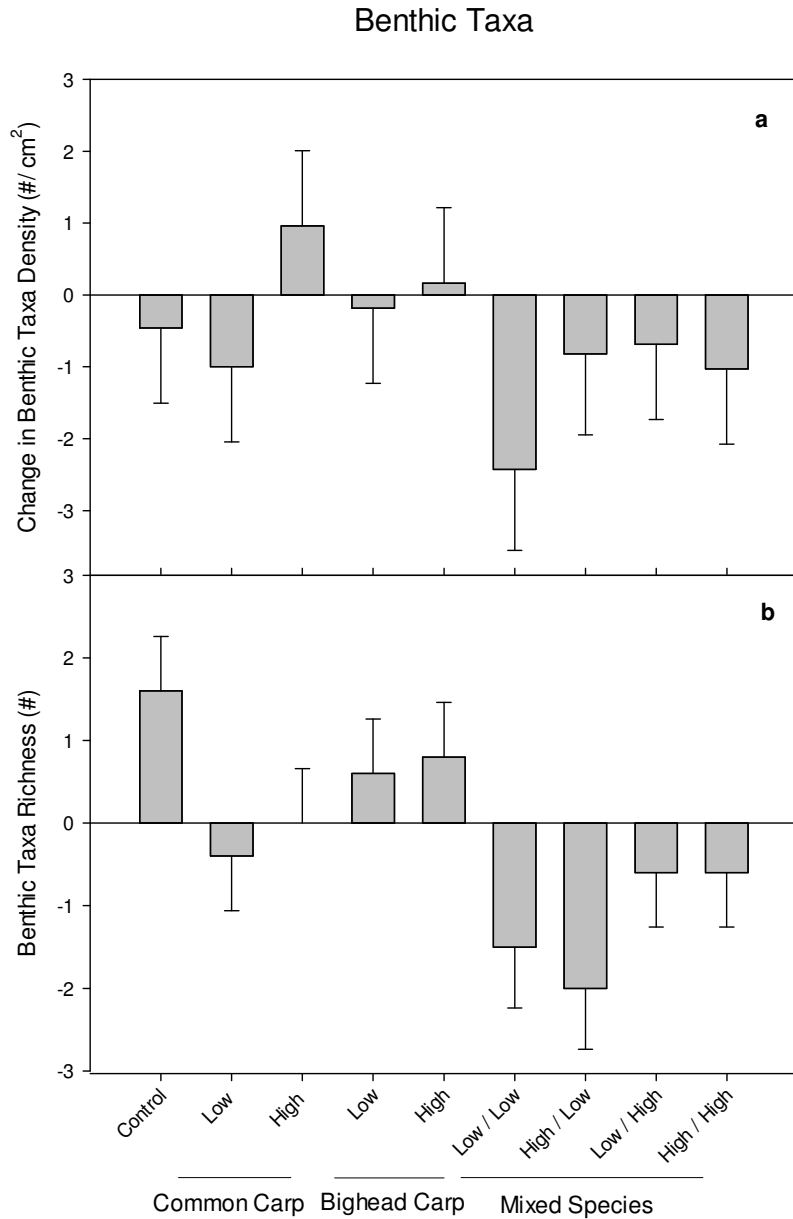


Figure 12. Mean change in total benthic taxa (a; total number of organisms from the final sample date subtracted from the total number of organisms from the initial sample date) by cm^2 and richness (b; total number of taxa from the final sample date subtracted from the total number of taxa from the initial sample date). Low common carp (*Cyprinus carpio*) and bighead carp (*Hypophthalmichthys nobilis*) treatments had a total of five fish/ mesocosm. High common carp and bighead carp treatments had a total of ten fish / mesocosm. For mixed species treatments, 'low' refers to a fish density of five and 'high' refers to a fish density of ten. Mixed species treatments had a total fish density of ten, fifteen, or twenty depending on the treatment. Error bars represent ± 1 standard error about the mean.

CHAPTER 4: THE RELATIVE IMPORTANCE OF INTER- AND INTRA-SPECIFIC COMPETITION FOR BLUEGILL PAIRED WITH INVASIVE BIGHEAD CARP IN EXPERIMENTAL PONDS

ABSTRACT

Invasive species may change nutrient cycling and ecosystem processes in novel habitats to the benefit or detriment of native species. We tested the relative importance of intra- and inter-specific competition between juvenile bluegill (*Lepomis macrochirus*) and juvenile bighead carp (*Hypophthalmichthys nobilis*) in a replicated 0.4-hectare experimental pond experiment. We also tested for influences on the aquatic community using three treatments of low bluegill density, high bluegill density, and mixed species with bluegill and bighead carp. Bluegill growth was weakly density-dependent, with reduced growth in the high-density treatment relative to the low-density treatment, although this result was not statistically significant. Bighead carp presence facilitated bluegill growth, resulting in significantly greater length and marginally greater weight. Bighead carp had a negative influence on zooplankton density and biomass, and bluegill consumed more macroinvertebrates with bighead carp present. Our results suggest community modifications in lentic systems due to bighead carp may benefit native taxa, such as juvenile bluegill.

INTRODUCTION

Concerns about aquatic invasive species effects on native taxa and their respective ecosystems are common (Simberloff and Von Holle 1999, Baxter et al. 2007, Elvidge and Ricciardi 2007, Simberloff 2011, Wahl et al. 2011, Simberloff et al. 2013). Aquatic invasive species have been shown to prey upon native species (Sepulveda et al. 2013), compete with them for resources (Baxter et al. 2007), hybridize (Boyer et al. 2008, Lamer et al. 2010), and spread disease (Gozlan et al. 2009). Invasion success is often due to a non-native species ability to exploit resources more efficiently than the native species present (Shea and Chesson 2002,

Fridley et al. 2007). The monopolization of food resources can trigger shifts in native species diets, which can potentially influence growth, reproduction, or even survival (Ross 1986, Chargulaf et al. 2011, Liso et al. 2013).

Areas with high native species diversity can also host many invasive species (Fridley et al. 2007). Invasive species will not necessarily have negative influences on all native species present (Altieri et al. 2010) because ecological interactions are complex and can interact in unexpected ways. Although understudied, evidence for neutral or even positive interactions between invasive and native species exists (Rodriguez 2006, Thomsen 2010, Thompson and Schiel 2012). For instance, adult yellow perch (*Perca flavescens*) were found to grow larger in the presence of zebra mussels (*Dreissena polymorpha*) due to modifications of benthic macroinvertebrate densities and community structure via sediment enrichment and greater habitat heterogeneity (Thayer et al. 1997). Facilitation of native species by invasive species can play an important role in community dynamics, and better understanding of such interactions is critical as rates of invasion increase (Rodriguez 2006)

Bighead carp (*Hypophthalmichthys nobilis*) have been cultured globally for water quality management and polyculture (Kirkendall and Smitherman 1990, Webber and Bayne 1990, Kolar et al. 2007). Bighead carp, along with silver carp (*Hypophthalmichthys molitrix*), were introduced to the United States in the 1970s for this purpose before escaping soon after into the Mississippi River Basin (Kolar et al. 2007). Some studies have found that bighead carp, coupled with silver carp, can alter energy pathways by shifting nutrients and organic carbon to the sediments (Opuszynski 1980b, Leventer and Teltsch 1990, Starling 1993). Shifts in energy flow have been attributed to their high consumption rates of plankton and subsequent excretion; both species have been shown to reduce zooplankton and phytoplankton (Opuszynski 1980b, Leventer

and Teltsch 1990, Starling 1993, Kolar et al. 2007). The removal of zooplankton by bighead carp is suspected to have a detrimental competitive effect on native fishes in the Mississippi River Basin (Chick and Pegg 2001, Irons et al. 2007, Mandrak and Cudmore 2010, Sass et al. 2014). Although some studies have found dietary overlap and reduced body condition of native planktivores in the presence of bighead and silver carp (Irons et al. 2007, Sampson et al. 2009), the potential influence of these carp on facultative planktivores remains largely uninvestigated.

Competitive interactions between bighead carp and a native facultative planktivore, bluegill (*Lepomis macrochirus*) were investigated in a replicated mesocosm experiment (Nelson et al. 2014). Bluegill showed density dependent decreases in growth and bighead carp presence increased chironomid densities (Nelson et al. 2014). Small scale mesocosm experiments can provide insight into mechanisms of species interactions, but observed patterns can disappear or change at larger spatial scales, making experiments with greater niche heterogeneity necessary to better understand real world processes (Carpenter and Kitchell 1992, Carey and Wahl 2011a). For these reasons, we conducted a replicated competition experiment with bluegill and bighead carp in experimental ponds. We hypothesized that density dependent intra-specific competition would have a greater influence than inter-specific competition, and juvenile bluegill would grow more rapidly when low fish densities were present. We hypothesized that bighead carp would have a negative influence on zooplankton density, which would remove an important food resource for juvenile bluegill. Partial dietary overlap was expected to have negative influences on bluegill growth, but not as great of an influence as the total dietary overlap experienced by conspecifics.

