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BIGHEAD CARP EFFECTS ON THE GROWTH, ABUNDANCE, AND SURVIVAL OF
LARVAL BLUEGILL

BY

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THESIS

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ABSTRACT

Bighead Carp (*Hypophthalmichthys nobilis*) are an invasive planktivore, native to Asia, that have established successful populations in the Mississippi and Illinois River systems after their unintentional introduction in the 1980's. Their ability to efficiently consume zooplankton, has generated enormous concern for the native fishes in these ecosystems and those in connected water bodies yet to be invaded. Current research on their competitive interactions with native fishes, especially facultative planktivores, is not well documented and inconsistent. Furthermore, inquiries into their effect on the larval stages of native fishes have yet to be made.

The objective of my thesis was to test for competitive interactions between Bighead Carp and a facultative planktivore as they relate to larval growth, abundance, and survival. Moreover, I aimed to compare the competitive effects of Bighead Carp to those of a native planktivore. I conducted two experiments at different spatial scales involving Bighead Carp, Golden Shiners (*Notemigonus crysoleucas*), and larval Bluegill (*Lepomis macrochirus*). My first experiment involved investigating the growth of larval Bluegill at varying densities of either Bighead Carp or Golden Shiners in a controlled mesocosm setting. The results of this experiment inconsistently suggested that Bighead Carp reduce the growth of larval Bluegill to a greater extent than Golden Shiners. My second experiment was at a larger scale in 0.4 hectare ponds and aimed to examine the recruitment success of Bluegill when either Bighead Carp or Golden Shiners were present. This experiment consistently showed that Bighead Carp reduce the daily growth rate, and ultimately recruitment efficiency, of larval Bluegill to a greater extent than Golden Shiners. Effects observed in both studies correlated with greater decreases in zooplankton by Bighead Carp compared to Golden Shiners. These results begin to indicate that an invasive planktivore may negatively affect the growth of larval Bluegill, and other native

fishes with similar life-histories, to a greater extent than a native planktivore. My results help to further understand the effects Asian Carp are having on the Illinois and Mississippi River systems and provide insight into their potential impacts on aquatic systems yet to be invaded.

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In loving memory of George D. Fletcher

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CHAPTER 1: GENERAL INTRODUCTION

Through dramatic increases in migration and commerce, there exist only a few places on earth untouched by the effects of non-indigenous species (Mack et al. 2000). Unfortunately, a large proportion of vertebrate invasions, especially aquatic, are facilitated through deliberate introductions of organisms for human benefit (Moyle 1986; Mack et al. 2000). Invasive species, whether anthropogenically introduced or not, have been increasingly blamed for native population loss and extinction (Paolucci et al. 2013). Through habitat alterations, changes in water quality, the introduction of new parasites and diseases, hybridization, and by changing spatial and trophic interactions, invasive fish introductions can have a large effect on native aquatic communities (Burr et al. 1996). Carps, members of the largest fish family (*Cyprinidae*), have been transported for human use dating back to the Roman Empire (Moyle 1986, Kolar et al. 2005). More recently, the introduction of Bigheaded Carps (genus *Hypophthalmichthys*) into North American waters has become an increasingly important topic of invasion ecology research.

First introduced into the United States from Taiwan in 1971, for the use of biofiltration of sewage lagoons, Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*) commonly referred to as Asian Carp, are among the most ecologically relevant aquatic invaders to take hold in the last quarter-century (Cremer & Smitherman 1980). In the 1980's both species escaped their aquaculture holdings, initiating their invasion into the Mississippi River and its major tributaries (Freeze & Henderson 1982). The ecological repercussions of this invasion are widely studied today as Asian Carp continue to increase in abundance and reproductive range (Sass et al. 2010; Collins et al. 2015).

Current research on both of these Carp species centers around preventing their expansion to other important aquatic systems, and understanding the current ecological effects they have on successfully invaded ecosystems (Kolar et al. 2005, Irons et al. 2007, Baerwaldt et al. 2013). Furthermore, speculation into their potential success in ecosystems yet to be invaded is becoming more widespread (Kolar et al. 2005, Cooke et al. 2009, Cooke & Hill 2010). Specifically, the Great Lakes are of the utmost concern as they host vital fishing, boating, and tourism industries that contribute upwards of 17 billion dollars to local economies (Patel et al. 2010). The combination of exponential growth of Asian Carp populations within the Mississippi River Basin with the presence of reproductive populations occurring just 50 miles south of Lake Michigan, (Butler et al. 2016) have generated great concern for these industries (Chick & Pegg 2001, Mandrak & Cudmore 2010, Patel et al. 2010, Sass et al 2010, Rasmussen et al. 2011, Sass et al 2014). Already, plagued by an increase of introductions following the opening of the St Lawrence Seaway system, the Great Lakes could face even greater ecological consequences if Asian Carp were allowed to establish (Cudmore et al. 2012, Cuddington et al. 2013).

To mitigate the ramifications of a potential invasion of Asian Carp into the Great Lakes or other aquatic systems, it is first important to fully understand their ecology and ecological impacts in currently invaded systems. Evidence suggests that Asian Carp are extremely efficient at reducing zooplankton populations within an aquatic ecosystem (Cremer & Smitherman 1979; Dong & Li 1994; Chick & Pegg 2001; Xie and Chen 2001; Radke & Kahl 2002; Cooke et al. 2009). Furthermore, zooplankton are a critical prey item for many fishes, especially at early life stages (Lemly and Dimmick 1982; Welker et al. 1994; Mayer & Wahl 1997; Claramunt & Wahl 2000). By reducing prey availability, Asian Carp have the potential to out compete native fishes,

reducing larval growth and ultimately recruitment success (Xie & Chen 2001; Schrank et al. 2003).

The factors that influence recruitment variability are extremely important for understanding a fish's population dynamics, as the slightest change in growth or early life stage duration can have noticeable effects on larval fish recruitment (Hjort 1914, Houde 1987). The early survival of many species is largely determined by growth made during the first few weeks after hatching (Keast & Eadie 1984, Mills & Mann 1985, Nunn et al. 2002). Moreover, short-term, early stage growth is critically dependent on food availability (Wieser et al. 1988a, Wieser et al. 1988b), and it is widely accepted that larval growth and survival is better when prey levels are high (Rilling & Houde 1999; Zenitani et al. 2007; Houde 2009). The availability of zooplankton prey is especially important for visual particulate feeders who are limited by their gape (Bremigan & Stein 1993). Given the linkages between prey availability, larval growth and survival, and recruitment success, in conjunction with the ability of Asian Carp to suppress zooplankton populations, the potential for negative interactions between these invasive planktivores and native larval fishes is clear.

We must consider how the newly established presence of Asian Carp could alter the larval stages of native fishes. Recent studies have revealed Asian Carp's negative effects on native planktivores (Chick & Pegg 2001, Schrank et al. 2003); yet little is known about their effect on economically important, sportfish, especially at the highly vulnerable larval stage. Through exploitative competition for prey resources, sportfish with larval stages relying on zooplankton could experience decreased growth when in the presence of Asian Carp (Xie & Chen 2001). Because larval growth is crucial for successful fish recruitment, these are important interactions to consider. My thesis will address the complex interfaces between Asian Carp, a

larval sportfish, and their shared zooplankton prey resource, to untangle these trophic interactions and to further understand the effect of this ecologically important invader.

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CHAPTER 2: BIGHEAD CARP EFFECTS ON THE GROWTH, ABUNDANCE, AND SURVIVAL OF LARVAL BLUEGILL

ABSTRACT

Evidence suggests that Asian Carp can reduce the abundance of zooplankton within the Mississippi and Illinois River systems. Recent studies indicate that exploitative competition between Asian Carp and native planktivores is inconsistent at the adult and juvenile stages; however, little is known about their effects on the early life stages of fishes, especially those with larval stages relying on zooplankton. A series of experiments in mesocosms and ponds were used to test the effect of Bighead Carp (*Hypophthalmichthys nobilis*) on the growth and abundance of larval Bluegill (*Lepomis macrochirus*). The effect of Golden Shiners (*Notemigonus crysoleucas*) on larval Bluegill was also assessed to differentiate the effects of a native compared to an invasive planktivore. We hypothesized that Bighead Carp would have a greater negative effect on larval Bluegill growth, abundance, and survival than Golden Shiners. In both mesocosms and ponds, larval Bluegill grew 65-86% less when in the presence of Bighead Carp. In contrast, larval Bluegill exhibited similar growth both when in the presence of Golden Shiners and when alone. Additionally, survival of larval Bluegill in mesocosms was 30% lower when low densities of Bighead Carp were present. In ponds, there was no effect of either Bighead Carp or Golden Shiner on the abundance of larval Bluegill. Differences in responses among species were correlated with differences in zooplankton abundance between treatments over time. These results demonstrate that Asian Carp, in comparison to a native planktivore, can have greater negative effects on the larval stage of native fishes within the Mississippi and Illinois River systems, with implications for potential range expansions into the Great Lakes.

INTRODUCTION

North America has been subjected to many invasive aquatic organisms, experiencing detrimental ecological effects from over 180 introduced species (Holeck et al. 2004; Cooke & Hill 2010). Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*H. molitrix*), hereafter referred to as Asian carp, are two of the most recent ecologically relevant aquatic invaders to the Upper Mississippi and Illinois River systems. Abundance of Asian carp in the Illinois River has increased exponentially (Sass et al. 2010; Collins et al. 2015) with current populations reaching levels of up to 1.6 bigheaded carp/1000m³ (MacNamara et al. 2016). It is likely that Asian carp will continue to numerically dominate the Upper Mississippi and Illinois Rivers (Sass et al. 2010), bringing into question their effect on native ecosystems.

