Effects of bluegill predation, lake productivity, and juvenile dispersal on common carp recruitment dynamics in lake-marsh systems in Minnesota

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Joseph D. Lechelt

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Abstract

Processes that regulate common carp (*Cyprinus carpio*) recruitment (i.e. survival of eggs, larvae and juveniles) are largely unknown. In interconnected lake-marsh systems of Minnesota, young of year (YOY) carp are generally found in marshes that winterkill and lack bluegill sunfish (*Lepomis macrochirus*), an abundant native predator. This suggests that bluegills might function as a biocontrol agent for carp. Further, whereas YOY carp are commonly found in winterkill marshes of south-central Minnesota, they are not found in similar systems in northern Minnesota where lake productivity is much lower, suggesting an aquatic productivity bottleneck on carp recruitment. Finally, in marshes where carp recruit (productive and bluegill-free), YOY must disperse into adjacent lakes to drive high population abundance. In this study, I conducted three experiments to test 1) the effect of bluegills on carp recruitment; 2) the effect of aquatic productivity on larval carp survival, growth and diet; 3) natural dispersal tendencies of YOY carp from a marsh into an adjacent lake. The first experiment employed four (20 m diameter) impermeable enclosures from 2011-2014. Each year, enclosures were stocked with carp eggs and every other one was stocked with bluegills. Backpack electrofishing surveys conducted five weeks later showed that carp catch per unit of effort (CPUE) was over 10-fold lower in the enclosures stocked with bluegills than in the controls. The second experiment, conducted in 2014 and 2015 used aquaria stocked with carp larvae and supplied with zooplankton densities and community structures from lakes of three different trophic states (oligo-, meso-, and eutrophic). It showed that carp larvae selectively consumed macrozooplankton (> 200 μm) and their growth rates were highest in the eutrophic lake and lowest in the oligotrophic lake. Survival, however, was high in all treatments. The third study was conducted in a natural lake-marsh system and utilized passive integrated transponder (PIT) tags to quantify the outmigration of YOY carp from the marsh to the lake. It showed that < 6% YOY carp outmigrated to the lake, supporting previous indirect estimates. The results of these three studies are important to understanding recruitment dynamics of carp in lake-marsh systems in Minnesota.

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Chapter 1: Thesis Introduction

Introduction

The common carp (*Cyprinus carpio,* hereafter "carp") is a large, long-lived cyprinid that evolved in the drainages of the Black, Caspian, and Aral Sea (Balon 1995). The carp has been of great importance as an ornamental fish and in providing people with animal protein since it was first cultured, nearly 3000 years ago (Moav et al. 1975). Today, it continues to be the one of the most commonly farmed and produced fish species across the globe (Naylor et al. 2000). The carp is an ideal species to be cultured globally, because of its low production costs, fast growth rates, and broad ecological tolerances (Koehn 2004, Zambrano et al. 2006). While carp hold many commercial benefits, its expansion in aquaculture and introductions as a sport fish has contributed significantly to its invasion across the globe. The carp has become invasive on every continent excluding Antarctica (Lehtonen 2002, Koehn 2004, Zambrano et al. 2006, Singh 2010, Vilizzi 2012). The following paragraphs will provide a short review of carp's invasion history in different regions of the world, followed by carp's ecological impacts, life history and factors influencing invasion success.

History of carp introduction worldwide

Carp appears to be especially invasive in North America, Australia and Africa. There are some disputes about when carp were first introduced to North America. The earliest reports date back to 1831 in New York when carp escaped from a pond into the Hudson River; however, it is uncertain whether they were carp or goldfish (*Carassius auratus*) (Cole 1905, Stickney 1996, Nico and Fuller 1999). Most reports suggest that carp were first brought to North America in 1872, when five carp from Germany were

stocked in ponds in Sonoma Valley, California (Cole 1905, Stickney 1996). However, the widespread invasion likely did not begin until 1877 when 345 carp were transported to Baltimore from Germany (Cole 1905). These fish were propagated for two years to supply a stocking program, which spread ~12,000 carp across 25 states and territories (Cole 1905). A more intensive stocking program followed in the 1880's and early 1890's, when the U.S Fish Commission authorized the stocking of over 2.4 million carp across the United States for food and angling purposes (Cole 1905). During this time, carp were introduced to many of the United States major river systems and the Laurentian Great Lakes, which further accelerated their spread (Cole 1905, Mills et al. 1994). Although most stocking efforts were halted by the end of the 19th century, carp continued to spread throughout the country and today can be found in all states except Alaska (Nico and Fuller 1999). In Canada, the carp was first introduced to Ontario during the 1880's to provide food (Crossman 1991). Today, the distribution of carp is primarily restricted to southern Canada (McPhail 2007). In Mexico, carp were first introduced in the late 1960's and widely spread throughout the country during the 1970's-1980's as part of a government program to provide protein to rural areas (Tapia and Zambrano 2003). Following their introduction, carp have invaded 95% of Mexico's waterways (Hinojosa-Garro and Zambrano 2004).

Carp have become invasive in many Australian waterways, especially in south-east Australia where they have become the dominant species, comprising > 90% of biomass (Koehn 2004). Initial introductions date back to the mid 1800's; however, these fish were contained in ponds and did not spread to natural waterways (Koehn et al. 2000). The invasion of carp truly began in 1964 when they were introduced to the Murray River

(Koehn et al. 2000). Carp quickly spread throughout the Murray-Darling River Basin through seasonal floods, which provided access to new habitats (Koehn et al. 2000). This spread was further exacerbated by the incidental releases via bait buckets (Koehn et al. 2000). In addition to south-east Australia, carp have been spread to Queensland, Western Australia, and Tasmania (Shearer and Mulley 1978, Koehn et al. 2000, Morgan et al. 2004). While carp have spread to Queensland and Western Australia, populations are restricted to certain water bodies and do not reach as high of densities as in the Murray-Darling River Basin (Koehn et al. 2000, Koehn 2004). In Tasmania, carp have been found and eradicated from the island on two separate occasions (1975 and1980), however in 1995 carp were found in Lake Crescent and Lake Sorell, which are currently undergoing an intensive removal project (Koehn et al. 2000, Diggle et al. 2012). Currently, 13% of the Australian continent is invaded by carp (Koehn 2004).

There have been multiple introductions in many different locales throughout Africa that have led to the spread of carp across the continent. In the 18th century, carp were first introduced in southern Africa as an ornamental fish (De Moor and Bruton 1988). Following this initial introduction, carp were commonly spread to other water bodies throughout southern Africa by anglers for food and sport (De Moor and Bruton 1988). The spread of carp rapidly increased across the rest of the continent in the 19th and 20th century when it became a popular aquaculture species (Moreau and Costa-Pierce 1997). Moreau and Costa-Pierce (1997) reviewed the history of aquaculture in 26 countries and found that carp were stocked in natural water bodies, man-made lakes, or escaped into natural water bodies in 17 of these countries, likely contributing to the widespread invasion across Africa (Matthews and Brand 2004, Vilizzi 2012).

Additionally, carp invaded one of Africa's most important water bodies, the African Great Lakes, in the 20th century (Ogutu-Ohwayo et al. 1997). New introductions have been recorded as recently as 1999, when juvenile carp escaped from an aquaculture facility during a flood into River Malewa and were transported downstream to Lake Naivasha, Kenya (Hickley et al. 2004, Britton et al. 2007).

Common Carp Impacts

Carp are widespread across the world, but it is the extensive environmental damage they cause that makes them a part of the "100 World's Worst Invasive Species" by the International Union for the Conservation of Nature (IUCN) (Lowe et al. 2000). Carp are known to be an ecosystem engineer, which means that they modify and alter the state of the water bodies they inhabit (Weber and Brown 2009). While carp are often brought into fish polyculture to improve the growth rates of other fishes (Hepher et al. 1989, Wahab et al. 1995), they are generally thought to negatively impact natural waterways (Weber and Brown 2009). Carp can become superabundant, >100 kg/ha, in certain regions (Bajer and Sorensen 2010) and can potentially displace native species (Koehn 2004, Weber and Brown 2011).

It is generally accepted that carp cause environmental damage through their destructive feeding habits (Zambrano et al. 2001, Miller and Crowl 2006, Weber and Brown 2009). Carp are benthivorous and have the ability to dig into the sediment in search of prey (Panek 1987), which can displace submerged macrophytes, increase suspended solids, and potentially increase nutrient cycling (Crivelli 1983, Zambrano et al. 2001, Miller and Crowl 2006, Bajer et al. 2009, Vilizzi et al. 2015). In a microcosm

experiment conducted by Crivelli (1983), the aquatic vegetation decreased with increasing carp biomass. These results were confirmed in a removal study, where aquatic vegetation cover significantly increased following the removal of carp from a Minnesota lake (Bajer and Sorensen 2015). Carp have also been shown to increase suspended solids, which leads to an increase in turbidity in aquatic ecosystems (Parkos III et al. 2003, Vilizzi et al. 2015). This increase in turbidity may have also an indirect effect on plant growth by limiting the amount of available light, although the extent of this effect remains unknown (Lougheed et al. 1998). Disruption of the sediment can also increase the amount of nutrients in the water column, which may increase phytoplankton growth and promote algal blooms (Matsuzaki et al. 2007, Weber and Brown 2009). All of these impacts can have direct and indirect effect on ecosystems and negatively alter zooplankton, invertebrate, amphibian, waterfowl and fish communities (Vilizzi et al. 2015). In shallow lakes, the introduction of carp can change the state of a system from clear water with abundant macrophytes to turbid with very few macrophytes (Matsuzaki et al. 2007, Weber and Brown 2009).

Common Carp Life History

Carp are believed to have evolved in large river systems that experience seasonal flooding (Balon 2004). These floodplains are highly productive, sheltered, and relatively predator-free environments, which carp utilize as spawning habitat. This behavior is emulated in invaded regions with rivers that still exhibit flood conditions, such as the Murray River in Australia where carp spawn in inundated red gum forests (Stuart and Jones 2006). However, the spawning behavior of carp is highly adaptable and can change according to the environment that they are introduced into. In interconnected

lake-marsh systems in the temperate region of North America, adult carp populations have been shown to spawn in lakes or migrate to outlying marshes to spawn (Bajer and Sorensen 2010). Carp are believed to be obligatory phytophiles and spawn on fresh aquatic vegetation to which their adhesive eggs stick.