MATERIALS AND METHODS

Experimental design

Inter- and intra-specific competition was tested for using juvenile bluegill and bighead carp in nine drainable 0.04-hectare ponds at Sam Parr Biological Station (SPBS), Kinmundy, Illinois, USA. Ponds were drained and allowed to dry for about two weeks, and then filled with water from Forbes Lake. Water was filtered through a 300 um mesh net to prevent larval fish introduction. Plankton and macroinvertebrates were allowed to populate for about two weeks before fish introduction.

Ponds were divided into three treatments with three replicates. The three treatments were low-density bluegill (400 bluegill·pond⁻¹), high-density bluegill (800 bluegill·pond⁻¹), and low-density bluegill with low-density bighead carp (400 bluegill·pond⁻¹ with 400 bighead carp·pond⁻¹; 800 total fish·pond⁻¹). Bluegill densities were within commonly observed range in natural waterbodies (Hackney 1979, Wolfe et al. 2009, Carey and Wahl 2011a, Wahl et al. 2011). Bighead carp density and biomass was matched to bluegill density and biomass. Bluegill were obtained from ponds at SPBS and bighead carp were provided from a commercial hatchery (Osage Catfisheries Inc., Osage Beach, Missouri, USA). Our experimental design tested for bluegill intra- and inter-specific competition without confounding density effects. However, our design was only able to address the inter-specific effect of bighead carp on bluegill. Intra-specific bighead carp competition and potential inter-specific bluegill effects on bighead carp could not be tested due to a limited number of ponds. Likewise, we chose to not add a fishless treatment to increase the number of replicates given the limited number of ponds. Prior to introduction into the ponds, fifty individuals of each species were measured (total length [1 mm]; weight [0.1 g]) for each replicate. Fish were enumerated and acclimated (water exchange,

minimum of 10 minutes) to each pond before release. Initial measurements for bluegill were 47.5 ± 13.3 mm and 1.9 ± 1.2 g, while initial measurements for bighead carp were 58.6 ± 6.4 mm and 1.9 ± 0.7 g. Initial fish mean biomass was similar among treatments ($F_{2,5.29} = 2.03$; $P = 0.22$) and between species ($F_{1,4.28} = 1.13$; $P = 0.34$). Initial fish mean length differed between species ($F_{1,10} = 158.41$; $P < 0.0001$) due to morphological differences.

Data collection

Limnological sampling was conducted immediately prior to fish introduction and then repeated on a biweekly basis for 80 days. Temperature and dissolved oxygen were measured at about 0.33 m below the water surface using a YSI meter (Wahl et al. 2011). Zooplankton were collected using a 70 mm diameter x 0.8 m long (3 L) vertical tube sampler and preserved in a 10% buffered formalin and rose Bengal mixture with baking soda (DeVries and Stein 1992, Chick et al. 2010). On each sample date, five tube samples were collected from various locations in each pond, combined, and filtered through a 55 μ m mesh net to estimate macrozooplankton densities and 20 μ m mesh net to estimate rotifer densities (Chick et al. 2010). Water samples were collected from the entire water column to determine total phosphorus (2 x 45 mL samples) and frozen within an hour of collection. Samples were stored frozen until they were processed by oxidizing with persulfate, adding a molybdate reagent, and measuring absorbance in a spectrophotometer (Wahl et al. 2011). One phosphorus sample was mishandled during processing. Chlorophyll *a* concentration was obtained by filtering 100 mL of water onto glass fiber filters (0.7 μ m pore size [Millipore, Billerica, Massachusetts, USA]), extracting chlorophyll *a* in 90% acetone for 24 hours, and then measuring fluorescence using a fluorometer (Turner Design, model TD700, Sunnyvale, California, USA) (Carey and Wahl 2010b). Benthic and littoral macroinvertebrates were collected monthly and preserved with ethanol colored with

rose Bengal. Benthic macroinvertebrates were collected from five randomly distributed samples per pond using a Standard 6''x 6'' x 6'' Ekman Bottom Grab (Wildco, Wildlife Supply Co.). Littoral macroinvertebrates were associated with habitat along the pond edge and collected from five randomly distributed samples (Dame 2005). Littoral macroinvertebrates were collected using an independently erect 18'' x 18'' x 33'' quadrat sampler, with the bottom open to the substrate and the sides enclosed with 64- μ m mesh (Hauer and Resh 2006). The sampler rested on the bottom of the substrate and was confined along the shoreline to span the entire water column. Sampling consisted of repeatedly agitating the entire water column within the quadrat sampler with a dip net (1 mm mesh), and sweeps were made until four consecutive sweeps resulted in no additional macroinvertebrates (Dame 2005). Any vegetation within the plot was collected with the rest of the sample for determination of macroinvertebrates in the lab (Dame 2005). Exact depth at each sample location was recorded (mm) to calculate sample area (m^3).

Final weight and length measurements were recorded for fifty fish per species per pond and the remaining fish were enumerated. In the laboratory, aquatic macroinvertebrates and zooplankton were enumerated and identified under a dissecting microscope to the lowest possible taxonomic level, genus, or species when possible (Carey and Wahl 2010b). Taxa-specific body dimensions were measured from a subset of macroinvertebrates and zooplankton (Carey and Wahl 2010b). Up to 400 rotifers were identified under a compound microscope to the lowest possible taxonomic level and final densities were estimated based on the identification (Chick et al. 2010).

Fish Analyses

Initial bluegill length and weight was tested for consistency across treatments and compared to initial bighead carp length and weight with a one-way ANOVA. Treatment

influences of fishes were tested for with three separate methods and comparisons among treatments were *a priori*. The first method tested for treatment effects on change in bluegill length, change in bluegill weight, percent survival, and production (g/ # surviving individuals) with a one-way ANOVA with a Kenward Roger correction (SAS[®], PROC MIXED). The MODEL statement contained Treatment, with Pond as a random variable. Bluegill change in length and weight were calculated by subtracting the initial values from the end values and dividing by the number of days of the experiment. Production was calculated as the per day change in weight multiplied by the number of days the experiment was conducted multiplied by the number of surviving fish. *A priori* CONTRAST statements were used to make specific comparisons among treatments. Statistical significance was determined at the $\alpha = 0.05$ level.

The second method used multiple linear mixed models to determine parameter estimates for per capita treatment effects on change in fish length and weight (Forrester et al. 2006, Asquith and Vonesh 2012). Independent variables in the regression models were bluegill and bighead carp density (Forrester et al. 2006). The interaction between bluegill and bighead carp density was not calculated due to limited degrees of freedom. This model tested the null hypothesis that the regression coefficients (β) had a slope equal to zero ($H_0: \beta=0$) for each response variable. Separate models were constructed for each response variable. Parameter estimates were obtained using the SOLUTION statement in PROC MIXED (SAS[®]). Errors were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Brown and Forsythe's Test for Homogeneity of Variance). Statistical significance was determined at the $\alpha = 0.05$ level.

The third method used an index of competitive effects to test whether inter- or intra-specific competition had a greater effect on bluegill for two response variables (change in fish

length and biomass; Hu and Tessier 1995, Caceres 1998). The competition index (CI) was calculated as:

Equation 1.
$$CI = \frac{(\bar{Y}_c - \bar{Y}_e)}{\bar{Y}_c}$$

where \bar{Y}_c is the mean of the response variable from the low bluegill density treatment (0.5 x) and \bar{Y}_e is the mean of the response variable from either the high bluegill density or mixed species treatments (1x for intra-specific competition, mix for inter-specific competition). The relative strength of inter-specific competition to intra-specific competition was estimated by calculating their ratio:

Equation 2.
$$\frac{CI \text{ INTERspecific}}{CI \text{ INTRAspecific}}$$

where a ratio of one indicates that the two species had an equivalent per capita influence on bluegill. Ratios > 1 indicated that inter-specific competition had a greater effect on bluegill, whereas ratios < 1 indicated that intra-specific competition had a greater effect.

Environmental Analyses

Initial measurements from the first sample date for each variable were tested for consistency across treatments using a one-way ANOVA. Length-weight regressions were used to estimate the average biomass of each prey type consumed (Smock 1983, Sample et al 1993) and the taxa-specific biomass estimates were multiplied by taxa density to estimate total biomass. Tests for differences in density and biomass of zooplankton, rotifers, benthic macroinvertebrates, and littoral macroinvertebrates, as well as zooplankton diversity, rotifer richness, benthic and pelagic macroinvertebrate diversity, water temperature, dissolved oxygen, Secchi disc transparency, chlorophyll *a*, and phosphorus among treatments were investigated with a repeated-measures ANOVA with a Kenward Roger correction (SAS[®], PROC MIXED).