Asian Carp are voracious planktivorous feeders who can filter out large quantities and reduce the abundance of phytoplankton and zooplankton (Cremer & Smitherman 1979; Dong & Li 1994; Chick & Pegg 2001; Xie and Chen 2001; Radke & Kahl 2002; Cooke et al. 2009). Additionally, this ability has been associated with increased rotifer abundances through a release from predation (Xie & Yang 2000; Sass et al. 2014). Alterations to plankton communities foster multifaceted interactions between Asian Carp and native adult planktivores through overlaps in diet composition (Sampson et al. 2009). Previous studies have shown reduced growth and condition of native species such as Paddlefish (*Polyodon spathula*), Gizzard Shad (*Dorosoma cepedianum*) and Bigmouth Buffalo (*Ictiobus cyprinellus*) (Kajak 1977; Opuszynski 1981; Chick & Pegg 2001; Schrank et al. 2003 Irons et al. 2007). Furthermore, Gizzard Shad and Bigmouth Buffalo body condition has significantly declined following the introduction of Asian Carp, which is likely driven by a decrease in zooplankton available to native planktivores (Irons et al. 2007). If native adult planktivores are being outcompeted for zooplankton, prey resources could

be limited for larval fishes of other non-planktivorous native species as well (Xie & Chen 2001). Previous studies focus primarily on the effects of Asian Carp on the adult and juvenile stages of native fishes; however, Asian Carp may impact fishes with early life stages reliant on zooplankton and incapable of switching to alternate prey resources due to gape limitations.

The potential threat that Asian Carp pose to facultative planktivores in the Illinois Mississippi ecosystems are unclear. Interactions between Bighead Carp and juvenile Bluegill (*Lepomis macrochirus*) in mesocosms found that, interspecific competition was asymmetrical in that Bluegill were negatively affected whereas Bighead Carp were not (Nelson 2014). In ponds, with increasing density of Bighead carp, Bluegill shifted their diets from predominantly zooplankton to predominantly benthic macroinvertebrates reducing interspecific competition for prey. (Collins et al. in review). Due to the large size of Bluegill in these studies (50-100 mm), they could forage on both zooplankton and benthic macro-invertebrates, thus lessening the impacts of Bighead Carp, and in some cases promoting growth of Bluegill. However, larval Bluegill (< 20 mm) lack such diet flexibility, limiting prey items to micro- and macrozooplankton, such that competitive interactions may be stronger at these sizes (Taylor 1977; Mallin et al. 1985).

Prey availability during the larval stage of development is a critical determinant of recruitment variability and early stage growth (Wieser et al. 1988a; Wieser et al. 1988b; Houde 2009). Slight changes in growth can prolong the duration these fishes are susceptible to predation, ultimately effecting fish recruitment (Hjort 1914, Houde 1987). In addition, factors crucial to larval development and survival, such as prey flexibility and predator avoidance, are often dependent on body size and gape limitations (Miller et al. 1988). Larger, faster growing larvae have a survival advantage, as they can avoid size-dependent mortality caused by predation

and starvation (Post & Prankevicus 1987; Miller et al 1988; Luecke et al. 1990; Partridge & DeVries 1999). Because larval growth and survival of many fish species is heavily reliant on zooplankton (Lemly and Dimmick 1982), and Asian Carp readily suppress zooplankton populations, they have the potential to negatively impact the recruitment success of native fishes (Xie & Chen 2001; Schrank et al. 2003).

Bluegill are a facultative planktivore native to the Illinois region, a popular sportfish throughout the Midwestern United States, and have a larval stage relying on zooplankton. This reliance increases the potential for direct and indirect, multi-trophic level interactions during their early life history (Taylor 1977; Becker 1983; Mallin et al. 1989; Harvey 1991). The growth of larval Bluegill is affected by the availability of zooplankton prey (Welker et al. 1994) as starvation decreases swimming ability (Toetz 1966), leading to reduced predator avoidance and ultimately greater larval mortality. Native planktivorous fish such as Gizzard Shad and Golden Shiners (*Notemigonus crysoleucas*) can also have negative effects on Bluegill and other facultative planktivores by reducing the abundance of zooplankton in the system, thus increasing competition for resources during a crucial time of development (Paszkowski 1986; Guest et al. 1990; Browman & O'brien 1992; Dettmers & Stein 1992; DeVries & Stein 1992; Welker et al. 1994; Stein et al. 1995; Aday et al. 2003; Carey & Wahl 2010). Additionally, like Asian Carp, Golden Shiners are highly abundant species (Hall & Ehlinger 1989), and have filtering capabilities and inter-gill raker spaces of a similar size (~ 0.1- 0.05 mm) (Ehlinger 1989; Opuszynski & Shireman 1993). Due to similarities in characteristics and zooplankton exploitation, we might expect invasive Bighead Carp to show comparable, if not more extreme effects on the growth, abundance, and survival of larval Bluegill as native Golden Shiners.

We hypothesized that through exploitative competition, Asian Carp would limit the prey available to larval fishes, ultimately decreasing their growth and survival. Our primary objective was to determine if Bighead Carp affect the growth, survival, and/or abundance of larval Bluegill through greater consumption of zooplankton resources in comparison to a native planktivore. We predicted that with increasing density of Bighead Carp we would observe greater declines in zooplankton prey and shifts in zooplankton community to smaller sized taxa, leading to decreased growth, survival, and abundance of larval Bluegill. By examining the larval stage, we were able to experimentally evaluate the interactions between invasive Asian Carp and other native fishes at a life stage that is important to the strength and success of future recruitment.

METHODS

In order to address our hypothesis, we conducted two experiments examining the interactions between larval Bluegill, an invasive planktivore (*Hypophthalmichthys nobilis*), a native planktivore (*Notemigonus crysoleucas*), and their zooplankton prey. First, manipulative mesocosm experiments were conducted using larval Bluegill and varying densities of either Bighead Carp or Golden Shiners. These controlled, small scale, experiments allowed for the direct observation of larval Bluegill growth and survival in the presence of both invasive and native planktivores. Second, a larger scale pond experiment was conducted to further observe these competitive interactions by measuring larval growth and abundance of Bluegill when allowed to spawn in the presence of each planktivore species. This field experiment not only provided further insight into the effect of each planktivore on the growth of larval Bluegill, but ultimately allowed us to observe effects on recruitment success in a more natural setting.

Mesocosm Experimental Design – Two trials of a mesocosm experiment using 1325-L polyurethane tanks were conducted over two 4-week time periods from late June 2015 to early September 2015 at the Sam Parr Biological Station in Kinmundy, IL (Trial 1: July 2-23, Trial 2: August 19 - September 11). The first trial consisted of 40 mesocosms and the second trial consisted of 35 mesocosms. The experimental design had five treatments (8 replications per treatment in trial 1, 7 replications per treatment in trial 2), each containing 20 larval Bluegill. One treatment contained only Bluegill, whereas the remaining treatments consisted of either high (6 individuals per mesocosm) or low (3 individuals per mesocosm) densities of either juvenile Bighead Carp or juvenile Golden Shiners. Additive experiments such as these are useful for addressing the effects of non-native species, yet also confound effects of competition with those of increased density (Faush 1998). By controlling for the density of Golden Shiners and Bighead Carp, we were able to differentiate the effects of native and invasive planktivores. Densities of all fish were within the natural ranges observed in lakes and rivers in this region (Carey & Wahl 2010; Butler et al. 2016; Collins et al. 2017).

Treatments were randomly assigned to each mesocosm, which were placed under a permanent overhead structure in order to reduce direct sunlight. Mesocosms were then filled with water from Forbes Lake, which was filtered through a 300 μm mesh to prevent the introduction of larval fish, yet allow for the establishment of a plankton community. In trial 1, plankton communities were given four weeks to establish prior to the introduction of fish. Due to time constraints, trial 2 had only a 2-week time frame for zooplankton establishment. In both trials, during this time, water was randomly interchanged to increase homogeneity between mesocosms.

Larval Bluegill were obtained from a rearing pond at the Sam Parr Biological Station. A subsample (N=50) of larval Bluegill were measured and weighed to obtain the mean length and weight of the population before adding them to each mesocosm (Trial 1: mean length = 18.6 mm, mean weight = 0.067 g; Trial 2: mean length = 19.8 mm, mean weight = 0.139 g). Bighead Carp and Golden Shiners were obtained from hatchery settings to avoid comparing wild-raised and hatchery-raised fish. A subsample (N=50) of each Bighead Carp and Golden Shiner were measured and weighed (Trial 1: BHC mean length = 85.6 mm, BHC mean weight = 5.22 g, GOS mean length = 85.14 mm, GOS mean weight = 5.82; Trial 2: BHC mean length = 65.96 mm, BHC mean weight = 2.54 g, GOS mean length = 65.74 mm, GOS mean weight = 2.36 g) to ensure each population was of statistically similar lengths and weights (t-test Trial 1: Length $t = 0.27$, $df = 98$, $P = 0.78$; Weight $t = -1.7$, $df = 98$, $P = 0.09$; t-test Trial 2: Length $t = 0.33$, $df = 98$, $P = 0.74$; Weight $t = 1.82$, $df = 98$, $P = 0.07$). Before being added to their respective mesocosms, each individual Bighead Carp and Golden Shiner was measured and weighed for growth analysis.