Carp engage in relatively synchronous spawning, where one female is followed by a group of males (Swee and McCrimmon 1966), with many groups spawning at the same time. In the northern temperate regions, spawning begins in the spring when water temperatures reach 15-18 °C (Swee and McCrimmon 1966, Crivelli 1981, Balon 1995). Female carp are highly fecund and can produce between 1 and 3 million eggs annually (Swee and McCrimmon 1966). Carp broadcast their eggs on vegetation in the littoral zone and do not provide parental care (Swee and McCrimmon 1996, Balon 1995). The eggs are fertilized externally and expand to 1.5 to 1.8 mm when released into the water (Balon 1995). Eggs adhere to vegetation and typically develop and hatch in 3 days in 20-23 °C (Balon 1995). However, hatching rate is temperature dependent and decreases at lower temperatures (Silbernagel 2011). Following hatching, larvae remain attached to the vegetation while endogenously feeding on yolk reserves for 2 to 3 days before beginning free-swimming (Geurden et al. 1999; Köprücü and Aydin 2004). Larvae then switch to feeding on zooplankton in the water column (Ahmed 2011, Jhingran and Pullin 1985). Mortality during this stage can be very high, due to predation and starvation.

Carp larvae transform into juveniles between 20-25 mm, when they begin feeding on benthic invertebrates (Vilizzi and Walker 1998). This also coincides with developing folds in the intestine and increased activity of amino peptidase (Dabrowski 1984). Carp can grow up to 1 mm/day during the first year of life (Phelps et al. 2008a), commonly

reaching 150 mm by the end of the first year. Following the first year of life, carp are often too large for most predators to consume and mortality rates among adult carp drop to 1-7% annually (Weber et al. 2011; Donkers et al. 2012). In temperate regions, female carp typically mature in 3 to 5 years and males in 2 to 3 years; however, carp have been shown to mature in less than 1 year in tropical environments (Parameswaran et al. 1972; Raina 1987). Adult carp can grow to over 1 m in length and live for more than 50 years (Gabelhouse Jr 1984; Bajer and Sorensen 2010; Koch 2014).

Factors Influencing Common Carp Invasion Success across North America

The factors that drive carp invasion success across broad geographical landscapes are often difficult to identify due to complex biological and environmental interactions. Typically, physical and biological characteristics of previously invaded regions and life history information of the species are used to create an ecological niche model, which can predict invasion potential and identify "at risk" environments (Marchetti et al. 2004; Herborg et al. 2007; Kulhanek et al. 2011a, b; Reshetnikov and Ficetola 2011). Ecological niche modeling suggests that most of North America is suitable for carp to invade (Zambrano et al. 2006). However, carp population abundance fluctuates dramatically across regions and also among locations within each region, showing that both coarse- and fine-scale processes regulate carp abundance in North America. Adult carp have broad ecological tolerances, are large enough to avoid predation, and have a low natural mortality rate (Swee and McCrimmon 1966; Zambrano et al. 2006; Weber et al. 2011; Donkers et al. 2012). Therefore, in environments with low population sizes it is unlikely that carp are limited by low adult survival, but rather

bottlenecks at earlier life stages; i.e. low recruitment rates are preventing these populations from becoming abundant.

Predation, lake productivity, adult density, and movement of adults and juveniles between interconnected systems of seasonally unstable habitats have all been suggested to have an effect on carp recruitment and population abundance in North America (Bajer and Sorensen 2010; Bajer et al. 2012; Silbernagel and Sorensen 2013; Weber and Brown 2013; Bajer et al. 2015a, b). Bluegill sunfish (*Lepomis macrochirus*), which have been shown to consume carp eggs and larvae (Bajer et al. 2012; Silbernagel and Sorensen 2013; Bajer et al. 2015a), have been hypothesized to function as an important biocontrol agent in many lakes in the Upper Mississippi region. However, this hypothesis has not been tested experimentally. Lake productivity has also been suggested to be an important driver of carp recruitment, possibly due to increased prey abundance for larval carp in productive lakes (Bajer et al. 2015a), but diets, growth and survival of larval carp have not been documented in lakes of varying productivity level. Finally, carp recruitment has a strong spatial component related to predator instability across the landscape. In lake-marsh complexes of central Minnesota, marshes often winterkill and lack bluegills. Adult carp employ spawning migrations to such habitats where they are able to produce strong year classes (Bajer et al. 2012). However, for this strategy to lead to high carp abundance throughout entire chains of lakes, juvenile carp must outmigrate from natal marshes into adjacent lakes before the next winterkill. While these juvenile outmigration rates have important management implications, they remain largely unknown and have not been measured directly.

Thesis Overview

The goal of this thesis is to identify and explore three specific aspects of common carp recruitment in Minnesota lakes: 1) the possibility that carp recruitment can be controlled by bluegill predation (biocontrol); 2) effects of lake productivity on larval carp diet, growth and survival; and 3) rates with which age-0 carp disperse from winterkill-prone marshes into lakes. This thesis consists of four chapters. The first chapter provides an overview of the thesis and the study organism, carp, its invasion history, environmental impacts, life history, and factors influencing invasion success. The second chapter describes a mesocosm experiment, which directly tested the ability of bluegill sunfish (*Lepomis macrochirus*) to control carp eggs and larvae through predation. The third chapter describes a laboratory experiment in which carp larvae were fed naturally occurring zooplankton communities from lakes of different trophic states to assess their diet, growth and survival. The fourth chapter describes a study that quantified the outmigration of age-0 carp from a winterkill-prone marsh into a lake using direct and indirect approaches.

Chapter 2: A Mesocosm Experiment Suggests Bluegill Sunfish (*Lepomis macrochirus*) are Effective Predators of Invasive Common Carp (*Cyprinus carpio*) Eggs and Larvae: Assessing the Potential for Biocontrol

Chapter Summary

Biological control refers to the process of using one organism to control a pest organism. This strategy is commonly used to control pest insect species, but its potential to control invasive fish remains largely unexplored. Bluegill sunfish (*Lepomis macrochirus*) have been hypothesized to be effective predators of common carp (*Cyprinus carpio*) eggs/larvae and could potentially serve as an important biocontrol agent in lakes of temperate North America. This hypothesis, however, has not been tested using controlled experiments. I conducted a mesocosm experiment in four consecutive years (2011-2014) in two lakes to test if bluegills can control carp recruitment through predation. Mesocosms were established using vinyl enclosures, which were stocked with fertilized carp eggs on natural spawning substrate and half were also stocked with representative densities of bluegills and the other half left fishless. The experiment lasted five weeks, the length of the juvenile carp vulnerability window, after which time I estimated the abundance of young of year (YOY) carp in each mesocosm (mean catch per unit of effort; CPUE). In addition, to determine if bluegills were primarily consuming carp eggs or larvae, I compared egg density in bluegill vs. fishless enclosures on day two of the experiment (one day before the eggs hatch). YOY CPUE was significantly lower in enclosures stocked with bluegill (mean = 0.83; SD =1.34; N = 4) than the control enclosures (mean = 13.30; SD = 3.66; N = 4; ANOVA; $p < 0.05$). However, egg density was only slightly lower in the bluegill enclosures (mean bluegill = 0.35; SD = 0.0094; N = 2; mean control = 0.51; SD = 0.28; N = 2). The results of this study suggest that bluegills might be an effective biocontrol agent of carp recruitment in North American lakes, and that their effects extend beyond the egg phase of carp development.

Introduction

Biocontrol is broadly defined as using one organism to control a pest organism (Thompson 1930) and is considered to be a fundamental element of integrated pest management (IPM) strategies (Kogan 1998; Stern et al. 1959; Zehnder et al. 2007). Biocontrol is often thought of in the classical sense, where a co-evolved predator, pathogen or parasitoid is imported from the pest's native range ("old enemy") to control the pest in new areas to which it has been introduced (Howarth 1991, Naranjo et al. 2015). While this process involves careful screening and quarantine procedures to ensure high specificity and low possibility of forming new associations with native non-target species, the introduction of a foreign biocontrol species can have many unintended consequences that can lead to a decrease or elimination of native populations of non-target species (Simberloff and Stiling 1996). A potentially safer approach, but less likely to occur since invaders are not expected to have co-evolved enemies in new areas to which they are being introduced, is the use of a native (local) species as the biocontrol agent, a process known as conservation biocontrol (Eilenberg et al. 2001). For example, establishing overwintering habitats or "beetle banks" for native arthropods can help in reducing the population of non-native pest aphids (Collins et al. 2002). Biocontrol has been primarily used to control terrestrial pests, including noxious weeds, insects, and rodents; however, the utility for fishes remains largely unexplored (Thresher et al. 2014).

While the introduction of "old enemies" might be needed to control most invasive insects, native biocontrol may be more plausible for vertebrates. Due to their high diversity (> 1 million species) it is typical for insects to have very specific, co-evolved enemies and it is less likely that a new enemy could be found among native species. This,

however, might be more plausible for vertebrates, or fish in particular, which are an order of magnitude less diverse and where few highly co-evolved predator-prey interactions exist. In other words, due to the fact that many fish species have broad, plastic diets, it may be more reasonable to expect that a native fish could control an invader, especially if the invader is similar to prey items in that native fish's natural diet (Iguchi and Yodo 2004; Balcombe et al. 2005). For example, the Japanese dace (*Tribolodon hakonensis*), which is an indigenous fish egg-eater to Japan, has been shown to consume > 90% of eggs in the nests of invasive smallmouth bass (*Micropterus dolomieu*) (Iguchi and Yodo 2004). Additionally, the European eel (*Anguilla anguilla*), which is native to the Netherlands and has been shown to feed on native crayfish species, is an effective predator of the invasive red swamp crayfish (*Procambarus clarkia*) (Aquiloni et al. 2010). Similarly, in the United States, high densities of native sunfish (*Lepomis* spp.) and rock bass (*Ambloplites ruspestris*) can dramatically reduce the population of invasive rusty crayfish (*Orconectes rusticus*) (Hein et al. 2006; Tetzlaff et al. 2011).

The possibility that a native predator can control an invasive fish is perhaps best developed for the common carp (*Cyprinus carpio*, hereafter "carp") (Bajer et al. 2012; 2015a). Carp's life cycle suggests that this species could be controlled by predators that target eggs, larvae and juveniles. Carp broadcast-spawn in shallow areas, where their small eggs adhere to vegetation and typically hatch in three days in 20-23 °C (Balon 1995; Swee and McCrimmon 1996). Carp employ no parental care. Newly hatched larvae are small and attach themselves to nearby vegetation, where they rely on endogenous yolk feeding for the first two to four days post-hatch (Balon 1995; Khadka and Rao 1986). As a result, carp are most vulnerable during these first few weeks of life

when they are small and defenseless. However carp have fast growth rates, 1 mm per day, and can quickly outgrow many potential predators (Phelps et al. 2008a). Studies of carp populations in North America suggest that small predatory fishes, such the bluegill, might play an important role in controlling the survival of carp eggs and larvae via predation, and may ultimately explain repeated recruitment failure of carp in many North American lakes (Bajer and Sorensen 2010; Bajer et al. 2012).