Abundant zooplankton taxa densities (individual taxa $\geq 5\%$ total density) were also investigated individually, as well as by the functional groups Cladocera, Copepoda, and Ostracoda. The order Cladocera consisted of Daphnia, Bosminidae, Sididae, Chydoridae, Ceriodaphnia, Simocephalus, Scapholeberis, and 'Other Cladoceran'. The subclass Copepoda consisted of Cyclopoida, Calanoida, and nauplii. The CLASS statement included Treatment, Pond, and Time. Pond was treated as a random variable. The full ANOVA model contained the terms Treatment, Time, and Treatment x Time. This model tested two null hypotheses for each response variable regarding differences in mean values among treatments or changes in response variables over time. The first null hypothesis was no difference in response variables across treatments, and the second null hypothesis was no change in the response variables over time. Errors were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Brown and Forsythe's Test for Homogeneity of Variance) to meet the assumptions of ANOVA. A \log_e transformation was applied if the initial residuals failed to meet the assumptions of ANOVA. Serial correlation among sampling dates due to repeated measurements was accounted for by fitting several covariance structures to the data (SAS[®], PROC MIXED). The best fitting covariance model was selected based on the corrected Akaike's information criterion (AICC; Littell et al. 2000). *A priori* CONTRAST statements were used to make specific comparisons among treatments. Significance was determined at the $\alpha=0.05$ level and levels between $0.05 < \alpha < 0.10$ were considered marginally significant.

RESULTS

Fish

Change in bluegill length was significantly different among treatments ($F_{2,6}=10.72$; $P=0.01$), with length increasing the most in the mixed species treatment, followed by the low-density treatment, and lastly the high-density treatment. Bluegill change in length in the mixed

species treatment was significantly greater than the low or high-density treatments (MIX vs. LOW; $F_{1,6}=7.86$; $P=0.03$; MIX vs. HIGH; $F_{1,6}= 21.10$; $P=0.004$; Figure 13 b). Change in bluegill length in low and high-density treatments did not differ ($F_{1,6}= 3.20$; $P=0.12$; Figure 13 b). Intra-specific interactions had a greater competitive influence on change in length than inter-specific interactions (Table 11). Regression parameters indicated a significant positive influence of heterospecific density on the change in bluegill length (Table 12). Bighead carp length increased over the duration of the experiment (Figure 13 b).

Change in bluegill biomass was marginally significant ($F_{2,6}= 4.42$; $P=0.07$) among treatments; however, biomass increased the most in the mixed species treatment, followed by the low-density treatment, and lastly the high-density treatment. Bluegill change in biomass in the mixed species treatment was similar to the low-density treatment ($F_{1,6}= 1.53$; $P=0.26$), but was significantly greater than the high-density treatment ($F_{1,6}= 8.77$; $P=0.03$; Figure 13 a). The low-density treatment was similar to the high-density treatment ($F_{1,6}= 2.98$; $P=0.14$; Figure 13 a). The competition index indicated that intra-specific interactions had a greater competitive influence on change in bluegill biomass than inter-specific interactions (Table 11). Regression parameters did not find a significant conspecific or heterospecific influence on the change in bluegill biomass (Table 12). Bighead carp biomass increased over the duration of the experiment (Figure 13 a).

Fish production was marginally significant in different treatments ($F_{2,6}=3.70$; $P=0.09$). The high-density treatment and mixed species treatments were similar ($F_{1,6}=0.02$; $P=0.88$), whereas the low-density treatment had marginally lower or lower production than the other two (LOW vs. HIGH; $F_{1,6}= 5.19$; $P= 0.06$; LOW vs. MIX; $F_{1,6}= 5.90$; $P= 0.05$; Figure 14 a). Bighead carp production was similar to total bluegill production ($F_{1,1.92}= 4.95$; $P= 0.16$; Figure 14 a).

Percent survival of bluegill varied among treatments ($F_{2,6}=6.32$; $P=0.03$). Survival in the mixed species treatment was greater than the low-density treatment, but similar to the high-density treatment (MIX vs. LOW; $F_{1,6}=12.59$; $P=0.01$; MIX vs. HIGH; $F_{1,6}=3.89$; $P=0.10$; Figure 14 b). High and low-density treatments had similar survival ($F_{1,6}=2.49$; $P=0.17$; Figure 14 b). Bighead carp survival was greater than bluegill ($F_{1,10}=8.01$; $P=0.02$; Figure 14 b).

Environmental Parameters

Initial environmental parameter measurements were consistent across treatments (all $P>0.05$). There were no significant treatment effects on water temperature (Treatment; $F_{2,6,25}=2.28$; $P=0.18$), dissolved oxygen (Treatment; $F_{2,6,01}=0.04$; $P=0.96$), Secchi disc transparency (Treatment; $F_{2,6}=0.63$; $P=0.56$), chlorophyll *a* (Treatment; $F_{2,6}=0.25$; $P=0.79$; Figure 17 a) or phosphorus (Treatment; $F_{2,6}=0.06$; $P=0.94$; Figure 17 b). Water temperature (Time; $F_{6,9,11}=4665.03$; $P<0.0001$), dissolved oxygen (Time; $F_{6,27,5}=76.2$; $P<0.0001$), chlorophyll *a* (Time; $F_{6,36}=6.45$; $P=0.0001$), and phosphorus (Time; $F_{6,36}=2.34$; $P=0.05$) varied significantly over time. Secchi disc transparency did not vary significantly over time (Time; $F_{6,27,9}=1.63$; $P=0.18$). No significant interaction between treatment and time was present for water temperature, dissolved oxygen, Secchi disc transparency, chlorophyll *a*, or phosphorus (Interaction: Temperature; $F_{12,9,87}=1.09$; $P=0.45$; Dissolved Oxygen; $F_{12,27,1}=2.05$; $P=0.06$; Secchi Depth; $F_{12,27,5}=0.34$; $P=0.97$; Chlorophyll *a*; $F_{12,36}=1.06$; $P=0.42$; Phosphorous; $F_{12,36}=1.45$; $P=0.19$).

Macrozooplankton

Macrozooplankton density was consistent across treatments in the initial sample ($F_{2,6}=0.79$; $P=0.50$). Macrozooplankton density was significantly affected by treatment (Treatment; $F_{2,42}=27.05$; $P<0.0001$), but not by time (Time; $F_{6,42}=1.28$; $P=0.29$), with no interaction between time and treatment ($F_{12,42}=1.57$; $P=0.14$). The high and low-density bluegill treatments

were not different ($F_{1,42}= 1.6$; $P= 0.21$). The mixed species treatment had significantly lower macrozooplankton densities than either of the bluegill treatments (LOW VS MIX; $F_{1,42}= 31.85$; $P<0.0001$; HIGH VS MIX; $F_{1,42}= 47.71$; $P<0.0001$; Figure 15 a).

The most abundant taxa (> 90% of total organisms) were Copepod calanoids, Copepod nauplii, Sididae (Order: Cladocera), and Ostracoda. Treatment and time (Treatment; $F_{2,9,97}= 13.93$; $P= 0.001$; Time; $F_{6,31.7}= 3.92$; $P= 0.005$) significantly influenced Cladoceran densities, however, the interaction was not significant ($F_{12,31.2}= 0.74$; $P= 0.71$; Table 13). Copepod densities varied by treatment (Treatment; $F_{2,42}= 23.59$; $P<0.0001$), but not by time or the interaction between treatment and time (Time; $F_{6,42}= 1.47$; $P= 0.21$; Treatment*Time; $F_{12,42}= 1.7$; $P= 0.10$; Table 13). Ostracod density was not affected by treatment or the interaction between treatment and time (Treatment; $F_{2,4,39}= 0.67$; $P= 0.56$; Treatment*Time; $F_{12,13,9}= 0.78$; $P= 0.66$), but varied by time (Time; $F_{6,13.5}= 14.3$; $P<0.0001$; Table 13).

Initial macrozooplankton biomass and diversity was similar across treatments (Biomass; $F_{2,6}= 0.80$; $P=0.49$; Diversity; $F_{2,6}= 0.75$; $P= 0.51$). Macrozooplankton biomass was significantly affected by treatment (Treatment; $F_{2,6}= 14.92$; $P=0.005$) and time (Time; $F_{6,36}= 2.32$; $P=0.05$), but not by their interaction (Treatment*Time; $F_{12,36}= 1.37$; $P=0.23$). High and low-density bluegill treatments had similar zooplankton biomass ($F_{1,6}= 1.30$; $P=0.30$) and had greater zooplankton biomass than the mixed species treatment ($F_{1,6}= 28.53$; $P= 0.002$; Figure 15 b). Macrozooplankton diversity varied by time, but not by treatment or interaction (Time; $F_{6,36}= 8.24$; $P<0.0001$; Treatment; $F_{2,6}= 0.70$; $P= 0.53$; Treatment*Time; $F_{12,36}= 1.10$; $P= 0.39$; Figure 15 c).