Throughout the duration of the experiment, larval Bluegill mortalities were removed and measured. If mortalities of Bighead Carp or Golden Shiners occurred within the first week of the experiment, an individual of the same size was used as a replacement. Mortalities of Bighead Carp and Golden Shiners in the following weeks were removed and replaced with a fin-clipped individual of the same size to maintain consistent biomass of fish throughout the experiment, yet to avoid using that replacement fish in the growth estimates. At the conclusion of the mesocosm experiments, all fish were removed for growth analysis and to determine survival.

Pond Experimental Design – A larger scale study using ten 0.04 ha experimental ponds was conducted over a 4-week time period in July 2015 at the Sam Parr Biological Station. The experiment consisted of three treatments, each containing male/female pairs of adult Bluegill (N=10 pairs) allowing for spawning to occur during the experiment. One treatment was left with just Bluegill, whereas the remaining treatments had either additional Bighead Carp (N=100) or additional Golden Shiners (N=100). Densities of juvenile Bighead Carp were within the range of those captured in the field (Butler et al. 2016; Collins et al. 2017), to which Golden Shiner densities were then matched. Each treatment had three replications with the Golden Shiner treatment having a fourth in order to utilize all 10 ponds.

Each pond was filled with water from Forbes Lake, which was filtered through a 300 μ m mesh to prevent the introduction of larval fish, yet allow for the establishment of a plankton community. Plankton communities were given four weeks to establish prior to the introduction of fish, after which adult Bluegill were added and given two weeks to acclimate before the addition of each treatment species. Bluegill were obtained from Forbes Lake via electroshocking and were only used if of reproductive maturity, and easily distinguishable as male or female. Bighead Carp and Golden Shiners were obtained from the same hatchery population as those used in the mesocosm experiment. At the conclusion of the pond experiment, two larval seines (5 m long, 1 m wide, 0.4mm mesh size) were conducted in each pond to assess abundance of larval Bluegill, and 30 larval Bluegill per pond were used for growth analysis.

Zooplankton Sampling – To observe changes in overall abundance of zooplankton as well as shifts in size-structure, one week prior to the addition of fish, and each week thereafter, zooplankton was sampled using a zooplankton tube sampler (1.5 L) at 3 different locations

within each mesocosm and pond. In trial 1 of the mesocosm experiment and in the pond experiment, each sample was filtered through a 55 μm mesh and preserved with Lugol's Iodine for each week prior to the final sampling event. In the final week, zooplankton samples were filtered through a 20 μm mesh and preserved in a 10% buffered formalin and rose Bengal solution with baking soda to observe rotifer abundances and community composition (Chick et al. 2010). In trial 2 of the mesocosm experiment, all zooplankton samples were filtered using the 20 μm mesh method to observe rotifer abundance shifts over time. In the laboratory, zooplankton samples preserved in Lugol's iodine were filtered through a 55 μm mesh and enumerated under a dissecting scope to the family level. The samples preserved in 10% buffered formalin, were first filtered through a 55 μm mesh and processed as above. The remaining solution was re-filtered through a 20 μm mesh and rotifers were enumerated using a Sedgewick-Rafter cell under a compound microscope (Olympus BH) to the genus level. When possible, the entirety of the sample was enumerated; otherwise subsamples were taken until at least 400 individuals were counted. Rotifer abundances from both the 55 and 20 micron sub-samples were combined to obtain the total rotifer abundance in each sample.

Limnological Sampling – Similarly, limnological parameters were measured one week prior to the addition of fish and each week thereafter for all experiments (Mesocosm: temperature, dissolved oxygen, chlorophyll-*a*, and light intensity; Pond: temperature, dissolved oxygen, chlorophyll-*a*, benthic macroinvertebrates, and percent vegetation cover). Total phosphorus concentrations were measured at the beginning and end of each experiment to reduce sample processing time. Temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/L) were measured in the center of each mesocosm and pond using a model 55 YSI meter. Total phosphorus was obtained through

water column samples (2 x 45 mL samples) 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 ($\mu\text{g} / \text{L}$; Murphy & Riley 1986). Chlorophyll-*a* was quantified 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 absorbance in a spectrophotometer ($\mu\text{g} / \text{L}$; Arar 1997). Light intensity (lx) was measured at the center of each mesocosm using an underwater photometer (Protomatic, Dexter, Michigan, USA). Benthic macroinvertebrates were sampled in the ponds (5 samples/pond) using a Hess sampler and preserved in an Ethanol and rose Bengal solution. Percent vegetation cover was sampled (5 samples/pond) using a randomly placed vegetation ring.

Larval Bluegill Analysis - Larval fish from all experiments were measured to the nearest 0.001 mm using a digitizing pad and Image J software. In addition, each fish was weighed to the nearest 0.0001 g using a micro-balance (Mettler Toledo XS205). For the mesocosm experiments growth of larval Bluegill was determined using the lengths and weights measured prior to and following the experiment. For the pond experiment, larval Bluegill length, total biomass, condition ($100000 \cdot (W/L^3)$), and abundance were simply compared between treatments. Due to the design of our pond experiment growth differences may have been a product of either treatment differences or differences in hatch date. To address these different causes, otoliths were extracted from a subsample of larval Bluegill (N=10/pond) and aged under a compound microscope (Olympus BH) at 400x magnification. Two readers independently aged each otolith and if they were within 10% of each other, the age was averaged. If counts were not within 10% of each other, readers tried to come to a consensus using a compound scope mounted camera

(OptixCam Summit K2) to display and read each otolith on a monitor. If a consensus could not be met, the otolith was removed and replaced with another.

Statistical Analysis - The initial level of each response variable was tested for differences using a one-way analysis of variance (ANOVA), and was concluded to be similar among all treatments for each experiment. At the conclusion of each mesocosm experiment, larval Bluegill growth was tested for treatment effects using a one-way ANOVA, blocked by trial. Change in length was log transformed and survival was squared in order to meet the assumptions of the test. If significant effects were found, contrast statements were written to compare Asian Carp and Golden Shiner treatments of the same density. Additionally, species level contrast statements were also written to compare the lumped response of both density treatments between species. At the conclusion of the pond experiment, larval Bluegill length, total biomass, condition, and abundance, along with rotifer abundance, were tested for treatment effects using a one-way ANOVA. Total biomass was log transformed to fit the assumptions of the test. Otolith ages were used to calculate average daily growth rates (g/day) of larval Bluegill in each pond, which were also analyzed for treatment effects using a one-way ANOVA. If significant results were found, post hoc student-t tests were conducted to discern which treatments were different from each other. For all experiments, because we expected zooplankton abundance, rotifer abundance, and environmental variables to change over the course of the experiment, those parameters were analyzed using a repeated measures analysis of variance over time to discern treatment effects, time effects, and their interaction. An indicator variable was used in the mesocosm analysis to identify trial as a source of variability. Chlorophyll-*a* concentration required a square root transformation and a Huynh-Feldt correction was used for any variable

when sphericity assumptions were not met (Mauchly 1940). Due to only having phosphorus measurements at the beginning and end of each experiment an ANOVA was used to analyze total end phosphorus concentrations as well as the difference accrued over time. For the mesocosm experiment, differences in phosphorus concentrations were made positive through the addition of a constant and then squared to meet the normality and homogeneity of variance assumptions of an ANOVA. To analyze the effect of additive planktivores on the rotifer community composition at the end of each experiment, a permutational multivariate analysis of variance (PERMANOVA) was used. This multivariate approach allowed us to avoid parametric assumptions that often are not met with species count data (Anderson & Walsh 2013).

RESULTS

Mesocosm experiments

Effects on Bluegill, Bighead Carp, and Golden Shiners

The majority of our growth parameters indicated that Bighead Carp had a greater impact on Bluegill than Golden shiners. Net weight gain of larval Bluegill was different among treatments ($F = 2.74$, $df = 4$, $P = 0.03$) and between trials ($F = 21.29$, $df = 1$, $P < 0.01$). As expected, the Larval Bluegill only treatment showed the greatest weight gain ($\mu = 67.95\%$, 0.05 g) over the course of the experiments. Bluegill in the low density Bighead Carp treatment showed the lowest weight gain ($\mu = 20.49\%$, 0.01 g); however, contrasts between treatments of similar densities showed no difference between Golden Shiners and Bighead Carp (Fig. 1A). Change in length was also different among treatments ($F = 4.45$, $df = 4$, $P < 0.01$) with larval Bluegill in both Bighead Carp treatments showing up to 65% lower growth than Bluegill with Golden Shiners or when alone (Fig. 1B). Additionally, contrast statements concluded that there

was a difference between the low density Bighead Carp and Golden Shiner treatments ($F(1,62) = 4.84, p = 0.03$) and between the Bighead Carp and Golden Shiner treatments as a whole ($F(1,62) = 5.55, p = 0.02$) (Table 1). There was no difference between the high density treatments ($F(1,62) = 1.33, p = 0.25$) nor was there a trial difference for change in length ($P > 0.05$). There was a treatment ($F = 4.17, df = 4, P < 0.01$) and trial effect ($F = 48.91, df = 1, P < 0.01$) on the survival of larval Bluegill. Bluegill alone had the highest survival ($\mu = 76\%$), with lowest survival occurring in the low density carp treatment ($\mu = 54\%$) (Fig. 1C). Contrast statements revealed a strong effect of planktivore species at low densities ($F(1,64) = 6.3, p = 0.01$) and a weak effect of planktivore species at high densities ($F(1,64) = 2.93, p = 0.09$).