Bluegill sunfish (*Lepomis macrochirus,* hereafter "bluegill") is one of the most abundant species in lakes of temperate North America east of the Rocky Mountains. Bluegills are a relatively small, laterally-compressed centrarchid that are adept at moving throughout and feeding in vegetation (Mittelbach 1981). They are visual predators whose mouth morphology makes them proficient at foraging on small organisms such as zooplankton and invertebrates in the littoral zone (Ehlinger and Wilson 1988). Bluegills are also known to feed on fish eggs and small fish (Azuma 1992). Therefore, it is possible that bluegills might control carp recruitment through predation, a theory first postulated in systems of lakes and hypoxia-prone marshes in the Upper Mississippi River Basin (Bajer and Sorensen 2010). In these systems, carp age structures coincided with winterkill events that led to collapses of bluegill populations in shallow marshes, which carp utilized as spawning habitat (Bajer and Sorensen 2010). A follow up study by Bajer et al. (2012) showed there were high catch rates of carp recruits in systems that winterkilled but not in those that did not. Additionally, they placed carp eggs attached to yarn in bluegill dominated lakes and those that lacked bluegills (and other fish) and observed high egg mortality in the bluegill dominated lakes. Concurrently, stomach surveys showed that bluegills were the main consumers of carp eggs. Finally, Silbernagel

and Sorensen (2013) used a laboratory experiment to show that bluegills also consume carp larvae and field surveys to show that the rate with which carp eggs disappear in natural spawning areas coincided with the presence of carp eggs in bluegill diet. While extant studies provided multiple pieces of evidence that bluegills might function as biocontrol agents for the carp, this hypothesis has not been tested using a controlled experiment.

In this study, I conducted a controlled experiment in large mesocosms to directly test if bluegills could control carp recruitment through predation on their eggs and larvae. I used experimental enclosures stocked with bluegills and carp eggs in a shallow productive lake to test this hypothesis. I hypothesized that bluegills will act as a biocontrol agent and decrease the number of YOY carp remaining at the end of the summer. Results of this study could provide one of a few examples of a controlled experiment showing a native fish controlling the recruitment of an invasive fish. The results from this study may also help explain why carp become super-abundant in some systems and not in others.

Methods

Study Area

To test if bluegills can control carp recruitment through predation, I conducted a mesocosm experiment in two productive lakes during 2011-2014. Experiments in 2011 and 2012 were pilot studies conducted prior my arrival (P. G. Bajer). In 2011, the experiment was conducted in Lake Casey (45°01’ N, 93°01’ W), a 4.8 ha, 1.5 m max depth, 1.0 m average depth, productive lake located in North St. Paul, MN. This lake was

selected because it had a consistent history of carp recruitment (and winterkills) suggesting that carp eggs and larvae had adequate conditions to survive there (Bajer et al. 2012). From 2012 to 2014, experiments were conducted in Lake Staring (44°84' N, 93°45' W), a 60 ha, 4.9 m max depth, 2.5 m average depth, productive lake located in Eden Prairie, MN. Lake Staring was chosen because rapid water level changes that occur after storms in Lake Casey caused flooding of some of the enclosures. Lake Staring had similar productivity to Lake Casey and also supported a large population of carp. Conducting the experiment in productive lakes was important because carp recruitment in meso- and oligotrophic lakes may be controlled by factors other than predation (Bajer et al. 2015a).

Experimental Design

During 2011-2013, rectangular 21.0 m x 21.0 m enclosures were constructed using impermeable vinyl panels that were 1.5 m tall. Each enclosure was constructed using four panels zipped together. The enclosures were set in a row in one area of the lake near shore where water depth was less than 1.0 m. In 2014, each enclosure was made using a single panel that was 54.9 m long and 2.0 m tall, to create a 17.5 m diameter circle (Figure 1). I modified the enclosures in 2014 to prevent flooding, which prematurely ended the experiment in 2011 and 2013. During all years, a lead line was strung through the bottom of the enclosures and metal stakes were driven into the sediment 1.0 m apart to anchor the enclosures and bury the lead line 0.1 m into the sediment. The enclosures remained afloat by placing swimming noodles (0.1 m diameter) in a sleeve attached to the top of the enclosure. Enclosures were cleared of native fish using a backpack electrofishing unit and a beach seine until no fish were caught in three

consecutive passes. After establishment, enclosures were checked on a quasi-daily basis to assess their physical integrity.

Two of the four enclosures were stocked with bluegills and the other two were left fishless each year. Bluegills were collected from Fish Lake (40°09' N, 93°46'W) using trap nets and transported to Lake Casey and Staring with the help of the Minnesota DNR. The goal was to establish and maintain a relatively abundant (~150 kg/ha) population of bluegills in each enclosure that resembled bluegill densities in neighboring lakes. This was achieved by overstocking the enclosures with ~250 kg/ha of bluegills, in order to account for the initially high level of mortality from handling and predation from birds. On a quasi-daily basis, enclosures were checked for dead bluegills. Any dead bluegills that were found were measured and removed from enclosures so that I could track bluegill biomass over time. If mortality reduced the biomass below the target biomass (150 kg/ha), additional bluegills were collected from Lake Staring via boat electrofishing and transferred to the enclosures. Ten kilograms (wet weight) of vegetation were placed in the enclosure to mimic carp spawning areas and provide cover and habitat for the bluegills (in addition to stocked vegetation, local vegetation also grew rapidly in the enclosures). I allowed bluegills to acclimate in the enclosures for one week, before beginning the experiment.

To collect carp eggs, I set up an additional 20.0 m x 20.0 m mesh enclosure into which I placed ~ 300 kg of coontail (*Ceratophyllum demersum*) to provide spawning substrate for carp. Five to ten sexually mature, pre-spawning adult male and female carp were captured using boat electrofishing, injected with 0.5 ml/kg of Ovaprim (Western Chemical Inc. ©), a synthetic hormone that stimulates spawning (Brzuska and Adamek

1999) and placed in the mesh enclosure. Spawning typically occurred the next morning by which time carp eggs were present on vegetation. To determine the density of carp eggs (# of eggs/gram of vegetation) in the spawning enclosure, I collected 20 random 10-40 gram subsamples of the vegetation and counted the number of eggs. The vegetation with carp eggs was then transported into the experimental enclosures in equal amounts so that each experimental enclosure was stocked with the same number of eggs. The number of eggs varied between 120,000 and 240,000 per enclosure between years.

One month after placing the eggs in enclosures, I began backpack electrofishing surveys to assess carp recruitment in each enclosure (by that time carp fry were larger than 20 mm and outgrew bluegill predation). These surveys were conducted every third day over a two-week period. Each survey consisted of a single pass lasting ~15 minutes and all carp captured were counted, measured, fin-clipped and released. I averaged the number of carp caught from the five surveys to estimate a mean catch per unit of effort (CPUE) in each enclosure for a given year. In addition, to determine whether the majority of bluegill predation was occurring during the egg or larval stage, I collected vegetation samples two days following egg stocking (one day before they hatched). I collected ten, 10 gram vegetation samples to calculate the mean number of eggs per gram of vegetation for each enclosure. Egg sampling was conducted only during the last year of the experiment (2014) to gain additional information and inform future experiments.

Statistical analyses

The difference in egg densities between treatments two days following egg stocking could not be tested statistically due to small sample size. To determine if carp

CPUE differed significantly between treatment, year and year*treatment interaction, I used two way analysis of variance (ANOVA; $p < 0.05$). For the ANOVA, the CPUE values were ln+1 transformed to account for heteroscedasticity and catch rates that were 0, however the untransformed values are shown in the figure to more accurately display observed catch rates.

Results

In 2011 and 2013, the experiment ended prematurely due to flooding following record rainfall events after only two electrofishing surveys were collected. These two surveys were used to compute CPUE in each of the enclosures. Additionally, the flooding in 2013 damaged one bluegill enclosure and one control enclosure before any data could be collected. These enclosures were removed from the analysis. The experiment ran its full course in 2012 and 2014. In 2011(N = 2 enclosures per treatment) and 2013 (N = 1 enclosure per treatment), there were no carp captured in enclosures with bluegills (CPUE = 0), whereas the control enclosures had a CPUE of 16 (SD = 19.8; N = 2) and 14.5 (SD = NA; N = 1), respectively. In 2012, the mean catch rate of YOY carp was 14.8 (SD = 8.2; N = 2) in the control enclosure and 2.8 (SD = 2.8; N = 2) in the bluegill enclosure. In 2014, the mean catch rates were 7.9 (SD = 2.7; N = 2) in the control enclosure and 0.5 (SD = 0.7; N = 2) in the bluegill enclosure. ANOVA showed that only the treatment effect was significant (df = 1; F = 20.59; p = 0.003) with control enclosures having significantly higher carp CPUEs (untransformed; mean = 13.30; SD = 3.66; Figure 2) than bluegill enclosures (untransformed; mean = 0.825; SD = 1.34; Figure 2). The effect of year or year*treatment interaction were not significant ($p > 0.5$)

The mean egg density in the bluegill enclosure (only 2014) was ~30% lower (mean = 0.35; SD = 0.0094; N = 2; Figure 3) compared to the control enclosure (mean = 0.51; SD = 0.28; N = 2; Figure 3).

Discussion

This study provides evidence from a controlled field experiment conducted in large natural arenas that a native fish can have a significant effect on controlling the recruitment of an invasive fish. The findings from this study support the results of Bajer and Sorensen (2010) and Bajer et al. (2012), which suggested that carp are unlikely to recruit in bluegill-dominated lakes. However, unlike the findings of Bajer et al. (2012) and Silbernagel and Sorensen (2013), who suggested that bluegills control carp recruitment mainly by egg predation, my results suggest that the main effect of bluegill on carp recruitment might occur via predation during the larval stage. Although I did not examine bluegill diets, previous work has shown that bluegills can consume large numbers of carp eggs and larvae (Bajer et al. 2012; Silbernagel and Sorensen 2013), which I have visually confirmed by collecting underwater videos in the enclosures. The most significant and novel contribution of my study is that this predation on eggs and larvae can lead to a more than a ten-fold reduction in carp recruitment rates.

Bluegills are well adapted to forage on carp eggs, because their body morphology allows them to maneuver in the vegetated habitats that carp select for spawning. Bluegills have exceptional visual acuity, small, protrusible mouths and buccal suction that allows them to forage on small prey items (Hawryshyn et al. 1988; Wainwright and Richard 1995; Ferry-Graham et al. 2003; Wainwright et al. 2007). Additionally, bluegills are

known to forage on prey that reduce time spent searching and handling (Werner and Hall 1974). Therefore, carp eggs are a likely food item for bluegills, because they are in high densities in small areas, stationary, and unguarded by adult carp (King et al. 2003). Their size (~ 1 mm) also matches that of zooplankton commonly consumed by bluegills (Mittelbach 1981). Given this, it was somewhat surprising that I did not observe a larger decrease in egg densities between treatments. A possible explanation for this is that I provided coontail as spawning substrate for carp, whereas Bajer et al. (2012) used yarn, on which carp eggs were more exposed to predators. Further, following placement into the enclosures, coontails (non-rooted vegetation) were blown by the wind into one corner of the enclosures, which created a very dense patch of vegetation. Previous studies have shown that larger bluegills avoid dense vegetation and feed in open water, and that juvenile bluegills, which are frequently found in vegetation, have decreased foraging success with increasing vegetation density (Werner and Hall 1988; Gotceitas 1990). Therefore, my study may have underestimated bluegills' ability to consume carp eggs, by creating dense patches of vegetation in which bluegills were unable to effectively forage.