Rotifers

Initial rotifer density, biomass, and richness were consistent among treatments in the initial sample (Density; $F_{2,6}= 1.21$; $P= 0.36$; Biomass; $F_{2,6}= 2.18$; $P= 0.19$; Richness; $F_{2,6}= 0.07$; $P= 0.93$). Rotifer density varied by time, but was unaffected by treatment or the interaction between time and treatment (Time; $F_{6,36}= 6.21$; $P= 0.0002$; Treatment; $F_{2,6}= 1.71$; $P= 0.26$; Treatment*Time; $F_{12,36}= 0.92$; $P= 0.53$; Figure 15 d). Rotifer density in the high and low bluegill treatments did not differ from the mixed species treatment ($F_{1,6}= 3.42$; $P= 0.11$; Figure 15 d). Rotifer biomass was influenced by time, but not by treatment or interaction of time and treatment (Time; $F_{6,32.2}= 3.91$; $P=0.005$; Treatment; $F_{2,8.98}= 2.64$; $P= 0.13$; Treatment*Time; $F_{12,31.6}= 0.91$; $P=0.55$; Figure 15 e), as was rotifer richness (Time; $F_{6,36}= 3.13$; $P= 0.01$; Treatment; $F_{2,6}= 1.10$; $P= 0.39$; Treatment*Time; $F_{12,36}= 0.88$; $P= 0.57$; Figure 15 f).

Macroinvertebrates

The most abundant benthic taxa (> 85% of total density) were Bivalvia (Class), Ceratopogonidae (Family; Order: Diptera), Chironomidae (Family; Order: Diptera), and Ostracoda (Class; Table 14). Initial benthic macroinvertebrate density, biomass, and diversity were similar among treatments (Density; $F_{2,6}= 0.19$; $P=0.83$; Biomass; $F_{2,6}= 2.17$; $P= 0.20$; Diversity; $F_{2,6}= 0.20$; $P= 0.98$). Benthic macroinvertebrate density was unaffected by treatment, time, or their interaction (Treatment; $F_{2,8.24}= 0.58$; $P=0.58$; Time; $F_{3,9.61}= 1.66$; $P=0.24$; Treatment*Time; $F_{6,10.1}= 0.10$; $P= 0.99$; Figure 16 d). Benthic macroinvertebrate biomass was influenced by time (Time; $F_{3,17}= 3.25$; $P= 0.05$), but not by treatment or interaction (Treatment; $F_{2,6.55}= 0.40$; $P=0.69$; Treatment*Time; $F_{6,17}= 1.06$; $P= 0.43$; Figure 16 e). Benthic macroinvertebrate diversity was not influenced by time, treatment, or their interaction (Treatment; $F_{2,7.17}= 0.23$, $P= 0.80$; Treatment*Time; $F_{6,17.2}= 0.56$; $P= 0.76$) and was marginally influenced by time (Time; $F_{3,17.2}= 2.86$; $P= 0.07$; Figure 16 f).

The most abundant littoral taxa (> 75% of total density) were Anisoptera (Suborder; Order: Odonata), Ceratopogonidae (Family; Order: Diptera), Chironomidae (Family; Order: Diptera), Zygoptera (Suborder; Order: Odonata), and Notonectidae (Family; Order: Hemiptera; Table 4). Initial littoral density, biomass, and diversity were similar (Density; $F_{2,6}= 0.10$; $P= 0.90$; Biomass; $F_{2,6}= 0.05$; $P= 0.96$; Diversity; $F_{2,6}= 0.73$; $P= 0.52$). Littoral macroinvertebrate density was unaffected by treatment, time, or their interaction (Treatment; $F_{2,6}= 1.78$; $P=0.25$; Time; $F_{3,8,62}= 0.81$; $P=0.52$; Treatment*Time; $F_{6,8,98}= 0.66$; $P=0.69$). At the end of the experiment, littoral macroinvertebrate density was significantly greater in the high-density bluegill treatment than in the mixed species treatment ($F_{1,20,5}= 4.94$; $P=0.04$; Figure 16 a). Littoral macroinvertebrate biomass was influenced by treatment and time (Treatment; $F_{2,6}= 5.93$; $P= 0.04$; Time; $F_{3,18}= 4.83$; $P= 0.01$), but their interaction was not significant (Treatment*Time; $F_{6,18}= 0.63$; $P= 0.70$; Figure 16 b). The low-density bluegill treatment had significantly greater littoral macroinvertebrate biomass than the mixed species treatment ($F_{1,6}= 11.86$; $P=0.01$; Figure 16 b), but both were similar to the high density treatment (Low vs. High; $F_{1,6}= 3.16$; $P=0.13$; Mixed vs. High; $F_{1,6}= 2.77$; $P=0.15$; Figure 16 b). When combined, both bluegill-only treatments had greater littoral macroinvertebrate biomass than the mixed species treatment ($F_{1,6}= 8.70$; $P= 0.03$). Littoral macroinvertebrate diversity was also unaffected by treatment or the interaction of time and treatment (Treatment; $F_{2,24}= 1.08$; $P= 0.36$; Treatment*Time; $F_{6,24}= 1.50$; $P= 0.22$), but varied significantly over time (Time; $F_{3,24}= 12.69$; $P<0.0001$; Figure 16 c).

DISCUSSION

Facilitation between species is an important ecological interaction that is widespread, but often unacknowledged (Altieri et al. 2010). When facilitation is considered among aquatic invasive species, it has often resulted in cumulative detrimental effects on native biota

(Simberloff and Von Holle 1999, Adams et al. 2003, Simberloff 2006, Griffen and Byers 2009). However, ecological processes are complex, and an introduced species may directly or indirectly modify the invaded ecosystem in ways that benefit individual taxa at certain stages of their life history (Kolar et al. 2007). Our first hypothesis, which stated that density dependent intra-specific competition would have a greater influence than inter-specific competition on bluegill, was partially supported. Bluegill growth was lower in the high-density treatment; however, the growth differences between the two treatments were not statistically significant. The CI supported the conclusion that intra-specific competition had a stronger influence on bluegill. Unexpectedly, we found that the presence of bighead carp significantly increased bluegill length and marginally increased bluegill weight. Bighead carp have negatively influenced heterospecific growth (Schrank et al. 2003, Irons et al. 2007, Sampson et al. 2009); however, these studies were focused on filter-feeding planktivores.

The unexpected increase in bluegill growth in the presence of bighead carp may be explained by several plausible mechanisms. First, bighead carp may have altered energetic pathways that led to an increase in macroinvertebrate density, biomass, or production. Bighead carp have been used in aquaculture facilities globally to reduce algal blooms (Opuszynski 1981, Kirkendall and Smitherman 1990, Kolar et al. 2007). Previous studies investigating bighead carp influences on nutrient uptake are varied; some studies have found that bighead carp transfer nutrients from pelagic areas to the benthos via excretion (Opuszynski 1980b, Ruan 2005, Kolar et al. 2007, Nelson et al. 2014) and aquatic macroinvertebrates have increased in density and biomass with nutrient addition due to increased periphyton (Cross et al. 2006, Miracle et al. 2006). One study concluded that bighead carp had a negative influence on benthic macroinvertebrate densities; however, the macroinvertebrate results were confounded by initial

macroinvertebrate densities and the presence of benthivores (Webber and Bayne 1990). An increase in organic carbon, nitrogen, and total phosphorus in the sediments could potentially have a positive indirect influence on either macroinvertebrate density or production, which could have benefited bluegill. There is potential for a positive feedback between adult bluegill and bighead carp when bluegill consume macroinvertebrates and excrete into pelagic areas (Mather et al. 1995, Schindler and Scheuerell 2002, Glaholt and Vanni 2005).

Standing stock estimates of macroinvertebrates did not reflect higher density or biomass, but instead indicated lower littoral macroinvertebrate biomass in the mixed species treatment.

However, these samples reflect snap shots of community composition (Johnson et al. 2013), and increases in macroinvertebrate density and biomass may have been exploited by bluegill more rapidly than our sampling could detect, resulting in greater bluegill growth in the mixed species treatment. Lower littoral macroinvertebrate biomass may have been a reflection of bluegill exploitation. Although we did not measure macroinvertebrate production or bluegill diet contents, nutrient addition has been found to increase macroinvertebrate production (Cross et al. 2006, Johnson et al. 2013).

Second, bighead carp presence may have influenced the behavior of the macroinvertebrates or altered community composition to taxa that are more vulnerable to bluegill predation. Generalists like bluegill tend to preferentially select larger, more active macroinvertebrates, and behavioral traits of macroinvertebrates can influence their vulnerability to predation (Diehl 1992). Many aquatic macroinvertebrates rely on zooplankton as a food resource (e.g. Coleoptera, Odonata; Burks et al. 2006, Magnusson and Williams 2009). Reduction of zooplankton in the water column due to bighead carp foraging may have forced these taxa to forage more actively, causing them to be more conspicuous to bluegill.

Alternatively, low zooplankton densities could have triggered a community shift to taxa that are more periphyton dependent (e.g. Physid, Trichoptera; Doremus and Harman 1977, Burks et al. 2006), which may have conveyed a benefit to bluegill.