Additionally, there were differences in the change in length ($F = 3.23, df = 3, P = 0.04$) and net weight gained ($F = 3.41, df = 3, P = 0.03$) of both Bighead Carp and Golden Shiners between treatments. Golden Shiners in the low density treatment showed the greatest change in length ($\mu = 6.3$ mm), whereas Golden Shiners in the high density treatment showed the smallest change in length ($\mu = 2.3$ mm). Bighead Carp in both high and low density treatments had intermediate changes in length (Fig. 2A). Similarly, the Golden Shiners in the high density treatment displayed the lowest net weight gain ($\mu = 1.5$ g); however, the Bighead Carp in the high density treatment showed the greatest ($\mu = 2.6$ g), with both other treatments being intermediate (Fig. 2B).

Limnological Sampling

Limnological parameters remained similar between treatments over the course of the experiments, with slight variation between trials (Table 2). There were no treatment differences in dissolved oxygen ($F = 1.16, df = 4, P = 0.34$), temperature ($F = 1.09, df = 4, P = 0.37$), and light intensity ($F = 0.82, df = 4, P = 0.52$) between treatments; however, temperature ($F = 28.14,$

df = 1, $P < 0.01$) and light intensity ($F = 7.73$, df = 1, $P < 0.01$) were lower in the second trial. All three parameters showed differences over time ($P < 0.01$) with dissolved oxygen consistently increasing and temperature and light intensity following similar variable patterns. Phosphorus concentrations dropped consistently between treatments ($F = 1.02$, df = 4, $P = 0.41$) over the course of the experiments, and did not differ between treatments at the end ($F = 0.98$, df = 4, $P = 0.43$). Chlorophyll-*a* concentrations remained stable between treatments ($F = 0.20$, df = 4, $P = 0.32$) and trials ($F = 3.88$, df = 1, $P = 0.05$).

Zooplankton

Zooplankton population trends over the course of both trials were as expected, but high variability prevented us from consistently distinguishing between Bighead Carp and Golden Shiner effects. There was a treatment ($F = 4.84$, df = 4, $P < 0.01$), trial ($F = 10.18$, df = 1, $P < 0.01$), time ($F = 161.83$, df = 4, $P < 0.01$), and time*trial interaction ($F = 20.27$, df = 4, $P < 0.01$) effect on total zooplankton abundance. All treatments decreased over time, with Bighead Carp treatments exhibiting the most dramatic declines; however, because of variability between replicates there was no treatment*time interaction (Fig. 3A and C). Similarly, macrozooplankton abundances exhibited effect differences for treatment ($F = 3.74$, df = 4, $P = 0.01$), trial ($F = 4.80$, df = 1, $P < 0.01$), and time ($F = 151.80$, df = 4, $P < 0.01$). Furthermore, there was a weak treatment*time interaction effect ($F = 1.53$, df = 4, $P = 0.09$) most evident at week 1, where both Bighead Carp treatments and the high density Golden Shiner treatments declined at a faster rate than the low density Golden Shiner treatment and the just Bluegill treatment (Fig. 3B and D). In trial two, rotifers showed an increasing trend over time ($F = 10.41$, df = 4, $P < 0.01$) in all treatments, but there was no treatment effect ($F = 0.02$, df = 4, $P = 0.95$) or treatment by time interaction ($F = 0.65$, df = 16, $P < 0.01$) (Fig. 4).

Pond Experiment

Effects on Bluegill

The results of the pond experiment were more consistent, and provide greater evidence that Bighead Carp and Golden Shiners differ in their effects on larval Bluegill. There was no treatment effect on the abundance of larval bluegill ($F = 1.49$, $df = 2$, $P = 0.29$) (Fig. 5E); however, total biomass of larval bluegill was different among treatments ($F = 5.37$, $df = 2$, $P = 0.04$) and 54% lower in the treatment containing Bighead Carp compared to Bluegill alone (Fig. 5B). There was a weak effect of treatment on the length of larval bluegill ($F = 3.99$, $df = 2$, $P = 0.06$) (Fig. 5C) and condition of larval Bluegill ($F = 4.61$, $df = 2$, $P = 0.05$) was lower in the treatment containing Bighead Carp (Fig. 5D). The mean age of larval Bluegill was not different between treatments ($F = 1.43$, $df = 2$, $P = 0.30$); however, the daily growth rate was different between treatments ($F = 6.02$, $df = 2$, $P = 0.03$) and 86% lower in the treatments containing Bighead Carp compared to Bluegill alone (Fig. 5A). A post-hoc student's t-test revealed that larval Bluegill in the treatments containing Golden Shiners did not differ from the Bluegill only treatment in mean daily growth rate, mean total biomass, nor mean condition, but exhibited a 13% lower change in length.

Limnological Sampling

As seen in the mesocosm experiments, limnological parameters remained similar between treatments over the course of the pond experiment (Table 1). There were no treatment differences in temperature ($F = 0.73$, $df = 2$, $P = 0.50$) or dissolved oxygen ($F = 0.57$, $df = 2$, $P = 0.54$), both of which showed consistent temporal variation. Similarly, percent vegetation cover ($F = 0.6$, $df = 2$, $P = 0.58$), secchi depth ($F = 1.49$, $df = 2$, $P = 0.25$), and benthic macro-invertebrate abundance ($F = 2.14$, $df = 2$, $P = 0.15$) were similar between treatments. Phosphorus

concentrations at the end of the experiment were statistically similar between treatments ($F = 3.87$, $df = 2$, $P = 0.08$), but Bluegill alone did show lower concentrations than the other treatments. Additionally, phosphorus concentrations in the just Bluegill treatment declined over the course of the experiment; whereas the other treatments increased; however, due to variation, and low sample size, no treatment effect in the difference of phosphorus was detected ($F = 2.61$, $df = 2$, $P = 0.15$). Chlorophyll-*a* concentrations stayed consistent throughout the course of the experiment ($P = 0.41$) and did not differ between treatments ($F = 0.05$, $df = 2$, $P = 0.17$).

Zooplankton

Zooplankton population declines exhibited high variability as in the mesocosm experiments, yet displayed clearer treatment differences. Total zooplankton abundance decreased over time ($F = 19.53$, $df = 2$, $P < 0.01$), but was not different between treatments (Fig. 6A) ($F = 2.92$, $df = 2$, $P = 0.13$). Macrozooplankton abundance showed a significant treatment ($F = 8.72$, $df = 2$, $P = 0.017$), time ($F = 20.29$, $df = 2$, $P < 0.01$), and treatment*time interaction ($F = 3.6$, $df = 4$, $P = 0.04$) (Fig. 6B). At week 0 and 4 there was no significant difference between treatments; however, at week 2 the treatment containing Bighead Carp had substantially lower abundances of macrozooplankton than the treatment containing just Bluegill ($P = 0.01$). The Golden Shiner treatment and the Bluegill alone treatment had similar macrozooplankton abundances at week 2 ($P = 0.89$).

At the conclusion of the experiment, rotifer communities exhibited treatment differences; however, due to high variance, we did not detect a difference in rotifer abundance between treatments ($F = 3.43$, $df = 2$, $P = 0.12$). Rotifer community compositions in ponds were dominated by *Trichocerca spp*, *Philodina spp*, and *Lecane spp* in all three treatments (Fig. 7). There was a treatment effect on the composition of the rotifer community (Pseudo- $F = 3.68$, $df =$

9, $P = 0.02$). *Philodina spp* accounted for 45% of the difference between the just Bluegill populations and the two treatments, making up 72% of the community, compared to 30% in the Golden Shiner treatment and 25% in the Bighead Carp treatment. Furthermore, a student t means separation confirmed community composition differences between both the Bighead Carp and the Golden Shiner treatment as compared to Bluegill alone ($P = 0.02$), but no difference between the Bighead Carp and Golden Shiner treatments themselves ($P = 0.65$).

DISCUSSION

We compared the effect of an invasive and native planktivore on the larval stage of a common sportfish, and assessed the complex interactions between planktivores, larval fish, and their zooplankton prey. Based on mesocosm and pond experiments, Bighead Carp may have the ability to reduce the growth of larval Bluegill to a greater extent than Golden Shiners, likely through more efficient exploitative competition of their zooplankton prey. We observed consistent patterns across all experiments and found some of the first evidence to suggest that Asian Carp, compared to a native planktivore, have greater negative effects on the early life stages of other fishes.

Although statistically inconsistent, in both mesocosms and ponds we observed alterations in the zooplankton community with the steepest decline of zooplankton abundance in treatments containing Bighead Carp. In both experiments, macrozooplankton populations were nearly immediately eliminated by Bighead Carp, causing a 94% decline in macrozooplankton within the first week of the mesocosm experiment (94% decrease at week 2 in ponds). The Bluegill alone (29% in mesocosms, 0.1% in ponds) and the Golden Shiner (72% in mesocosms, 70% in ponds) treatments experienced less drastic declines. The patterns we observed followed our hypothesis

that Bighead Carp would be the most effective at reducing zooplankton populations. Additionally, our results agree with those of previous controlled experiments (Cremer & Smitherman 1979; Lewkowitz & Lawkowitz 1991; Cooke et al. 2009; Collins & Wahl 2017). Furthermore, the compensatory increases in rotifers observed in mesocosms, following reduced macrozooplankton abundances, reflects patterns detected in various other studies on planktivore effects on rotifer communities (Dettmers & Wahl 1999; Domaizon & Dévaux 1999; Nielson et al. 2000; Attayde & Hansson 2001; Attayde & Menezes 2008). The ability of Bighead Carp to reduce and alter zooplankton populations is well established (Cremer & Smitherman 1979; Dong & Li 1994; Chick & Pegg 2001; Xie and Chen 2001; Radke & Kahl 2002; Cooke et al. 2009; Nelson 2014; Collins et al. in review); however, how altered invertebrate assemblages affect larval growth and early life histories of native fishes has previously been undocumented.