Following hatching, carp larvae remain vulnerable to bluegill predation for at least several days due to their small size and low predator avoidance (Smallwood and Smallwood 1931; Silbernagel and Sorensen 2013). Like many fish species, bluegill gape increases with size, which allows larger bluegills (>135 mm) to feed on larger prey items (> 20 mm) (Keast 1978). Carp larvae grow ~1 mm/day in productive environments (Phelps et al. 2008a; Chapter 3), which would suggest that larger bluegills may be able to feed on carp larvae for a few weeks. However, bluegills have been shown to forage optimally by reducing handling time and increasing net energy intake (Werner and Hall

1974). Werner (1974) showed that handling time for bluegills increases exponentially as the prey diameter reaches gape size. Given that carp larvae increase body depth (i.e. diameter) and mobility fairly rapidly throughout development, it may not be metabolically beneficial for bluegills to target large carp larvae or small fry (Vilizzi and Walker 1998). Therefore, the vulnerability of carp to bluegill predation is likely less than what would be predicted by gape alone. This may be especially true in hypereutrophic lakes where larval carp growth rates tend to be highest (Chapter 3). For that reason, bluegills might be less effective biocontrol agents in hypereutrophic lakes.

Carp recruits were captured in the bluegill enclosures, despite previous studies suggesting that carp recruitment only rarely occurs in bluegill-dominated lakes (Bajer et al. 2012; Bajer et al. 2015a). While, my study shows bluegills are adept at feeding on carp eggs and larvae, other species of native fish likely assist in controlling carp. Those species include commonly occurring larval and fry predators that might forage on juvenile carp that outgrow bluegill predation. The larval and small fry predators include black and white crappie (*Pomoxis* spp.), other sunfish species (*Lepomis* spp.), yellow perch (*Perca flavescens*), and black bullhead (*Ameiurus melas*). Whereas, northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), and walleye (*Sander vitreus*) could potentially feed on larger fry. However, following the first year or two of life, carp outgrow most aquatic predators. Additional research is required to fully understand the ability of these other fish species to assist in controlling carp recruitment.

Although bluegills are common throughout the Upper Mississippi River Basin, carp continue to be invasive in many lakes and watersheds throughout the region due to the high propensity of some shallow lakes and marshes to winterkill. Carp are highly

mobile and are able to avoid the predation pressure of bluegills by moving to outlying wetlands and marshes, which may, at least occasionally, lack bluegills (Bajer et al. 2012). Marshes in this region periodically winterkill, which creates a predator-free spawning habitat that carp can exploit (Bajer and Sorensen 2010; Bajer et al. 2012). Bluegills are particularly sensitive to hypoxia and perish when oxygen concentrations decrease below 1.5-2.0 mg/L (Cooper and Washburn 1949; Petrosky and Magnuson 1973; Rahel 1984). As a result, sporadic but strong year classes that coincide with winterkills often drive carp populations in this region. Nonetheless, because bluegills (and other fish) are able to control carp recruitment in most lakes and recruitment may occur infrequently and only in external hypoxia-prone marshes. Many populations of carp could be controlled using sustainable approaches that target the adults, such as removal of carp winter aggregations with seine nets (Lechelt and Bajer 2016).

Increasing the abundance of the natural enemy is an important tenant of conservation biocontrol (Eilenberg et al. 2001). In agriculture, this can consist of providing additional food plants or artificial food sprays, overwinter shelter, and planting vegetation that attracts natural enemies, all of which can increase the abundance, diversity, and fitness of the natural arthropod community (Jonsson et al. 2008). Creating or improving spawning habitat for bluegills might be used to increase their abundance. Bluegills prefer to spawn on hard, gravel substrate and may not be able to reach high densities in lakes with soft, mucky bottoms (Gosch et al. 2006). Merz et al. (2004) showed that improving spawning habitat for salmonids by adding gravel increased embryo survival. Adding gravel to the littoral zone could increase the number of suitable nesting sites and increase bluegill recruitment (Gosch et al. 2006). Installing aerators in

winterkill-prone marshes that carp exploit for spawning might also minimize the occurrence of winterkills and stabilize bluegill populations in many systems. While increasing and stabilizing populations of bluegills via winter aeration or other means may not be practical in many lakes, especially shallow (< 1 m) marshes and prairie lakes, such strategies could be used as a key element of carp IPMs in other locales. For example, winter aeration appeared to have been effective in curbing carp recruitment in Lake Susan (Bajer and Sorensen 2010), located in the Upper Mississippi River Basin, which eventually allowed for carp control in that system. A final option is stocking bluegills, but this approach can have unintended consequences, such as predation of resident species' eggs and larvae or increased competition for food resources, so it is generally not recommended and therefore unlikely to be sustainable. Lake managers should carefully consider local conditions and system-specific nuances of carp life history, such as migrations to specific marshes to spawn but not to others, before implementing schemes to control carp populations via biocontrol.

Figures

Figure 1

Photo of the experimental enclosures installed in Lake Staring during the spring of 2014. Carp spawning area (net enclosure) in the distance.

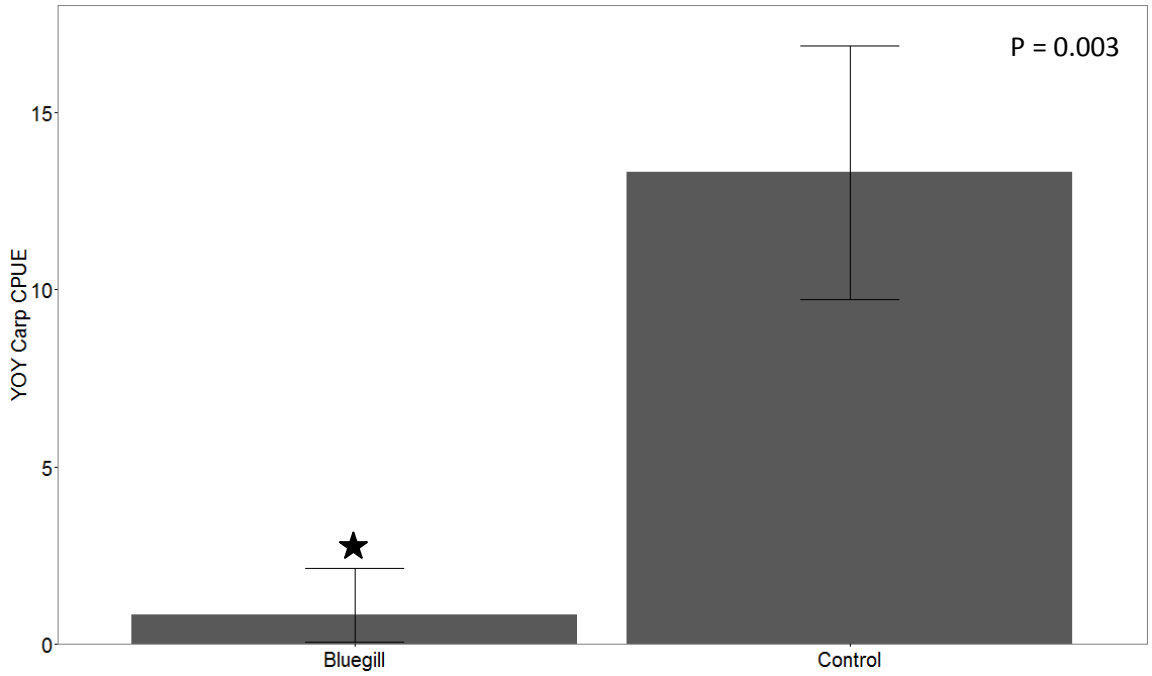

Figure 2

Mean CPUE of YOY carp in bluegill and control enclosures. The error bars represent the 95% confidence interval. The CPUE was significantly lower in the bluegill enclosures than the control enclosues, as indicated by the black star (ANOVA; df = 1; F = 20.59; p = 0.003).

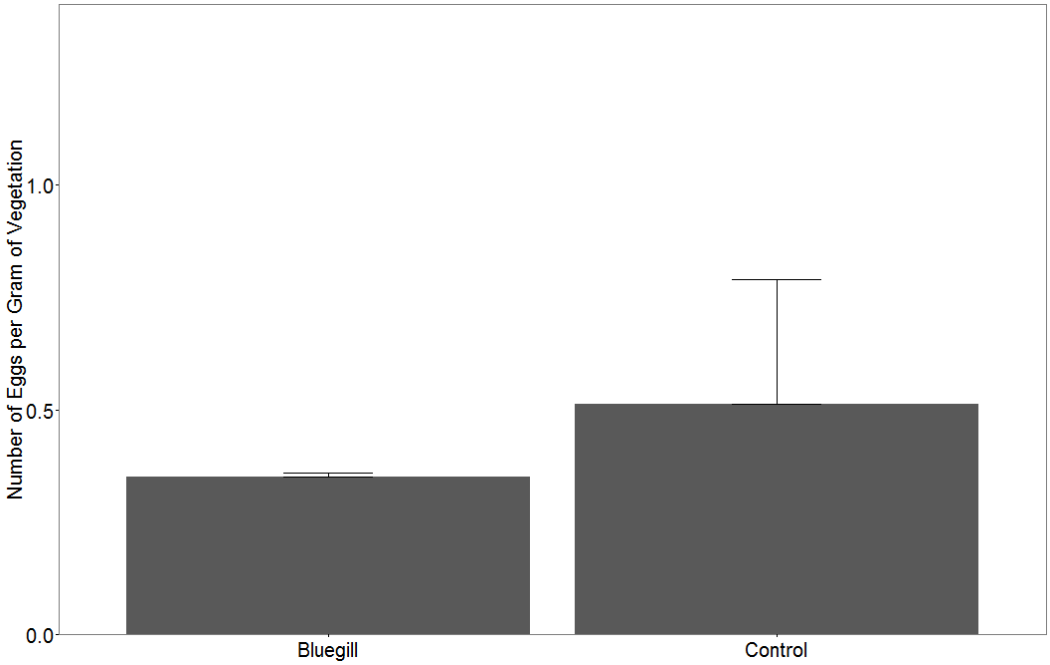

Figure 3

Mean number of eggs per gram of vegetation in bluegill and control enclosures two days after placing the eggs in the enclosures. The error bars represent the standard deviation.