Finally, differences in bluegill foraging among treatments may have been responsible for the observed growth patterns, with bluegill experiencing greater growth with mixed species than low-density bluegill only. Bluegill have been found to exploit either large zooplankters or aquatic macroinvertebrates, depending on the individual fish, time of year, relative prey abundance, presence of competitors, or presence of predators (Werner and Hall 1979, Mittelbach 1981, Werner et al. 1981, Werner et al. 1983, Ehlinger and Wilson 1988, Mittelbach 1988, Ehlinger 1989, 1990, Dewey et al. 1997, Olson et al. 2003). Macroinvertebrates and zooplankters (e.g. *Daphnia* spp.) have similar energy content (Ehlinger 1989, 1990, Breck 1993). Although macroinvertebrates are much larger than zooplankton with greater total energy, they are more difficult for bluegill to locate among sediments and macrophytes and require longer handling time for consumption (Mittelbach 1983). The presence of bighead carp, a pump filter feeder and superior competitor for zooplankton (Burke et al. 1986, Kolar et al. 2007), may have reduced the encounter rates of macrozooplankton to levels too low to be energetically profitable for bluegill, triggering a reliance on macroinvertebrates. Littoral macroinvertebrate biomass was lower with mixed species compared to the low-density bluegill treatment, despite having the same number of bluegill, suggesting bluegill relied more heavily on macroinvertebrates as a food source in the mixed species treatment. The benthic and littoral macroinvertebrate density and biomass in the ponds was similar to other studies conducted in Illinois (Stone et al. 2005, Walther and Whiles 2008) with high littoral to pelagic habitat ratios. In the low-density treatment, bluegill may not have accurately assessed foraging potential or selected prey based on

another mechanism that ultimately reduced foraging return. Possible mechanisms influencing bluegill foraging differences among treatments include phenotypic variations in morphology (Ehlinger and Wilson 1988, Ehlinger 1990), temperature preferences (Wildhaber 2001), or differences in vegetation densities (Harrel and Dibble 2001, Shoup et al. 2012). Suboptimal foraging in bluegill is well-documented (Mittelbach 1981, Harrel and Dibble 2001, Spotte 2007, Shoup et al. 2012) suggesting the mechanisms driving bluegill foraging patterns are varied. Regardless, our results demonstrate that bighead carp are capable of modifying habitats via changes in environmental processes that, in some cases, convey benefits to certain native taxa such as juvenile bluegill.

Although bluegill had greater growth in the presence of bighead carp, we caution that bighead carp still have the potential to negatively influence bluegill and other fishes. The experimental ponds are relatively shallow (maximum depth 1.4 m) with aquatic macrophytes present, thus providing ample habitat for benthic and littoral macroinvertebrates compared to the pelagic area. In aquatic systems with few macrophytes or large pelagic areas, heavy reliance on macroinvertebrates may be inadequate for positive growth. The ponds were also void of piscine predators such as largemouth bass (*Micropterus salmoides*) and predation risk can influence bluegill behavior and habitat choice (Carey and Wahl 2010a, Oplinger et al. 2011). The presence of piscine predators coupled with plankton community effects by bighead carp may limit bluegill from adequately accessing food resources. Additionally, larval bluegill rely exclusively on zooplankton, and inadequate plankton densities have been negatively correlated with bluegill growth (Welker et al. 1994), suggesting that bighead carp have the potential to negatively influence larval stages of bluegill populations.

Consistent with our second hypothesis, bighead carp suppressed zooplankton density and biomass, but not rotifers. Littoral macroinvertebrate biomass was greater in the low-density bluegill treatment compared to the mixed species treatment. The responses of several parameters may have been due to low replication. Mesocosm experiments are relatively inexpensive and often have the advantage of many replicates and treatments, leading to statistical power and inferences about species interactions, but can occasionally produce misleading results (Carpenter 1996, Drenner and Mazumder 1999). Experimental ponds can incorporate increased environmental complexity such as larger spatial scale, resource heterogeneity, and habitat heterogeneity (Carey and Wahl 2011a). The disadvantage of experiments at larger spatial scales is fewer replicates, treatments, and a longer time scale; however, experiments at larger spatial scales are necessary to build upon results found at smaller scales (e.g. mesocosms) and elucidate if findings are consistent (Carpenter 1999, Drenner and Mazumder 1999). Our pond results yielded different results compared to our previous mesocosm study testing for competitive interactions between bighead carp and bluegill (Nelson et al. 2014). Our mesocosm study found that bluegill were negatively influenced by inter- and intra-specific effects; however, there was a significant interaction between the densities of the two fishes, indicating the effect of one species was dependent upon the other (Nelson et al. 2014). At the larger spatial scale, we found that bluegill were facilitated by bighead carp presence. Previous studies have found varying results at differing spatial scales, likely due to increased environmental heterogeneity and increased niche space (Carey and Wahl 2011a). Testing for the influences of bighead carp on bluegill at different life stages in natural systems may further expand our understanding of the effects of these invasive species.

Interactions among fishes in structurally complex habitats with partial dietary overlap can be difficult to quantify, and in our study, bighead carp unexpectedly facilitated bluegill growth. Although bighead carp negatively influenced native planktivores (Schrank et al. 2003, Irons et al. 2007), they may have the ability to influence trophic dynamics in unpredictable ways that may benefit native species under certain conditions (Kolar et al. 2007). Our results demonstrated that bighead carp presence could alter communities, most notably by suppressing zooplankton densities, an important food resource for both aquatic vertebrates and invertebrates. Our observation of zooplankton suppression by bighead carp has also been supported at an ecosystem scale on the Illinois River, Illinois, USA (Sass et al. 2014). This may have triggered a shift in energetic pathways, macroinvertebrate communities, and/or behavior, and these trophic dynamics warrant future investigations to better understand the complex array of influences bighead carp may have on native communities.

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TABLES AND FIGURES

Table 11. Competition Indices (CI) for change in length and biomass of bluegill (*Lepomis macrochirus*) in an 80-day experiment testing for inter- and intra-specific competition of bluegill with bighead carp (*Hypophthalmichthys nobilis*) in experimental ponds. Values were calculated as the ratio of CI inter-specific values (CI inter) to CI intra-specific values (CI intra). Ratios > 1 indicated that inter-specific competition had a greater effect on the focal species; ratios < 1 indicated that intra-specific competition had a greater effect, and a ratio of one indicates that the two species had an equivalent per capita effect. See text for details on calculating the CI (Hu and Tessier 1995, Caceres 1998).

	Bluegill		
	CI Intra	CI Inter	Ratio
Change in Biomass	0.26	-0.36	-1.38
Change in Length	0.16	-0.26	-1.63

Table 12. Regression models testing effects of conspecific and heterospecific density on changes in length and biomass of bluegill (*Lepomis macrochirus*) in an 80-day experiment testing for inter- and intra-specific competition of bluegill with bighead carp (*Hypophthalmichthys nobilis*) in experimental ponds. The interaction between bighead carp and bluegill was not tested due to limited degrees of freedom. Displayed are model r^2 values, regression coefficients (β) and P-values for an associated significance test ($H_0: \beta=0$) for each term in the model.

	r^2	Intercept	Conspecific density		Heterospecific Density	
			β	P	β	P
Bluegill Responses						
Change in Length (mm/ day)	0.78	0.48 (± 0.06)	-0.0002 (± 0.0001)	0.12	0.0003 (± 0.0001)	0.03
Change in Biomass (g/ day)	0.60	0.11 (± 0.03)	-0.0001 (± 0.00005)	0.26	0.0001 (± 0.00005)	0.14

Table 13. Repeated measures ANOVA testing for the effects of treatment, time, and their interaction on the most abundant zooplankton taxa (# / L) in experimental ponds during an 80-day experiment. Pond was included as a random variable. Individual taxa were considered abundant if their density·L⁻¹ was ≥ 5% of the total number of organisms. Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), F-statistics, and P-values are presented for each analysis. Kenward-Rodger correction was used to obtain degrees of freedom. The covariance matrix for each response variable was determined from lowest AICC score.

Zooplankton	NDF	DDF	F	P
Copepod				
Calanoida				
Treatment	2	5.92	28.79	0.0009
Time	6	35	4.20	0.003
Treatment x Time	12	35	2.91	0.007
nauplii				
Treatment	2	11.8	2.84	0.10
Time	6	31.4	4.17	0.003
Treatment x Time	12	31	1.96	0.07
Cladocera				
Sididae				
Treatment	2	6.26	24.36	0.001
Time	6	25.1	7.83	<0.0001
Treatment x Time	12	25.1	1.20	0.33
Ostracoda				
Treatment	2	4.39	0.67	0.56
Time	6	13.5	14.3	<0.0001
Treatment x Time	12	13.9	0.78	0.66

Table 14. Repeated measures ANOVA testing for the effects of treatment, time, and their interaction on the most abundant benthic (#/m²) and pelagic (#/m³) macroinvertebrate taxa in experimental ponds during an 80-day experiment. Pond was included as a random variable. Individual taxa were considered abundant if their density·L⁻¹ was ≥ 5% of the total number of organisms. Numerator degrees of freedom (NDF), denominator degrees of freedom (DDF), F-statistics, and P-values are presented for each analysis. Kenward-Rodger correction was used to obtain degrees of freedom. The covariance matrix for each response variable was determined from the lowest AICC score.