In conjunction with greater reductions in macrozooplankton prey, we observed lower growth of larval Bluegill when Bighead Carp were present. Additionally, larval Bluegill experienced lower survival in mesocosms and lower condition and daily growth rate in ponds when Bighead Carp were present as compared to with Golden Shiners or when alone. Studies examining larval Bluegill growth in the presence of Gizzard Shad (*Dorosoma cepedianum*), another efficient planktivore, observed lower growth and recruitment success of Bluegill when Gizzard Shad were present (Welker et al. 1994; Stein et al. 1995). Our observations of reduced zooplankton abundance over time and treatment differences in growth and survival suggest that suppression of zooplankton prey by Bighead Carp contributed to reduced growth of larval Bluegill to a greater extent than native Golden Shiners.

Contrary to our predictions, at high densities of Bighead Carp in the mesocosms, we observed greater growth and survival of larval Bluegill. We expected a high density of Bighead

Carp to result in greater zooplankton suppression and thus decreased growth and survival of larval Bluegill. Although we observed high exploitation of zooplankton, that effect did not correspond to a decrease in growth or survival. Furthermore, we observed higher weight gain than expected of Bighead Carp at high densities. We would have expected increased density to result in density dependence or intraspecific competition for prey (Hepher 1989), and thus decreased growth; but this was not the case. These facilitation effects have been increasingly observed in the literature (Nelson 2014; Seibert et al. 2016; Collins et al. in review) yet the underlying mechanisms are still unknown. Some hypotheses involve “bottom up” effects including increased rotifer populations, increased nutrient recycling, and anti-predatory prey behaviors, or some combination of the three (Collins et al. in review)

We observed heavy suppression of macro-zooplankton when Bighead Carp were present; however, we also observed increased abundances of rotifer populations, as has been observed in the field (Sass et al. 2014). These rotifers may have been an important prey source for larval Bluegill in treatments containing high densities of Bighead Carp (Siefert 1972; Tanner & Knuth 1996). Preying on rotifers may be less calorically efficient than preying on larger macrozooplankton; however, rotifers can contain more calories than copepod nauplii despite being smaller in size (Theilacker & Kimball 1984). High rotifer abundance may have been beneficial to the growth of larval Bluegill. Additionally, increased nutrient recycling when high densities of Carp were present may have outweighed the consequences of zooplankton predation (Du et al. 2014). Excretion of nitrogen and phosphorus by fishes can provide a large proportion of the nutrients required for primary production and growth of other organisms, thus affecting species composition (Vanni & Layne 1997; Vanni 2002). Additionally, egestion of nutrient-rich waste shunts resources from planktonic to benthic habitats, potentially subsidizing benthic

organisms increases fish biomass as observed for age-0 channel catfish after consumption of Silver Carp fecal pellets (Yallaly et al. 2015; Collins & Wahl 2017). It is clear that some indirect effects occurred in our mesocosms; however, our data does not lend itself to distinguishing among hypotheses, and will require future studies.

Despite the ability of Bighead Carp to effectively outcompete larval Bluegill for zooplankton, there was no effect on the overall abundance of larval Bluegill in ponds. These results support that prey-availability, although important, is not the only factor influencing age-0 mortality (Houde 2009). The indirect feedbacks we observed within the mesocosm food web dampened the impact of Bighead Carp and indicate that competition is not the only mechanism at play (Nelson et al. in review; Collins & Wahl 2017). Furthermore, effects on survival in mesocosms may have been masked by the short duration of the experiment. With time, we may have observed zooplankton communities shifting to smaller and less energy efficient prey (Lewkowitz & Lawkowitz 1991; Dong & Li 1994) causing further decreases in growth (Breck 1993). Smaller Bluegill unable to outgrow the gape limitations required to switch to benthic prey items could then induce greater mortality or susceptibility to predation, ultimately leading to lower recruitment success (Bremigan & Stein 1994).

There were no differences in rotifer abundances between treatments; however, rotifer community composition shifts were observed in both planktivore treatments. Removal of large zooplankton is commonly associated with shifts in rotifer assemblages through increased phytoplankton biomass or decreased density of predatory zooplankton (Jack & Thorp 2002; Thorp & Casper 2003; Hunt & Matveev 2005). Both Bighead Carp and Golden Shiners passively feed on rotifers through pump filter feeding (Ehlinger 1989; Browman & O'Brien 1992; Dong & Li 1994). Conversely, larval Bluegill are visual particulate foragers that can

reduce rotifer community size-structures through size-selective foraging (Rettig 2003).

Philodina contributed over 45% of the difference between both treatments and Bluegill alone.

Although not much is known about the ecology of Bdelloid rotifers, we do know that their adult form is relatively small, they are highly fecund, and have a short-life cycle (Moreira et al. 2016). Greater numbers of macro-zooplankton predators in the Bluegill alone treatments in addition to size-selective foraging by larval Bluegill may help to explain the differing rotifer communities we observed.

Understanding the growth of larval populations is an important indicator of foraging success, recruitment, and ultimately community composition. Whereas other work has presumed there might be negative effects of Asian Carp on larval native species (Chick & Pegg 2001; Xie & Chen 2001), our study is one of the first to directly detect these effects of invasive Bighead Carp on the growth of a native larval fish. The ability of Bighead Carp to reduce zooplankton populations ultimately resulted in decreased growth of larval Bluegill at both spatial scales. Lower growth of larvae has the potential to extend the period larvae are susceptible to predation (Rice et al. 1987; Miller 1988), lengthen their reliance on zooplankton prey, decrease foraging ability (Blaxter 1986; Pepin 1991), and increase susceptibility to overwinter mortality (Adams et al. 1982). Ultimately these effects could alter Bluegill recruitment to the juvenile and adult stages, and further, influence the community composition of aquatic systems.

With the possibility of Bigheaded Carp reaching the Great Lakes and other lakes in the United States (Butler et al. 2016; Cooke & Hill 2010) it is important to understand how they may affect native fishes in these ecosystems. Bluegill, and functionally similar species, are important sportfish throughout the Midwestern United States, such that invasion effects on economically important fisheries would warrant action from managers and practitioners alike. Future work

focusing on these potential negative interactions as well as possible positive feedback loops (Collins & Wahl 2017) will further our understanding of the effect these invaders can have on our riverine and lacustrine systems, helping prepare us for future expansions and invasions.

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TABLES AND FIGURES

Table 1. Results of the contrast statements on length, weight, and survival of larval Bluegill in the mesocosm experiments. Results were obtained using JMP software. Each density of Bighead Carp (3,6) was compared with the same density of Golden Shiners, and then pooled to compare entire species effects against one another. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.

3BHCvs3GOS	Length	Weight	Survival
Sum of Squares	2.30	0.003	53783
Degrees of Freedom	62	64	64
F-value	4.84	1.73	6.30
P-value	0.03	0.19	0.02
<u>6BHCvs6GOS</u>			
Sum of Squares	0.63	0.002	24790
Degrees of Freedom	62	64	64
F-value	1.33	1.12	2.93
P-value	0.25	0.29	0.09
<u>BHCvsGOS</u>			
Sum of Squares	2.64	0.00004	2166
Degrees of Freedom	62	64	64
F-value	5.55	0.02	0.25
P-value	0.02	0.88	0.62
<u>GOSvsBLG</u>			
Sum of Squares	2.30	0.01	48847
Degrees of Freedom	62	64	64
F-value	4.85	5.72	5.72
P-value	0.03	0.02	0.02
<u>BHCvsBLG</u>			
Sum of Squares	8.56	0.01	71009
Degrees of Freedom	62	64	64
F-value	18.02	6.66	8.32
P-value	0.00001	0.01	0.005

Table 2. Mean and 95% confidence intervals for all environmental parameters in the mesocosm and pond experiments. Due to a lack in treatment differences, averages and confidence intervals were calculated between all tanks/ponds over the course of the entire experiment.

Trial 1	Mean	C.I.
Light Intensity	80.87 lx	± 24.14 lx
Phosphorus	150.27 µg/L	± 43.57 µg/L
Chlorophyll- <i>a</i>	114.64 µg/L	± 2.15 µg/L
Temperature	22.38 °C	± 0.16 °C
Dissolved Oxygen	7.56 mg/L	± 0.17 mg/L
<u>Trial 2</u>		
Light Intensity	45.86 lx	± 20.79 lx
Phosphorus	200.57 µg/L	± 32.64 µg/L
Chlorophyll- <i>a</i>	118.25 µg/L	± 2.48 µg/L
Temperature	21.56 °C	± 0.19 °C
Dissolved Oxygen	7.81 mg/L	± 0.25 mg/L
<u>Pond</u>		
Phosphorus	46.45 µg/L	± 19.71 µg/L
Chlorophyll- <i>a</i>	116.34 µg/L	± 7.87 µg/L
Temperature	25.36 °C	± 0.36 °C
Dissolved Oxygen	2.20 mg/L	± 0.39 mg/L
Vegetation Cover	33.00%	± 24.06 %
Benthic Inverts	20.01 ind/sample	± 12.44 ind/sample
Secchi Depth	0.68 ft	± 0.12 ft

Figure 1. Difference in mean weight gain (g) (A), change in length (mm) (B), and survival out of 20 (C) of larval Bluegill between treatments in mesocosms. Treatments consisted of Bluegill alone and Bluegill with a high (6) and low (3) density of either Bighead Carp or Golden Shiners. All comparisons were made using an ANOVA, and post-hoc comparisons were made using a Tukey's honest significance test. Error bars represent the standard error, and values with different letters are significantly different. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.