Chapter 3: Effects of Natural Zooplankton Community Structure from Lakes of Different Trophic States on Larval Common Carp (*Cyprinus carpio*) Growth, Survival, and Diet Selectivity

Chapter Summary

Poor survival during the larval stage can create significant recruitment bottlenecks for invasive fish in many geographic areas. It has been shown that common carp, *Cyprinus carpio*, recruitment is primarily restricted to productive systems. A possible explanation is that productive systems have higher concentrations of zooplankton, the primary food source for larval carp, which may result in faster larval growth rates and higher survival. This study assessed how zooplankton community structure from different trophic states (oligo-, meso-, and eutrophic lakes) affected larval carp survival, growth and diet selectivity. Larval carp were cultured in aquaria and fed zooplankton (at naturally occurring densities) from three lakes of varying trophic states for 20 days. Growth rates were highest when larvae fed on zooplankton from a eutrophic lake (mean = 18.5 mm; SD = 1.2) and lowest when larvae fed on zooplankton from an oligotrophic lake (mean length = 11.7 mm; SD = 1.3). However, survival was high in all treatments regardless of trophic state. Carp larvae consistently selected for large zooplankton (0.3-0.6 mm) even though they often occurred in small abundance. The results of this study suggest that increased recruitment of carp in productive lakes might be related to fast larval growth rates in such systems that might aid in escaping gape-limited predators.

Introduction

The success of invasive fish might be affected by the ability of their larvae to overcome survival bottlenecks in areas to which they are introduced. While native predators have been shown to pose larval survival bottlenecks for invasive fishes in some geographic areas (Bajer et al. 2015a; Chapter 2), it is less know whether dietary requirements might create similar bottlenecks elsewhere. Because virtually all larval fish are zooplanktivorous, zooplankton abundance and species composition is likely to have an effect on growth and survival of invasive fish larvae. Larvae need to find, manipulate and consume prey, which can be limited by gape (Schael et al. 1991; Bremigan and Stein 1994; Devries et al. 1998), capture efficiency (Hunter 1972), or prey defense mechanisms (Swaffar and O'Brien 1996; Kolar and Wahl 1998). The size of invasive fish larvae can vary substantially among species and so do their dietary preferences, abilities to withstand starvation and escape predators. Very little information exists on the diet, growth and survival of invasive fish larvae in different types of environments to which they are being introduced but such information could increase our understanding of invasion patterns across geographic regions.

The common carp (hereafter "carp") is one of the most invasive fish in the world. The success of carp has been hypothesized to be related to ecosystem productivity through the availability of zooplankton prey for larvae. Carp tend to be abundant only in hypereutrophic waters (Kulhanek et al. 2011 a, b) and Bajer et al. (2015a) showed that carp recruitment is generally only found in productive lakes, despite the fact that adults are also commonly found spawning (although in low abundance) in meso- and oligotrophic lakes. One possible explanation for this pattern is that zooplankton

community structure and abundance in oligo or mesotrophic lakes may limit the survival of carp larvae due to starvation, nutritional deficiencies or reduced growth and associated with it increased vulnerability to predators. The hypothesis that carp larvae require highly-productive environments to successfully develop and survive is supported, although indirectly, by three pieces of evidence. First, zooplankton abundance, both microzooplankton (20-200 µm) and macrozooplankton (> 200 µm), often increases with lake productivity (Pace 1986). Further, in its native range, adult carp spawn over freshly inundated floodplains, that tend to be warm and productive (Balon 2004). Finally, in aquaculture, pond fertilization is commonly used to spike productivity and promote seasonal zooplankton blooms, which are carefully monitored to determine appropriate times to stock ponds with carp larvae to ensure dietary match (Khadka and Rao 1986).

While rarely studied in natural systems, dietary and nutritional requirements of larval carp have received much attention in the aquaculture industry (Dabrowska et al. 1979; Dabrowski et al. 1983; Geurden et al. 1995; Radunz-Neto et al. 1996; Carvalho et al. 1997; Geurden et al. 1998). It has been shown that larval carp gape is large enough to consume organisms up to 0.5 mm in length during first feeding and that feeding carp larvae a natural diet (zooplankton) is important for increasing survival and growth rates before switching to artificial diets (Dabrowski et al. 1983). It has also been shown that carp larvae can survive up to a week without food (Geurden et al. 1995; Geurden et al. 1998; Fontagne et al. 1999). Dabrowski (1984) described ontogenetic shifts in the morphology and physiology of larval carp's digestive tract and the activity of associated digestive enzymes during the first month of life, which likely coincides with an important shift in dietary preferences during this time. While much of the aquaculture work has

focused on creating artificial larval carp diets to reduce the reliance on natural food sources, there has been very little research on larval carp diets in natural environments. It is generally not known what food items carp larvae select in natural environments, the plasticity of their diets, and how naturally occurring differences in zooplankton abundance in different geographic areas might affect larval diet, growth and survival.

In this study, I used a controlled laboratory experiment to test how naturally occurring zooplankton communities in eutrophic, mesotrophic, and oligotrophic lakes, found within a region in which carp show pronounced regional differences in abundance, impact larval carp diet selectivity, survival and growth. I hypothesized that carp larvae feeding on zooplankton from oligotrophic lakes would have the lowest survival and the slowest growth rate, while larvae feeding on zooplankton from eutrophic lakes would have the fastest growth and highest survival. Additionally, I examined early larval carp diet selectivity, whether a shift in diet selectivity occurs throughout development, and whether carp larvae maintain the same dietary preferences if exposed to different zooplankton communities from different lakes.

Methods

Study Lakes

I collected zooplankton from three lakes located in the Upper Mississippi River Basin near Minneapolis, Minnesota, USA, a region where carp shows pronounced differences in abundance and recruitment among lakes of different ecoregions (Bajer et al. 2015a). Each year (2014 and 2015) my goal was to sample the same set of three lakes comprised of one eutrophic, one mesotrophic, and one oligotrophic lake. I defined a

lake's trophic state by calculating the Trophic State Index (TSI), which is used to determine the trophic state of a lake on a scale from 1-100 (eutrophic: TSI > 50; mesotrophic: TSI 40-50; oligotrophic TSI < 40; Carlson and Simpson 1996). TSI was calculated from the mean 10 year summer (June to September) secchi depth in meters (Carlson 1977; Minnesota Pollution Control Agency). The eutrophic lake was Lake Staring (44°84' N, 93°45' W), a 60 ha, 4.9 m max depth lake, TSI of 70.0, located in Eden Prairie, MN. The mesotrophic lake was Lake Ann (44°87' N, 93°56' W), a 47 ha, 13.7 m max depth, TSI of 46.0, located in Chanhassen, MN. The oligotrophic lake was represented by Courthouse Lake (44°79' N, 93°59' W), a 4 ha, 17.4 m max depth, TSI of 39.8, located in Chaska, MN. Total phosphorus concentrations (mean May-September epilimnetic values over the last 10 years) over ranged from 17 µg/L in Courthouse Lake to 23 µg/L in Lake Ann and 111 µg/L in Lake Staring (Minnesota Pollution Control Agency). I collected samples from the oligotrophic lake only in 2015, because our first choice oligotrophic system (Christmas Lake (44°90' N, 93°54' W); TSI of 34.0) became infested with and treated for zebra mussels (*Dreissena polymorpha*) shortly before sampling began in 2014, and we did not secure water collection permits to collect water from another oligotrophic lake during that year. For the remainder of this chapter these treatments will be referred to by their trophic state and year: Courthouse 2015 = "Oligo 2015"; Ann 2014 = "Meso 2014", Ann 2015 = "Meso 2015". Staring 2014 = "Eu 2014"; and Staring 2015 = "Eu 2015".

Experimental tanks and conditions

To test if lake productivity and its associated zooplankton communities impacted larval carp growth, survival and diet, I set up aquaria in a controlled environment, under 12 hour ambient light conditions, which I supplied with zooplankton from the three study lakes on a daily basis. Each aquarium was equipped with an air stone, and each was subject to a daily water exchange (see below); to increase control over zooplankton densities, the aquaria were not set as flow-through systems.

In 2014, I established 18, 18-L aquaria in a block design to achieve six replicates per treatment: two treatment lakes (Eu 2014and Meso 2014) and one control (well water). The tanks were initially filled with well water. Carp eggs were collected with vegetation from a carp spawning area in Lake Staring on 6/24/14, transported to the laboratory and put in an aerated holding tank. I stocked 18 fertilized eggs (1 egg/L) in each aquarium on 6/26/14 (clear eggs with larvae's eyes visible). The eggs were stocked one by one on small fragments of vegetation to which they were attached. The larvae hatched one day after placing them in the aquaria and were monitored (without feeding) for the next two days while they continued to absorb their yolk sacs and rested on tank walls. The first feeding with zooplankton collected from our study lakes occurred on 6/30/14 once yolk reserves were absorbed and larvae were actively swimming throughout the tanks, which marked the beginning of the 20 day experiment. The larvae were fed daily while temperature and dissolved oxygen were also recorded daily. Temperature ranged between 25.6-20.9° C; average 22.8° C, and dissolved oxygen ranged between 5.45-7.23 mg/L; average 6.64 mg/L.

In 2015, I established 18 aquaria in a block design with six replicates per treatment (Eu 2015, Meso 2015, and Oligo 2015). I omitted the well-water control in agreement with animal care protocols and also because mortality rates from the control aquaria in 2014 were consistent with previous studies for carp larvae deprived of food (Geurden et al. 1995; Geurden et al. 1998; Fontagne et al. 1999). Carp eggs were collected from Lake Staring on 5/17/15 and transported to the laboratory. On 5/18/15, 24 fertilized eggs were added to each aquarium (1.27 eggs/L). I stocked an additional 6 eggs in each aquarium to collect more larval carp samples on the first and third day after feeding to increase data resolution, which is lacking in the literature and which I determined to be particularly important in light of the 2014 experiment. One tank in Eu 2015 was accidentally understocked by 5 larvae and was excluded from the survival and growth analysis but used for diet selectivity analysis. The eggs began to hatch on 5/19/15 and the larvae were once again given two days to feed on their yolk reserves. Feeding began on 5/22/15 and the experiment ran for 20 days. Mean daily water temperatures ranged from 18.8-29.1° C, matching ambient conditions, with an average temperature of 23.7° C. The temperatures remained near the mean, except for a two day period 5/27/15-5/28/15 where outdoor temperatures approached 35° C. Dissolved oxygen in the aquaria ranged between 6.04-8.52 mg/L.