Benthic Macroinvertebrates	NDF	DDF	F	P	Littoral Macroinvertebrates	NDF	DDF	F	P
Bivalvia					Anisoptera				
Treatment	2	6	0.00	0.99	Treatment	2	11.7	1.45	0.27
Time	3	18	7.43	0.002	Time	3	17.6	4.84	0.01
Treatment x Time	6	18	2.36	0.07	Treatment x Time	6	17.8	0.34	0.91
Ceratopogonidae					Ceratopogonidae				
Treatment	2	6	0.10	0.91	Treatment	2	13.7	14.42	0.0004
Time	3	18	1.16	0.35	Time	3	15.8	6.84	0.004
Treatment x Time	6	18	0.98	0.47	Treatment x Time	6	16.2	2.71	0.05
Chironomidae					Chironomidae				
Treatment	2	6	0.27	0.77	Treatment	2	6	0.68	0.54
Time	3	18	5.45	0.005	Time	3	18	2.26	0.12
Treatment x Time	6	18	0.36	0.90	Treatment x Time	6	18	0.80	0.58
Ostracoda					Zygoptera				
Treatment	2	6	0.03	0.97	Treatment	2	6	0.92	0.41
Time	3	18	0.12	0.95	Time	3	18	6.00	0.003
Treatment x Time	6	18	1.49	0.24	Treatment x Time	6	18	0.63	0.71
					Notonectidae				
					Treatment	2	11.9	1.44	0.28
					Time	3	19	90.54	<0.0001
					Treatment x Time	6	19.1	0.59	0.73

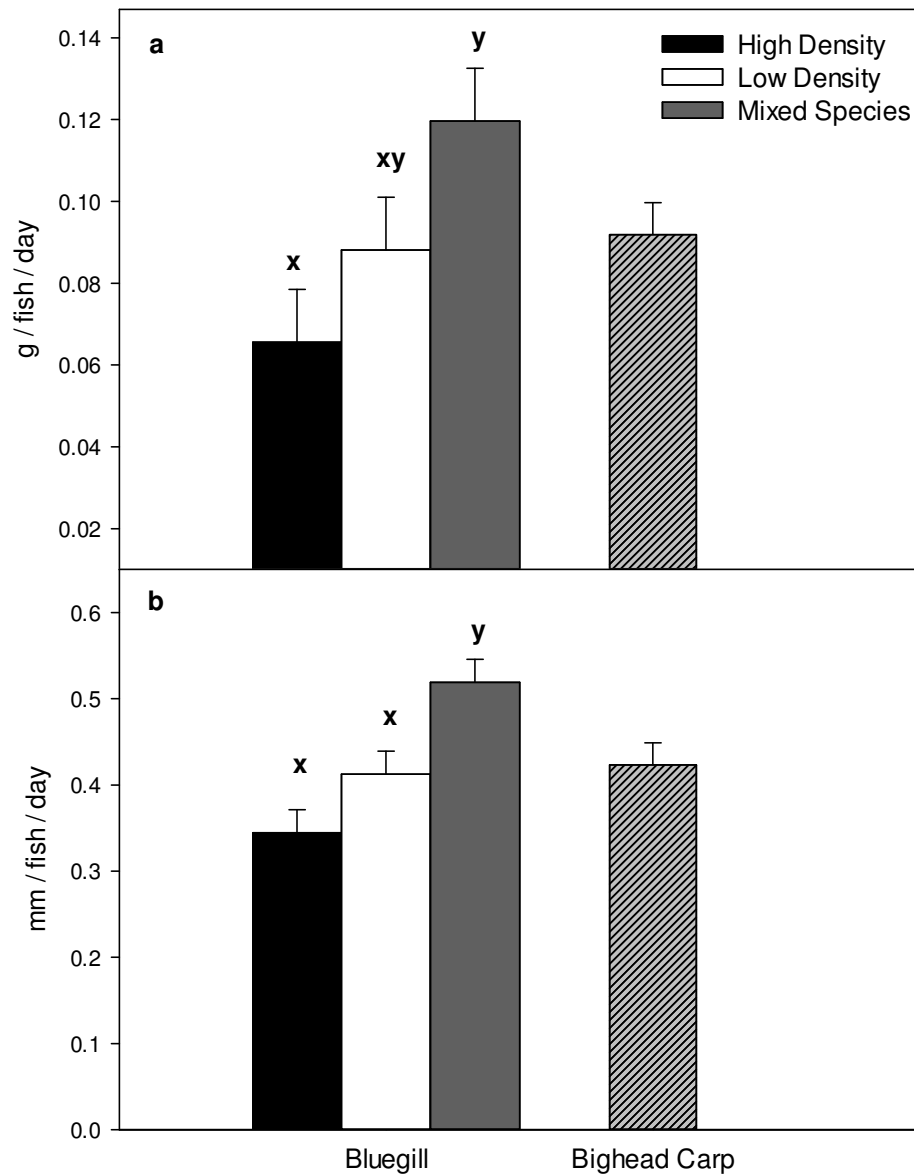


Figure 13. Mean change in biomass (a) and length (b) per fish per day by treatment in 0.04-hectare experimental ponds during an 80-day experiment testing for inter- and intra-specific competition of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). ‘High Density’ refers to treatments with 800 bluegill / pond. ‘Low Density’ refers to treatments with 400 bluegill / pond. ‘Mixed Species’ refers to treatments with 400 bluegill and 400 bighead carp / pond. Each treatment had three replicates. Different letters indicate significant differences between treatment combinations (CONTRAST statements, $P < 0.05$). Error bars represent ± 1 standard error about the mean.

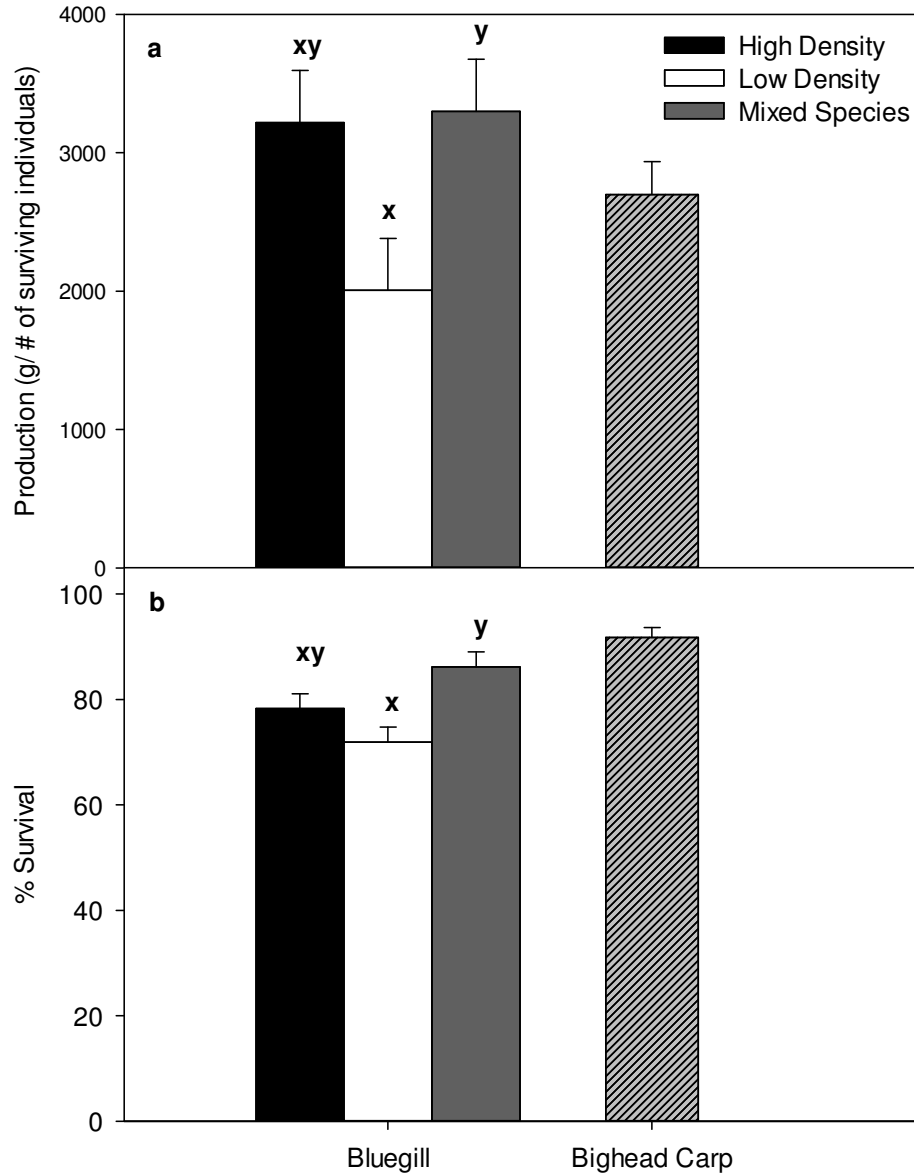


Figure 14. Production (a) and percent survival (b) of fishes by treatment in 0.04-hectare experimental ponds during an 80-day experiment testing for inter- and intra-specific competition of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). Production was calculated as grams·day⁻¹ multiplied by number of days the experiment ran multiplied by number of surviving individuals. ‘High Density’ refers to treatments with 800 bluegill / pond. ‘Low Density’ refers to treatments with 400 bluegill / pond. ‘Mixed Species’ refers to treatments with 400 bluegill and 400 bighead carp / pond. Each treatment had three replicates. Different letters indicate significant differences between treatment combinations (CONTRAST statements, P < 0.05). Error bars represent ± 1 standard error about the mean.