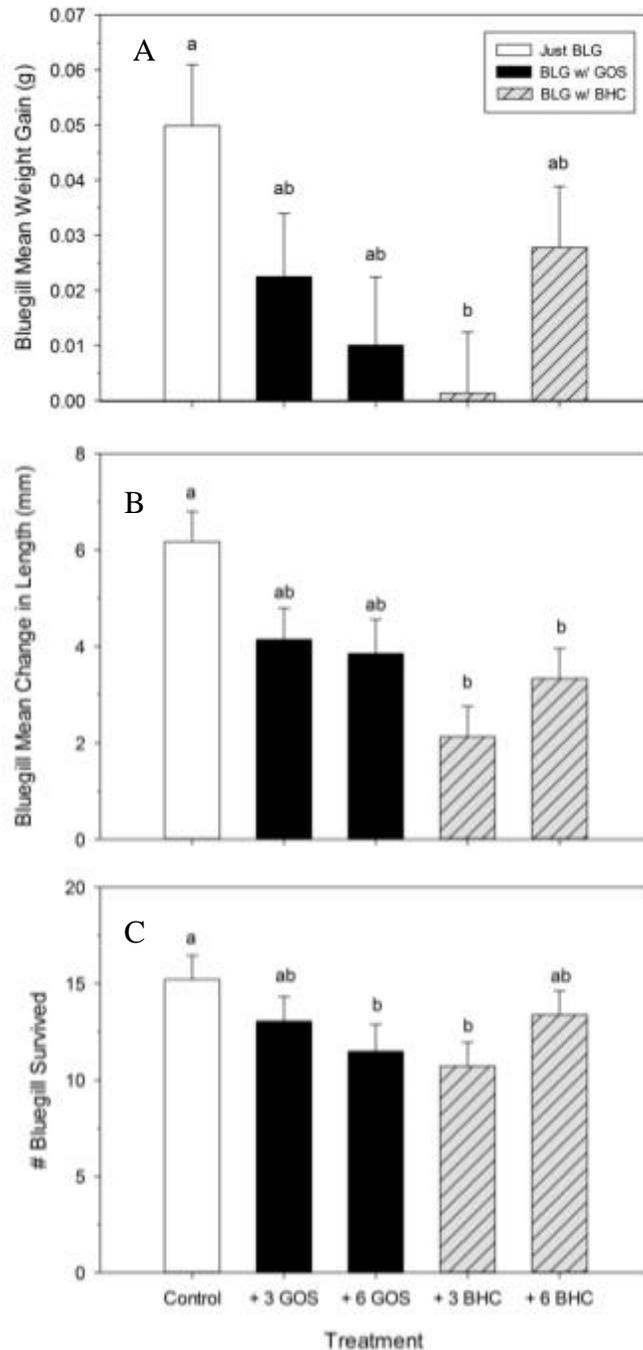


Figure 2. Difference in mean change in length (mm) (A) and mean weight gain (g) (B) of Bighead Carp and Golden Shiners at two density levels, 3 or 6, in mesocosms. All comparisons were made using an ANOVA, and post-hoc comparisons were made using a Tukey's honest significance test. Error bars represent the standard error, and values with different letters are significantly different. GOS = Golden Shiner, and BHC = Bighead Carp.

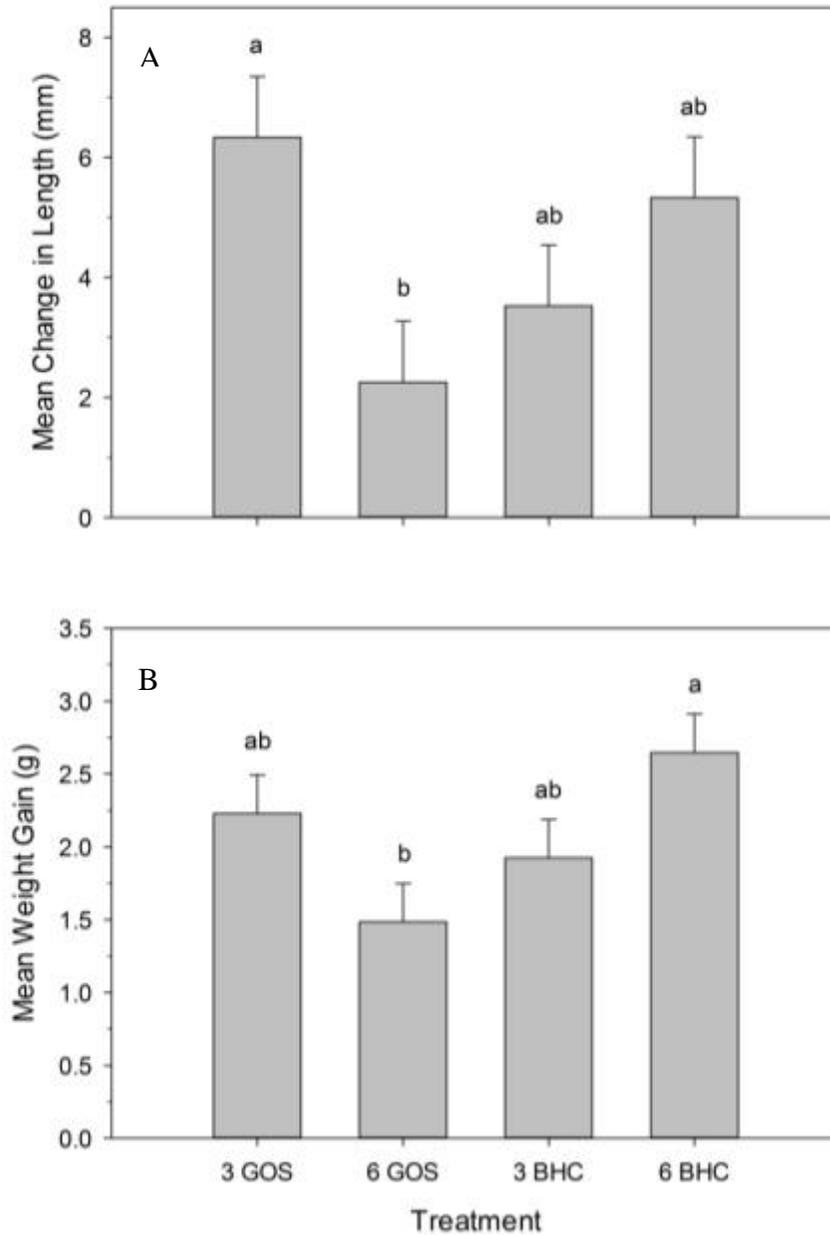


Figure 3. Change in total zooplankton abundance (A) and macrozooplankton abundance (B) between treatments over the course of the first trial and second trial (C and D) of the 4 week mesocosm experiment. Treatments consisted of Bluegill alone and Bluegill with a high (6) and low (3) density of either Bighead Carp or Golden Shiners. All comparisons were made using a Repeated Measures ANOVA. Error bars represent the standard error. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.