Zooplankton Collection and aquaria water exchange

I collected the zooplankton from the littoral zone (carp spawn in the littoral) in each lake using a WILDCO® Wisconsin Plankton sampler with 20-µm mesh size. I took 12 bottom-to-surface vertical zooplankton tows (four tows at three different sites) from

each lake from areas that were ~1 m in depth. The 12 tows, which filtered 147.19 L of water from each lake, were concentrated to 1 L and transferred to the laboratory within one hour of sampling to ensure that plankton did not perish in transport. In the laboratory, the 1 L samples were diluted in 36.85 L of aerated well water to create zooplankton stock. At this point, the zooplankton were 3.8 times more concentrated than in the lake. The previous day's water was then carefully siphoned out of each aquarium until ~2 L of water remained; carp larvae remained in the tank throughout the water exchange process. The aquaria were then refilled with well water to a volume of 13.93 L to which I added 5 L of the concentrated zooplankton stock. By doing so, I added zooplankton to each aquarium at a density equal to that in the lake. We chose to concentrate zooplankton from each lake and dilute them with well water rather than transport undiluted lake water to ensure that my results were attributable to differences in zooplankton communities rather than differences in water chemistry among the lakes. Zooplankton samples and water exchanges were conducted daily throughout the experiments.

To analyze the differences in zooplankton density and community structure in each lake, I collected a 1 L subsample of the concentrated zooplankton stock daily from each lake and strained it through the Wisconsin Plankton sampler (20 µm mesh size) to a volume of 50 mL. I then fixed these 50mL samples with ethanol and concentrated them further to 10 mL. A 1 mL aliquot of the concentrated 10 mL sample was placed in a 20 x 50 grid counting well (Pyser-SGI S52 Sedgewick Rafter Counting Chamber). These samples were counted under a microscope using 40 x magnification. Rotifers were identified to the phylum (*Rotifera*), cladocera were identified to the family or genus

(*Bosmina* spp., *Daphnia* spp., *Ceriodaphnia* spp., *Chydoridae, Leptodora* spp., *Sididae*), and *Copepoda* were identified as either nauplia or adults. *Annelida*, such as segmented worms, were also noted. *Leptodora* spp., *Sididae*, and *Annelida* were combined into the "other" category, because they were rarely found in the samples. All cells on the slide were examined except when counting rotifers, in which only the first 5 columns were counted because rotifers were present in very high densities. A subset of zooplankton (~5 per day per treatment) were also measured, so the groups could be classified into size classes following Pace (1986): macrozooplankton > 200 µm (*Bosmina* spp., *Daphnia* spp., *Ceriodaphnia* spp., *Chydoridae, Leptodora* spp., *Sididae* and adult *Copepoda*) and microzooplankton < 200 µm (*Rotifera* and *Copepoda* nauplia).

Larval sampling

In 2014, two random larvae were sacrificed from each tank on days 1, 3, 10, and all larvae were sacrificed on day 20 (last day of the experiment). In 2015, to increase the resolution of early larval diet selectivity, which is lacking in the literature, I sacrificed four larvae from each aquarium on days 1 and 3. I then sacrificed two larvae per aquarium on days 6 and 10, and all larvae on day 20. I added sampling on day 6 in 2015, because visually larval size began to differentiate between treatments on this day. All larvae were collected one hour after feeding. Collected larvae were euthanized in MS-222 (Western Chemical Inc. ©) and placed in a plastic vial with 50% ethanol solution. Larvae from each tank were placed in separate vials in 2015, but were combined by treatment in 2014. At the completion of the experiment, the larvae were measured for length (after accounting for ethanol shrinkage; Appendix 1) to the nearest 0.01 mm, using a digital micrometer, weighed (after accounting for ethanol shrinkage; Appendix 1) to

the nearest 0.1 mg and analyzed for stomach content. In 2015, photographs were taken of the larvae to highlight the differences in growth and development between treatments. In addition to collecting larvae for growth and diet analyses, I visually inspected all tanks for dead larvae daily to determine mortality rates. The dead larvae were collected and placed in separate vials with 50% ethanol.

To determine larval stomach contents, I followed the protocol outlined in Chick and Van Den Avyle (1999). Intestines (carp lack a true stomach) were extracted from the larvae under 40 x magnification using a dissecting scope. The contents of the intestines were teased out using a pig's eyelash or deer's hair. Samples were then preserved using lacto-phenol aniline blue (Thermo Scientific™ Remel™), which stained the zooplankton and other prey items making them easier to identify. Prey were identified and measured to the nearest 0.1 μm using an ocular micrometer under 100 x magnification. Zooplankton lengths were transformed to dry weight using published equations (*Rotifera*-Dumont et al. 1975; *Chydoridae*-Lemke and Benke 2004; *Copepoda, Bosmina* spp., *Daphnia* spp., *Ceriodaphnia* spp.-Watkins et al. 2011). These prey items were also classified into the micro- and macrozooplankton categories defined above. Approximately one third of larger prey items, primarily *Daphnia* spp., were too damaged to be accurately measured, in which case their lengths were assumed to equal the mean for that particular prey category in a given sample.

Statistical analyses

For zooplankton abundance and larval carp diet analyses, I first calculated zooplankton density and composition for each treatment (i.e. lake) and sampling day.

Zooplankton consumed by carp larvae (by number, weight and length frequency) were also identified from each sampling day and treatment. Diet selectivity (*I*) was determined using Ivlev's (1961) index: $I = (r_i - p_i) / (r_i + p_i)$, where r_i is the proportion of prey items in the fish's stomach and p_i is the proportion of prey items in the water.

Survival data for each tank were analyzed using the *survival* package (Therneau 2015) in R (R Development Core Team 2015). Kaplan-Meier survival curves were created for each treatment and plotted with 95% confidence intervals. To compare survival between treatments, final day survival estimates from the Kaplan-Meier analysis were compared using a one way analysis of variance (ANOVA). Tukey's multiple comparison was then used to determine significant differences between individual treatments ($p < 0.05$). A single ANOVA was conducted for all treatments and years combined because large differences in zooplankton abundance occurred among lakes and years, and grouping lakes by their trophic status (oligo-, meso- and eutrophic) to conduct a two-way ANOVA (trophic status and year) was not biologically meaningful.

To test for differences in larval growth between treatments, larval weights and lengths were compared on the final day of the experiment (day 20) using a one way ANOVA followed by Tukey's multiple comparison test ($p < 0.05$).

Results

The density of microzooplankton, specifically rotifers, was greater than the density of macrozooplankton for all treatments and ranged between 692.29 and 4784.14 individuals per liter (Figure 1; Table 1). The density of rotifers was highest in the eutrophic lake followed by the mesotrophic and oligotrophic lakes (Table 1). The mean

concentration of macrozooplankton, ranged between 30 and 100 individuals per liter in all lakes and years, but was markedly higher in Eu 2015 when it exceeded 200 individuals per liter (Figure 1, 2; Table 1). Macrozooplankton was comprised primarily of *Bosmina* spp., *Daphnia* spp., and adult *Copepoda* (Figure 2; Table 1).

The total number and mass of prey items consumed by larval carp was distinctly higher in Eu 2015 than all other treatments (Figure 3). Whereas *Bosmina* spp., *Chydoridae*, and *Rotifera* were abundant numerically, *Bosmina* spp., *Daphnia* spp., *Ceriodaphnia* spp., and adult *Copepoda* comprised most of the consumed food by mass (Figure 3). A histogram of zooplankton lengths showed that, even during the first and third day of exogenous feeding, most zooplankton in the stomachs of larvae were macrozooplankton (Figure 4): Day 1 mean length = 371.50 µm (quartile 1 = 288.00 µm, quartile 3 = 436.00 µm) and Day 3 mean length = 425.30 µm (quartile 1 = 308.00 µm, quartile 3 = 496.00 µm). Although infrequent, larvae could consume prey as large as 0.95 mm on the first day and 1.25 mm on third day of endogenous feeding (Figure 4). The number of prey items and composition of prey were consistent among individual larvae within each treatment and day (Appendix 2).

Selectivity values suggested that in all treatments, microzooplankton were avoided (Figure 5), whereas macrozooplankton were selected, except for the first day in Eu 2014 when macrozooplankton were very scarce and not selected (Figure 5). The patterns in selectivity of specific zooplankton organisms were relatively consistent among treatments (Figure 6). Excluding Eu 2014, whenever *Bosmina* spp. were present they were generally selected for, especially on days 1 and 3 (Figure 6). Selection of *Daphnia* spp. and *Copepoda* adults increased on days 6 and 10 (Figure 6).

Larval survival differed significantly among treatments (ANOVA, df = 4, F = 25.02, $p < 0.0001$). Survival was highest in Eu 2015, but was not significantly higher than Oligo 2015 and Meso (2014, 2015) (Figure 7), Eu 2014 was significantly lower than all other treatments due to unexpected die-offs of all larvae in four tanks on days 9 to 12. All larvae perished in the control treatment by day 7 of the experiment (Figure 7).

Final day lengths were significantly different between treatments (ANOVA, df = 4, F = 186.7, $p < 0.0001$). Final day lengths were highest in Eu 2015 (Figure 8). Final day lengths were smallest for Oligo 2015, but did not significantly differ from Meso 2014 (Tukey $P < 0.05$; Figure 8). Meso 2015 and Eu 2014 had intermediate final day lengths (Tukey $P < 0.05$; Figure 8). Final day weights followed a similar pattern with Eu 2015 being the largest, Oligo 2015 the smallest, and all other treatments having intermediate values (Figure 8, 9; Tukey $P < 0.05$).

Discussion

I explored how zooplankton communities from lakes of different trophic states impacted larval carp survival, growth, and diet selectivity. Specifically, I tested the hypothesis that carp recruitment, which tends to occur predominantly in eutrophic systems, might be driven by nutritional deficiencies that carp larvae might face in oligotrophic lakes where zooplankton concentrations tend to be lowest (Pace 1986; Bajer et al. 2015a). My results partially support this hypothesis in that growth was slowest in larvae fed zooplankton from the oligotrophic lake, and highest in larvae fed zooplankton from the eutrophic lake. However, survival was relatively high in all treatments including the oligotrophic system. Although the experiments were relatively short and did not

address potential long-term effects of malnutrition, it suggests that recruitment of carp in oligotrophic systems is more likely to be reduced by slow larval growth rates, which likely increases their vulnerability to predators, but it is less likely to be caused by larval mortality due to starvation.

Slower growing carp larvae might spend more time foraging and be less agile, which might increase their risk of predation as has also been shown in juvenile yellow perch (*Perca flavescens*; Post and Prankevicius 1987). Additionally, carp larvae might spend more time foraging in low prey density environments, which might further increase their searching time and vulnerability to predators (Norberg 1977; Munk 1995; Puvanendran and Brown 1999). In northern temperate regions, rapid growth rates are often essential to gain enough resources to survive the winter (Sogard 1997). Sogard (1997) showed that small size classes of many temperate species including walleyes (*Sander vitreus*), bluegill sunfish (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and yellow perch were at a greater risk for overwinter mortality. This is likely a result of smaller fish having low energy reserves and suffering from starvation over the winter (Oliver et al. 1979). While this may be important in some instances, Bajer et al. (2015a) showed that carp recruitment failure occurs before winter and must therefore result from processes that take place in the first spring, summer and fall.