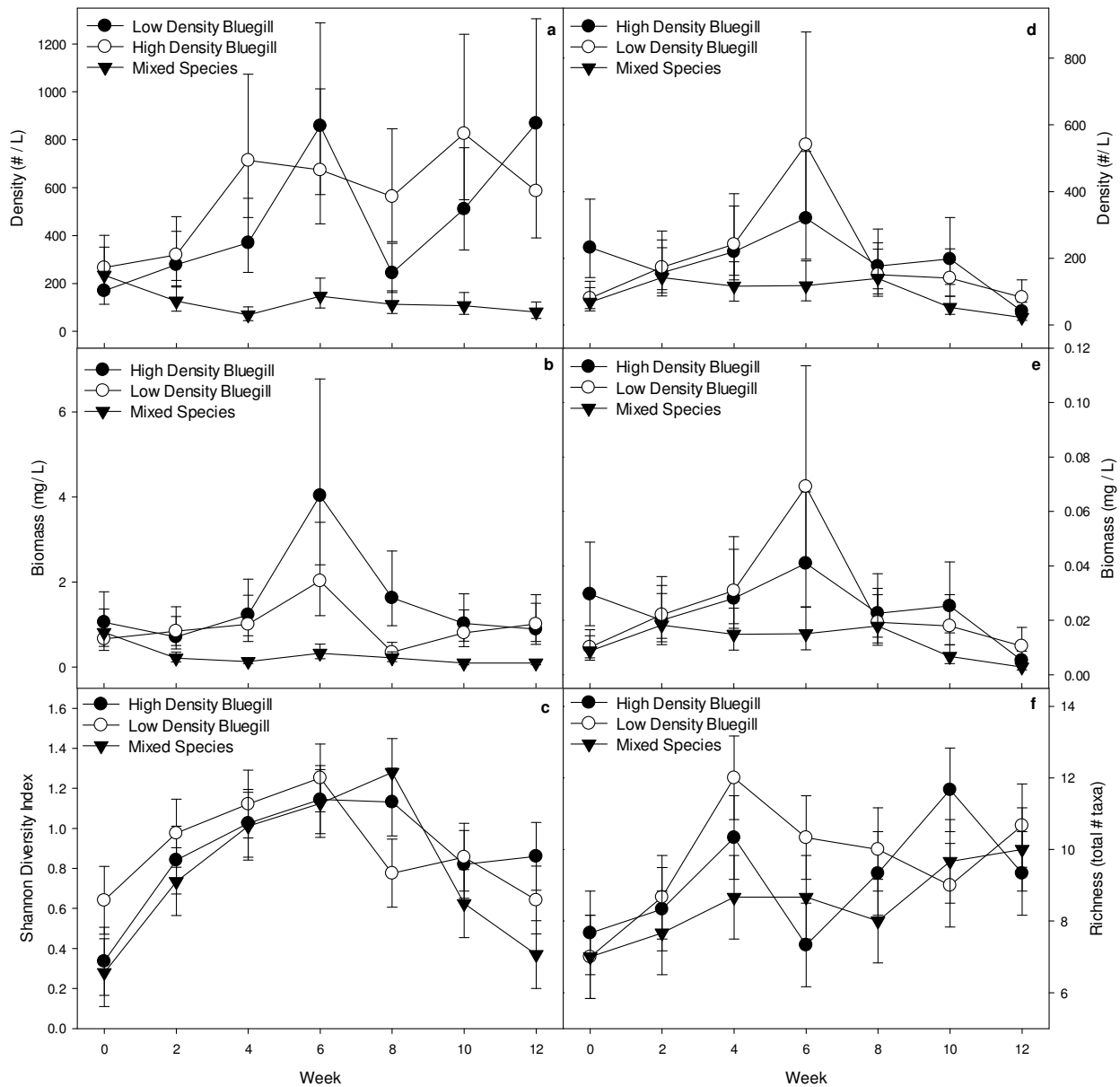


Figure 15. Mean density (a, d), biomass (b, e), Shannon diversity index (c), and richness (f) of zooplankton (left panels; a, b, c) and rotifers (right panels; d, e, f) by treatment in 0.04-hectare experimental ponds during an 80-day experiment testing for inter- and intra-specific competition of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). Density and biomass required a \log_e transformation to meet the assumptions of ANOVA. ‘High Density Bluegill’ refers to treatments with 800 bluegill / pond. ‘Low Density Bluegill’ refers to treatments with 400 bluegill / pond. ‘Mixed Species’ refers to treatments with 400 bluegill and 400 bighead carp / pond. Each treatment had three replicates. Error bars represent ± 1 standard error about the mean.

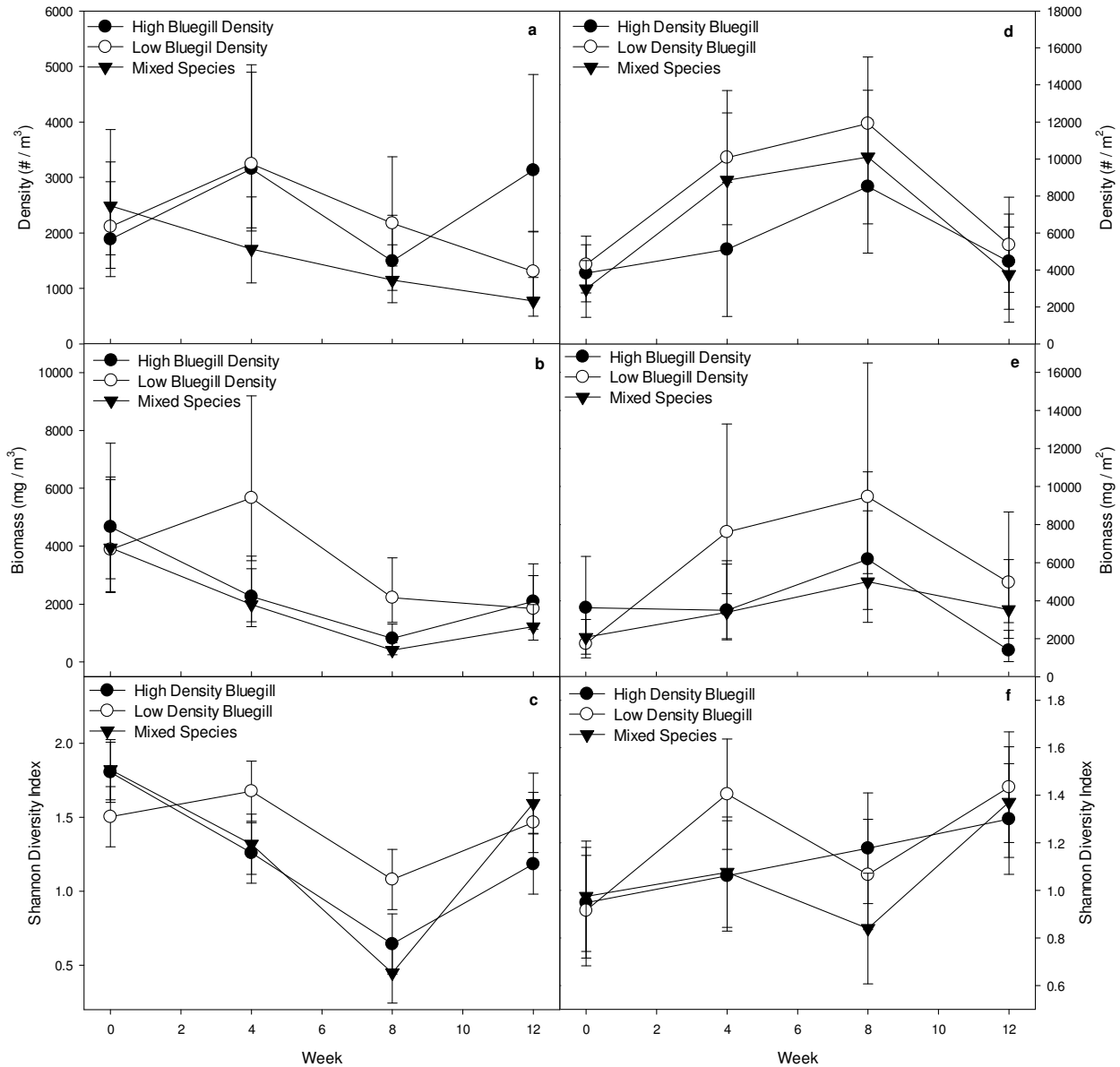


Figure 16. Mean density (a, d), biomass (b, e), and Shannon diversity index (c, f) of littoral (left panels; a, b, c) and benthic (right panels; d, e, f) macroinvertebrates by treatment in 0.04-hectare experimental ponds during an 80-day experiment testing for inter- and intra-specific competition of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). Littoral density (a), benthic density (d), and benthic biomass (e) required a \log_e transformation to meet the assumptions of ANOVA. ‘High Density Bluegill’ refers to treatments with 800 bluegill / pond. ‘Low Density Bluegill’ refers to treatments with 400 bluegill / pond. ‘Mixed Species’ refers to treatments with 400 bluegill and 400 bighead carp / pond. Each treatment had three replicates. Error bars represent ± 1 standard error about the mean.