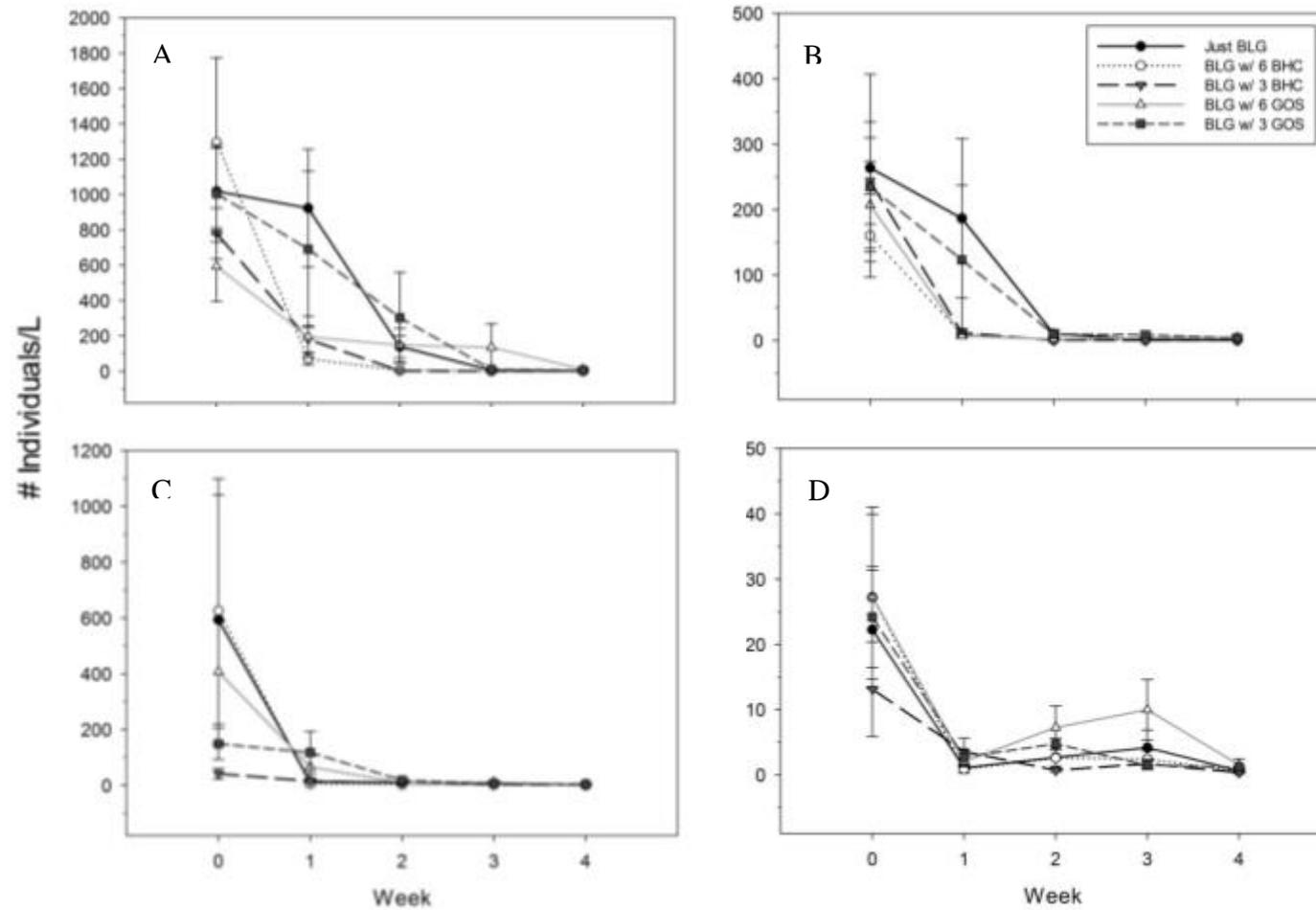


Figure 4. Change in total rotifer abundance between treatments over the course of the second trial of the 4 week mesocosm experiment. Treatments consisted of Bluegill alone and Bluegill with a high (6) and low (3) density of either Bighead Carp or Golden Shiners. All comparisons were made using a Repeated Measures ANOVA. Error bars represent the standard error. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.

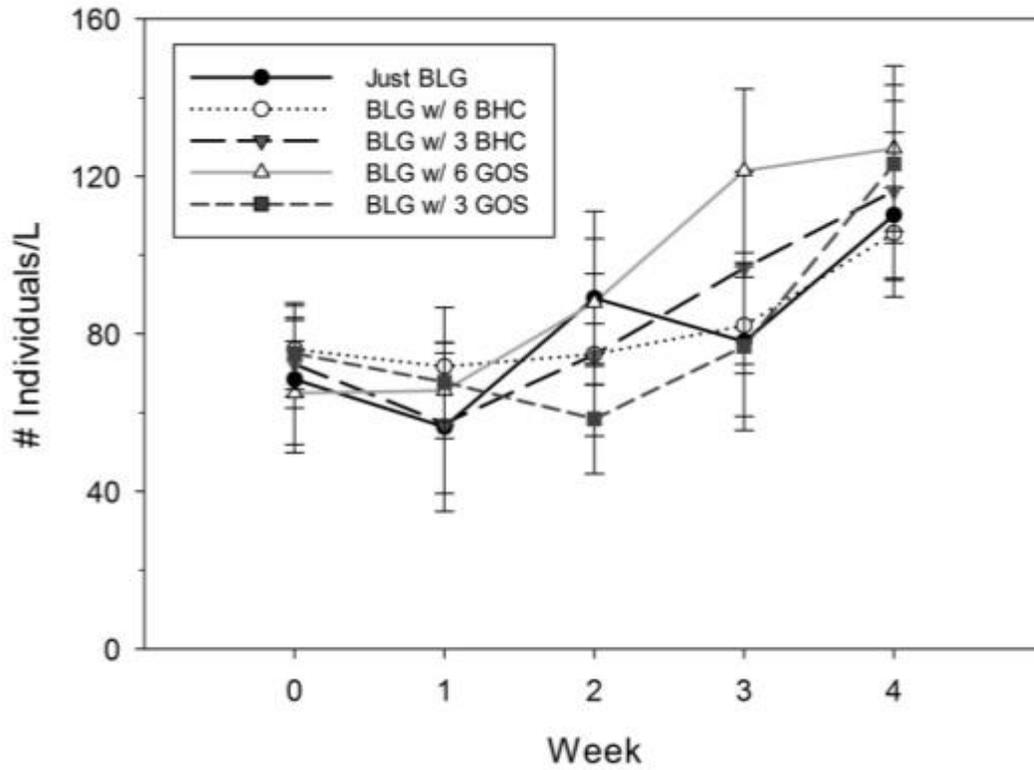


Figure 5. Difference in the mean daily growth rate (g/day) (A), mean total biomass (g) (B), mean length (mm) (C), mean condition (D), and mean abundance (E) of larval Bluegill per pond between treatments. Treatments consisted of Bluegill alone and the addition of either 100 Bighead Carp or 100 Golden Shiners. All comparisons were made using an ANOVA, and post-hoc comparisons were made using a Student's t-test. Error bars represent the standard error, and values with different letters are significantly different. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.

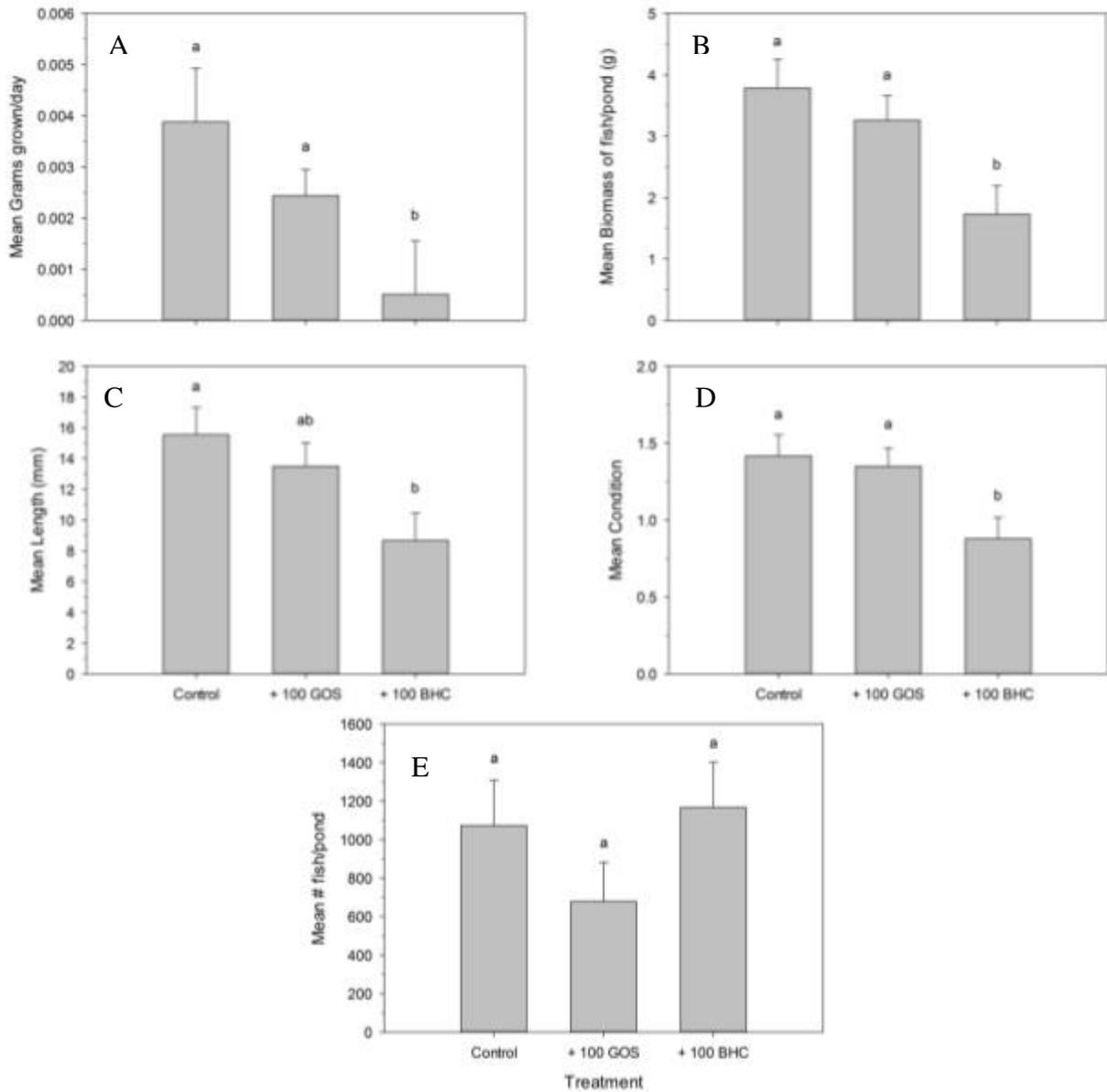


Figure 6. Change in total zooplankton abundance (A) and macrozooplankton abundance (B) between treatments over the course of the 4-week pond experiment. Treatments consisted of Bluegill alone and the addition of either 100 Bighead Carp or 100 Golden Shiners. All comparisons were made using a Repeated Measures ANOVA. Error bars represent the standard error. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.