This study provides the first evidence of the number of prey items and diet selectivity of larval carp during first exogenous feeding when fed zooplankton from natural lakes of different trophic states. Larval carp showed preference for macrozooplankton such as *Bosmina* spp., *Daphnia* spp., or *Chydoridae*, even though these organisms were often in relatively low abundance. These results are consistent with

Dabrowski et al. (1983), who suggested that larval carp can consume particles sizes of 0.5 mm as first food. Although infrequent, I documented that prey items up to 0.95 mm can be consumed. While *Bosmina* spp. were consumed throughout the experiment, larval carp began selecting for larger prey as they grew, primarily *Daphnia* spp. and adult *Copepoda* that ranged in size from 0.40 to 1.50 mm. A similar pattern was shown in an experiment where the sizes of available prey items were artificially manipulated (Khadka and Rao 1986). Carp larvae avoided rotifers even in treatments where macrozooplankton were scarce. This was surprising given that rotifers were abundant and their size allowed for their easy consumption. However, many zooplanktivorous fish exhibit size selectivity, avoiding certain prey sizes, and foraging behavior is generally determined by search time, handling time, and net energy gain (Werner and Hall 1974; Eggers 1977; Drenner et al. 1978; Bremigan and Stein 1994; Nandini and Sarma 2000). My results suggest that rotifers either do not offer high nutritional value for carp or are not recognized as edible, but the mechanisms behind larval carp food recognition remain largely unknown. While this study provides new information on diet selectivity of carp larvae, it is potentially hindered by the constraints of laboratory conditions. Zooplankton I collected and transported to the laboratory might not have been fully representative of the lake community. Further, my design could not account for patchy zooplankton distribution and its vertical and horizontal diel movement patterns that often occur in lakes. Future research is required to enhance the understanding of larval carp diet selectivity in natural settings.

Even in lakes that have reoccurring carp recruitment, the strength of recruitment can vary among years (Phelps 2006). A possible explanation is that zooplankton

communities fluctuate throughout time within individual lakes (McCauley and Murdoch 1987). Results from my study, and specifically those from Eu (2014 and 2015), suggest these fluctuations might impact larval growth and survival. The experiment in Eu 2014 was conducted ~5 weeks later in the season than the experiment in Eu 2015. The concentration of macrozooplankton was much lower in Eu 2014 than in Eu 2015, possibly due to the seasonal pattern of large zooplankton (*Daphnia* spp. and *Bosmina* spp.) abundance that tends to decline in June and July (Threlkeld 1979; DeMott and Kerfoot 1982). The 2014 experiment was conducted towards the end of carp spawning season when the eutrophic lake was already dominated by algal blooms. The experiment in 2015 began at the beginning of the spawning season (in May) during the clear-water phase when the densities of large zooplankton are often highest. The timing of carp spawning in relation to the blooms of large-bodied zooplankton might explain inter-annual variability in carp recruitment in productive lakes. Similar patterns have been shown in marine species, such as Atlantic cod (*Gadus morhua*), where a mismatch between the timing of reproduction and primary production might decrease the survival in young of year (Cushing 1990; Gotceitas et al. 1996).

Reduced ability of carp to recruit in hypereutrophic lakes (especially if spawning occurs late in the season) may also be related to shifts among primary producers caused by high nutrient concentrations. Davis et al. (2010) conducted a nutrient enrichment study in a stream and found that while increased nutrients increases the number of primary consumers, it did not extend throughout the food web. The reason being that increased nutrient loading increased the number of predator resistant primary producers, effectively halting the flow of energy (Davis et al. 2010). Increased productivity may also promote

the growth of more inedible prey items (Powers et al. 2008; Davis et al. 2010). This is often the case in hypereutrophic lakes where inedible cyanobacteria dominate phytoplankton communities in the summer, which can lead to declines in zooplankton filter feeders such as daphnia that are important prey organisms for more advanced carp larvae.

I observed complete die-offs of larvae in four aquaria in Eu 2014. These die-offs occurred on days 9-12 of the experiment. Specific explanations of these die-offs are unclear. Oxygen concentrations appeared to be high throughout the experiment, although I did not measure daily lows that typically occur before daybreak, and are likely in environments with high algal densities (high oxygen demand at night) such as the ones in Eu 2014. Additionally, these low oxygen levels may have made larvae more susceptible to disease or toxins. Also, carp larvae in this treatment had extremely poor diets and the mean number of prey found in the digestive tract of the larvae during days 1 and 3 in Eu 2014 was the lowest of all treatments. It is possible, therefore, that larval carp perished due to starvation, much like larvae in well-water controls. Interestingly, the concentration of macrozooplankton in Eu 2014 was similar to other treatments (except Eu 2015), suggesting that larval carp had difficulties capturing their prey. High densities of algae in the Eu 2014 treatment might have obstructed the visual acuity of carp larvae (Lazzaro 1987) or caused them to strike at wrong targets increasing their metabolic demands ("confusion effect"; Czesny et al. 2001). Future studies should examine the effect of algal density on the ability of carp larvae to locate and capture their prey because this might explain some of the density-dependent mechanisms in carp recruitment; e.g. carp

recruitment tends to decline in populations with high adult density, which usually coincides with degraded lakes and heavy algal blooms.

Carp recruitment has received much attention over the last decade. Identified drivers of carp recruitment include adult abundance (Weber and Brown 2013; Bajer et al. 2015b), egg and larval predator abundance (Chapter 2; Bajer et al. 2015a), and weather conditions, such as wind, during spawning season (Phelps et al. 2008b; Weber and Brown 2013). This study complements these extant studies by showing that lake productivity is likely to have a positive effect on carp recruitment via faster larval growth rate and possibly also predator avoidance. My results also suggest that the abundance of specific macrozooplankton species, such as *Bosmina* spp., might be useful in identifying environments where carp can recruit consistently. The interaction between lake productivity and predator abundance is particularly interesting. It appears that abundant populations of egg and larval predators can control carp recruitment in eutrophic lakes (Chapter 2), but it is not known if predatory control might also extend into hypereutrophic lakes where the growth rates of larval carp might be even higher. I suggest that this hypothesis should be addressed in future studies.

Tables

Table 1

The mean daily concentrations (number per L and (SD)) of zooplankton over the 20 day (N = 20) experimental period in each treatment. Bos = *Bosmina* spp., Chyd = *Chydoridae*, Dap = *Daphnia* spp., Cerio = *Ceriodaphnia* spp., Cop_a = *Copepoda* adults, and Cop_n = *Copepoda* nauplii. "Other" = *Sididae, Leptodora* spp. and *Annelida* combined.

Treatment	Bos	Chyd	Dap	Cerio	Cop_a	Cop_n	Rotifera	Macro	Micro	Other
Oligo 2015	9.4	1.1	3.2	0.4	17.2	23.0	669.4	31.3	692.3	0.1
	(8.4)	(1.6)	(4.5)	(1.0)	(14.3)	(26.8)	(518.3)	(17.7)	(522.0)	(0.3)
Meso 2014	49.7	8.1	4.5	5.7	26.8	16.9	1095.6	94.8	1112.5	2.7
	(68.9)	(11.1)	(6.6)	(8.4)	(18.7)	(18.9)	(770.3)	(87.6)	(771.5)	(1.7)
Meso 2015	4.4	8.9	4.6	0.4	17.1	11.3	766.1	35.4	777.4	0.1
	(3.5)	(10.9)	(5.7)	(1.0)	(10.5)	(11.5)	(448.2)	(16.0)	(449.2)	(0.3)
Eu 2014	1.9	5.7	14.5	0.9	24.4	25.4	4758.8	47.5	4784.1	0.9
	(2.5)	(4.9)	(10.7)	(1.6)	(17.6)	(23.3)	(2933.7)	(24.0)	(2951.0)	(0.8)
Eu 2015	163.7	8.5	41.6	5.2	17.3	28.3	1254.8	236.3	1283.1	2.7
	(127.9)	(5.8)	(23.5)	(4.7)	(13.6)	(33.2)	(773.8)	(149.2)	(792.3)	(2.4)

Figures

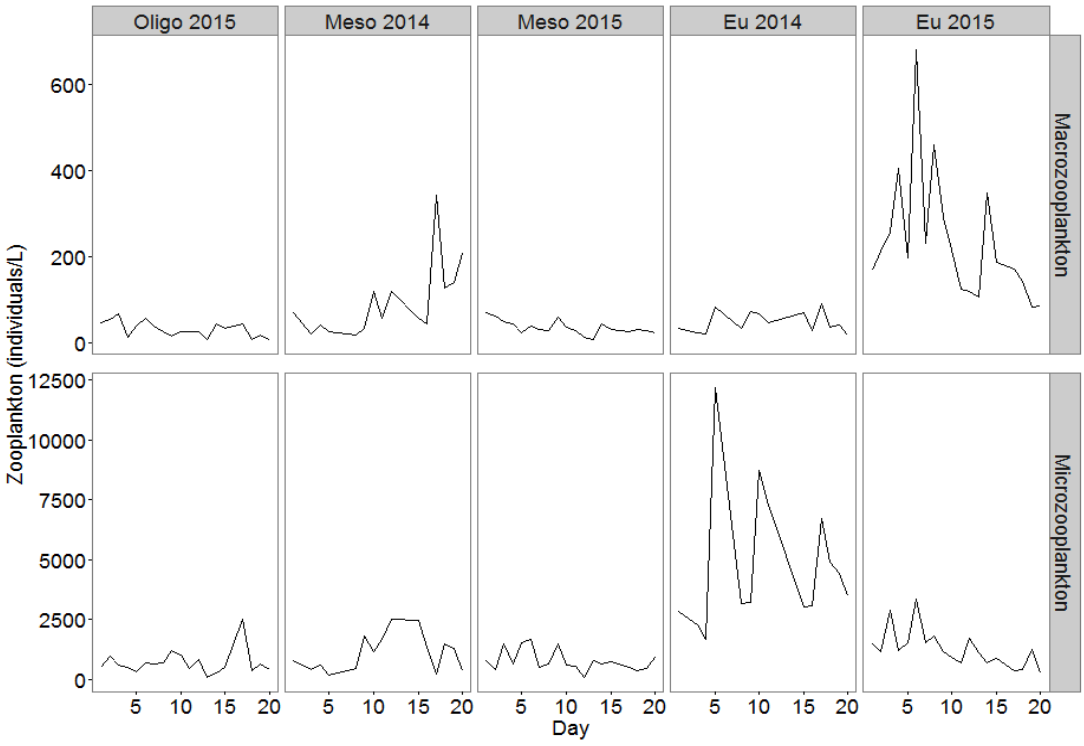

Figure 1

The concentration (individuals/L) of macrozooplankton (> 200 µm; top panels) and microzooplankton (< 200 µm, bottom panels) in the water supplied to each aquarium throughout the experiment in each treatment.