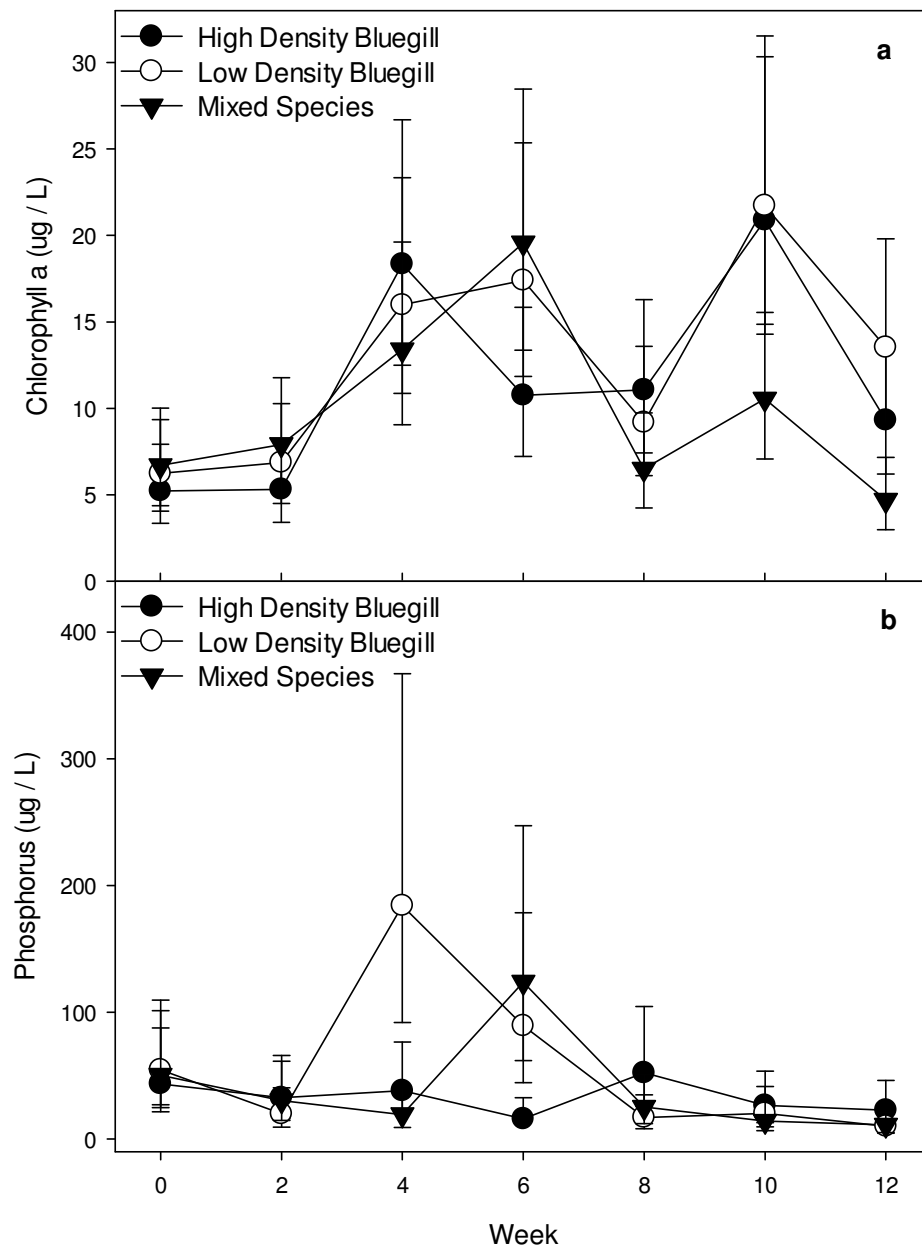


Figure 17. Mean chlorophyll *a* ($\mu\text{g}\cdot\text{L}^{-1}$; a) and mean total water column phosphorus ($\mu\text{g}\cdot\text{L}^{-1}$; b) by treatment in 0.04-hectare experimental ponds during an 80-day experiment testing for inter- and intra-specific competition of bluegill (*Lepomis macrochirus*) and bighead carp (*Hypophthalmichthys nobilis*). Means were obtained from LSMEANS following a \log_e transformation. ‘High Density Bluegill’ refers to treatments with 800 bluegill / pond. ‘Low Density Bluegill’ refers to treatments with 400 bluegill / pond. ‘Mixed Species’ refers to treatments with 400 bluegill and 400 bighead carp / pond. Error bars represent ± 1 standard error about the mean.

CHAPTER 5: GENERAL CONCLUSION

I tested for potential competitive interactions among native and invasive fishes at differing spatial scales to elucidate whether bighead carp may be influencing facultative planktivores. Competitive interactions between bighead carp and filter-feeding planktivores have been tested for in previous studies because bighead and silver carp have generated great concern that their plankton consumption may have detrimental effects on native fishes. Previous research has focused exclusively on filter-feeding planktivores, making my experiments the first to test for potential competitive interactions with facultative planktivores. My results suggested that facilitative and competitive influences can occur between native and invasive fishes, and these relationships can change at differing spatial scales. My studies highlight the complex relationships that can develop among species from ecosystem modifications resulting from invasive species introductions.

Previous studies investigating bighead carp and filter-feeding planktivores have found evidence of competition manifested in reduced body condition or planktonic dietary overlap. The results from my first two chapters demonstrated that intra-specific competition often had a stronger influence than inter-specific competition. Bluegill, a popular native sportfish, was negatively influenced by intra- and inter-specific competitive interactions; however, an interaction between fish densities resulted in the total competitive influence difficult to elucidate. Intra-specific competition played a greater role at low densities, but the effect was reduced at higher densities likely due to food limitation. Alternatively, common carp clearly experienced greater intra-specific competition. Bighead carp were facilitated by the presence of bluegill, but not by common carp, which may have been due to differences in nutrient cycling, the size of the fishes used, or dietary preferences. Evidence of benthic enrichment was observed when bighead

carp were paired with bluegill, a result that was also supported in the pond experiment. In both mesocosm experiments, bighead carp had a strong negative influence on macrozooplankton densities. My findings suggest that for some facultative planktivores, coexistence with bighead carp is likely; however, the presence of bighead carp may lead to resource partitioning as macrozooplankton become scarce. Additionally, the strong negative influence bighead carp have on macrozooplankton populations suggests that bighead carp are capable of negatively impacting fishes that are entirely reliant on macrozooplankton, such as obligate planktivores or larval fishes.

Increasing habitat and niche complexity provides an increasingly realistic platform to investigate competitive interactions. Increased complexity can modify species responses and highlight the importance of investigating interactions at different spatial scales. The pond experiment from my third chapter found that bluegill were facilitated by the presence of bighead carp. Several plausible mechanisms may explain the cause of the facilitation: 1) bighead carp may have shifted energetic pathways to the benthos, causing an increase in macroinvertebrate densities, biomass, or production; 2) bighead carp presence may have altered the macroinvertebrate community; and/or 3) bighead carp presence caused differences in bluegill foraging behavior in such a manner that they were benefited. Consistent with the previous chapters, bighead carp exerted a strong negative influence on macrozooplankton, providing evidence that this invasive species is capable of reducing plankton resources for native fishes and altering aquatic communities.

The establishment and spread of invasive bighead carp is suspected to have detrimental influences on native fishes. My research found that intra-specific competition played a stronger role than inter-specific competition, and at larger spatial scales, bighead carp facilitated bluegill.

The consistent suppression of macrozooplankton densities and the possibility of shifting nutrients to the benthos point to the ecosystem-wide modifications bighead carp may have on an invaded system. Collectively, my research provides insight into potential interactions between bighead carp and facultative planktivores. Future directions regarding bighead carp research may want to consider competitive interactions with larval fishes, nutrient cycling modifications, or influences on macroinvertebrate communities.