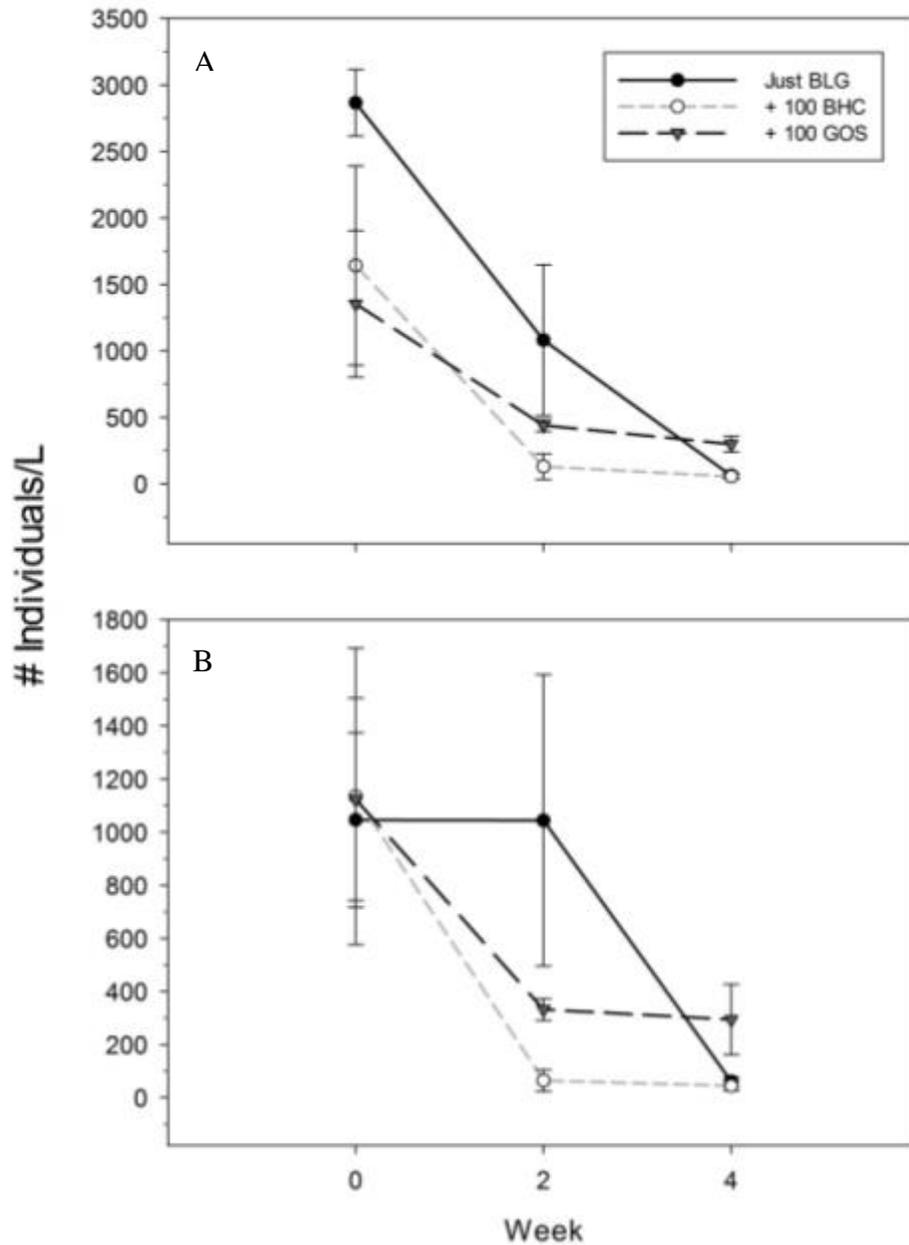
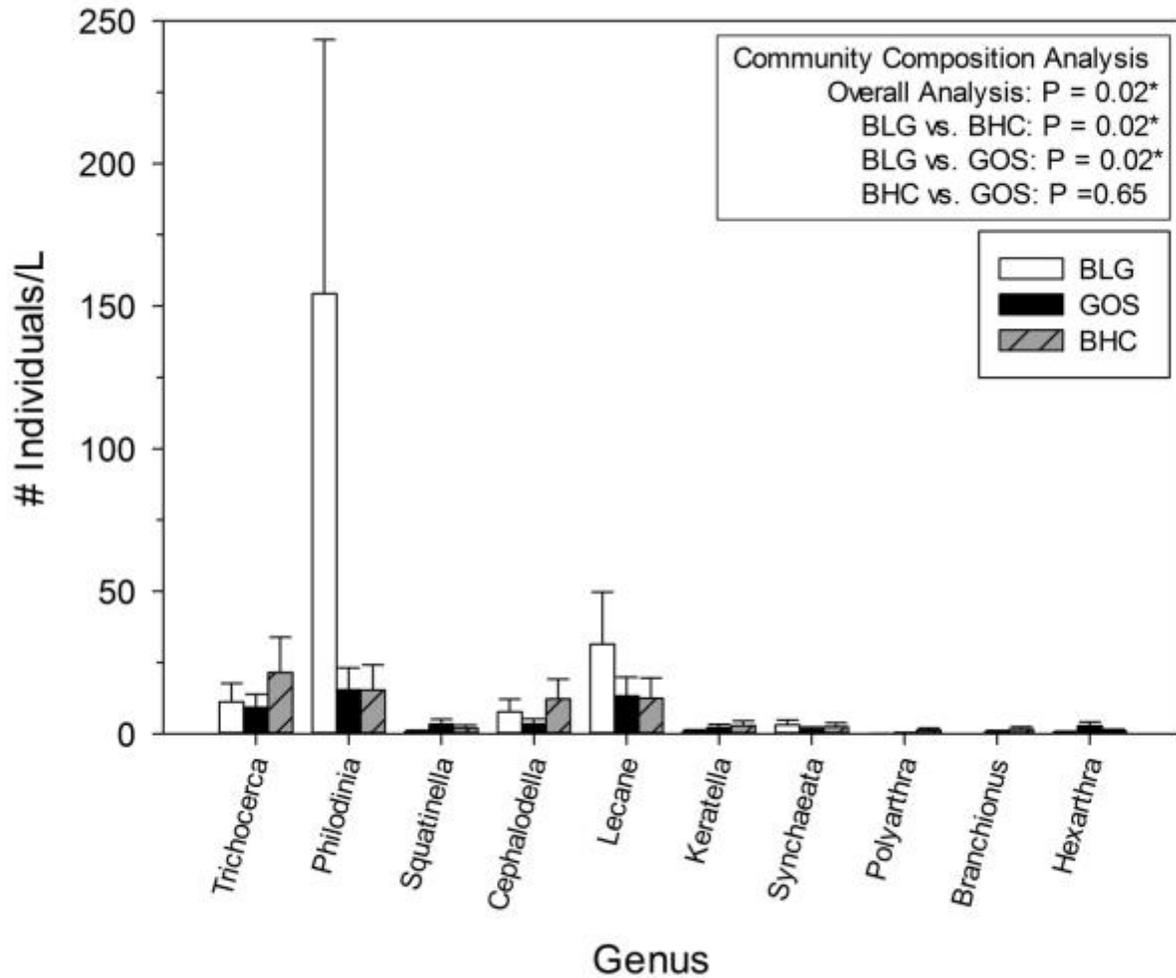


Figure 7. Mean abundance of each rotifer genus between treatments sampled at the conclusion of the pond experiment. The community composition analysis was conducted using a PERMANOVA test, followed by a Student's t-test to separate treatment means. Error bars represent the standard error. BLG = Bluegill, GOS = Golden Shiner, and BHC = Bighead Carp.



CHAPTER 3: GENERAL CONCLUSION

I tested for competitive interactions between Bighead Carp, Golden Shiners, and larval Bluegill at two different spatial scales to determine if an invasive planktivore has a greater negative effect than a native planktivore on the growth, survival, and abundance of a larval native sportfish. Competitive interactions between Bighead Carp and native species have previously been studied; however, the results of these studies are inconsistent. Although Bighead Carp have been shown to negatively affect native planktivores, effects on facultative planktivores are understudied and not fully understood. Bighead Carp and Bluegill interactions have been studied at the juvenile stage, and resulted in facilitation of growth rather than decreased growth due to exploitative competition. However, my study is the first to observe these interactions at the larval stage, directly comparing the effects of an invasive planktivore to those of a native one.

Bighead Carp have been shown to reduce zooplankton populations and alter zooplankton size structures. Concurrently, due to gape limitations, Bluegill are reliant on zooplankton prey for successful growth and survival at the larval stage. Given these linkages, the potential for competitive interactions between Bighead Carp and larval Bluegill is dramatically increased. Through both mesocosms and ponds, I was able to observe the effects of both Bighead Carp and Golden Shiner on the growth, abundance, and survival of larval Bluegill in order to make predictions about recruitment success.

In mesocosms we observed decreased growth and survival when low densities of Bighead Carp were present as compared to Golden Shiners. At higher densities of Bighead Carp, we detected facilitation effects that have been increasingly observed in the literature. In ponds, we again saw decreased larval growth of Bluegill that spawned in the presence of Bighead Carp

compared to Golden Shiners. No effects on abundance of larval Bluegill were detected. All Bighead Carp treatments between both experiments exhibited greater suppression of zooplankton populations over time than native Golden Shiners. Through a synthesis of both experiments, it is clear that Bighead Carp can reduce the larval growth of Bluegill to a greater extent than Golden Shiners. Effects of high densities of Bighead Carp need to be studied further to fully understand the mechanisms involved in the facilitation of larval Bluegill growth we observed.

With the range of Asian Carp expanding, concern for the aquatic ecosystems of the Great Lakes and other connected tributaries increases as well. Bluegill are one of the most abundant and sought after sportfish in the Midwestern United States in addition to being functionally similar to many other native species. My research shows that when larval Bluegill are present alongside these invaders, reduced growth can occur, providing the first examination of the effects of Asian Carp on the recruitment success of native fishes. It is important to keep these effects in mind as we prepare for further expansions and continue to preserve the natural biodiversity of our aquatic ecosystems.