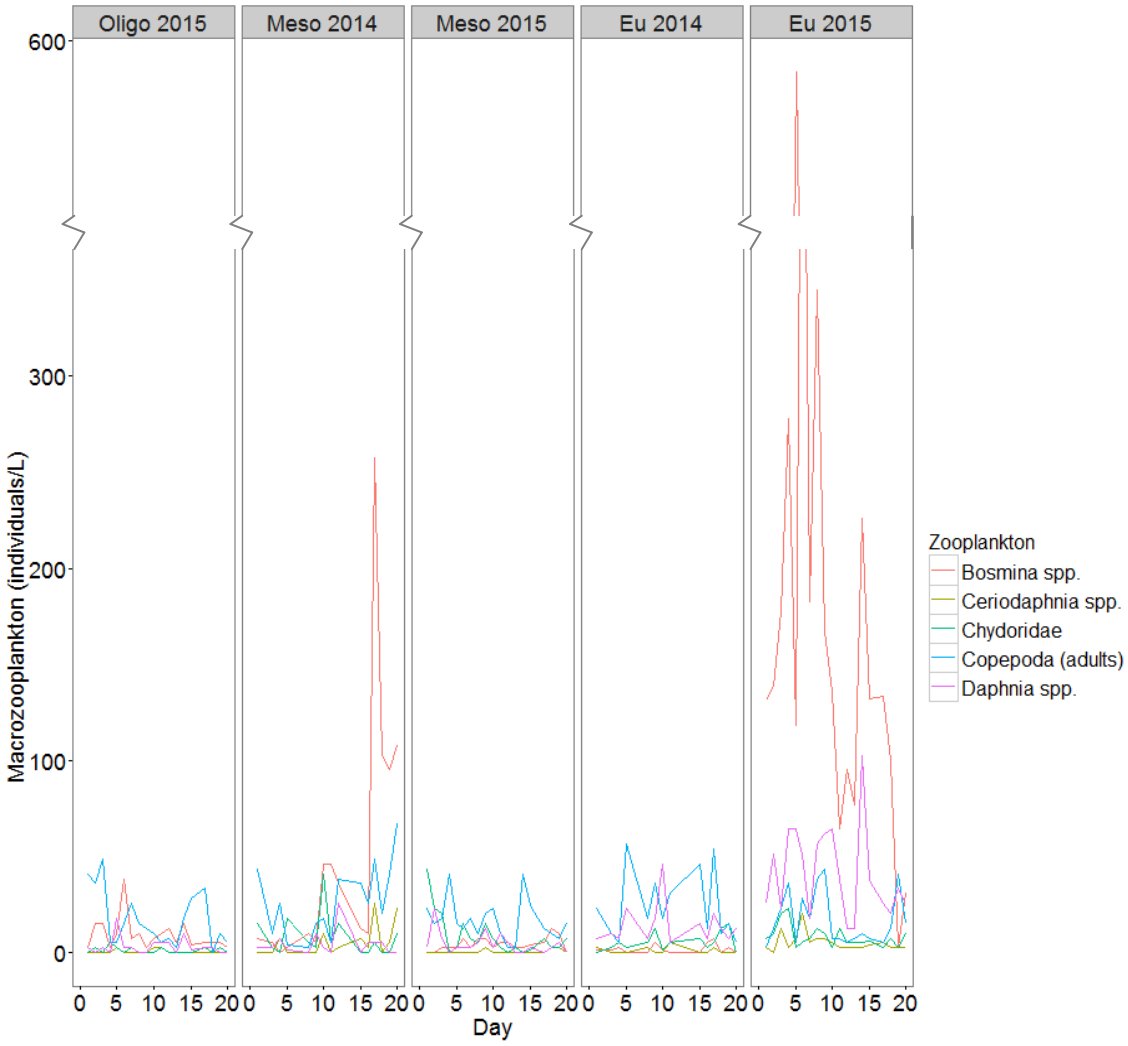

Figure 2

The concentration (individuals/L) of macrozooplankton (> 200 µm) by group in the water that was supplied to each aquarium throughout the experiment in each treatment (Note break in y-axis between 300 and 600).

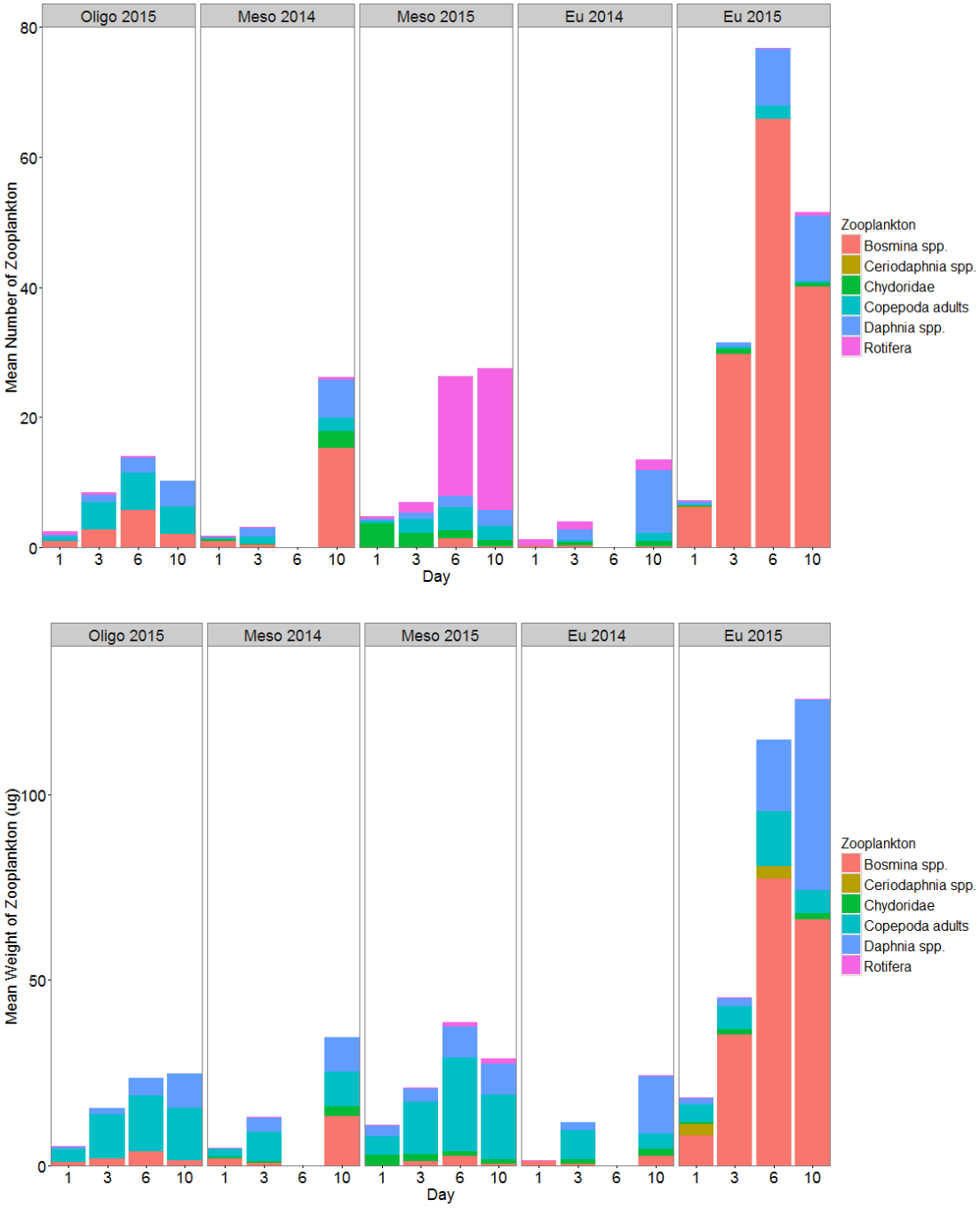

Figure 3

Mean number (top panel) and weight (µg; bottom panel) of the prey items found in the intestines of larval carp by treatment on days 1, 3, 6 and 10 in 2014 (no samples collected on day 6) and 2015.

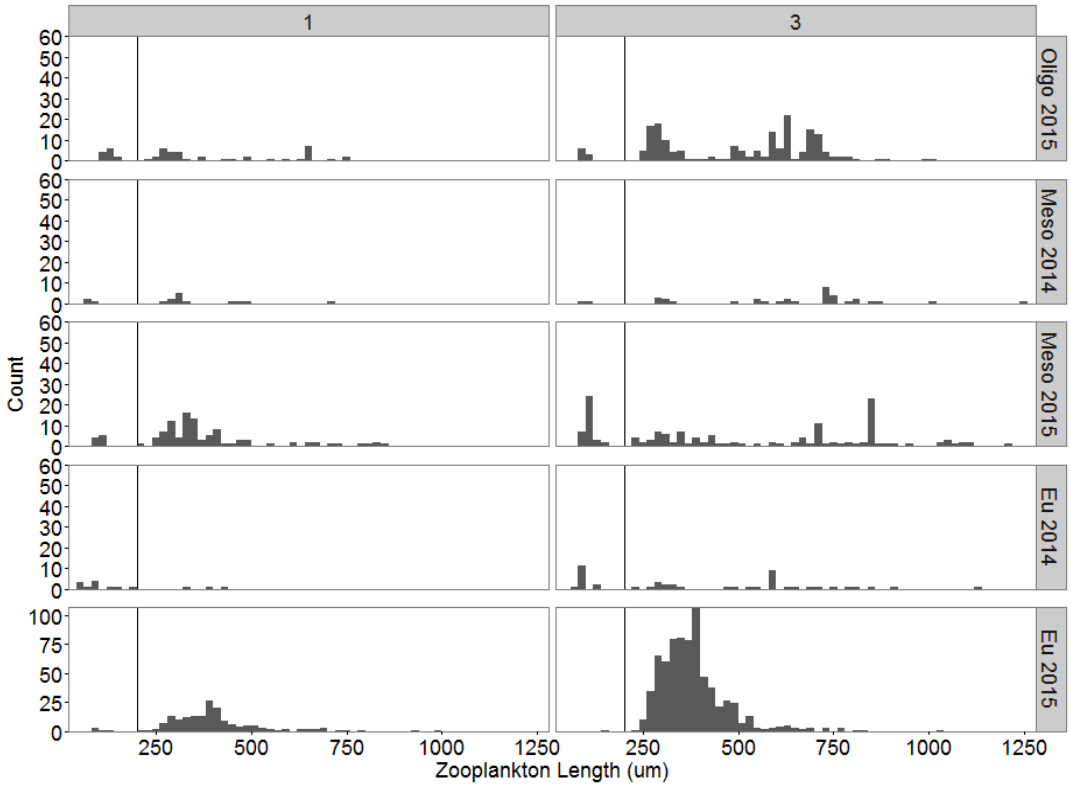

Figure 4

Length distribution of zooplankton consumed by common carp larvae on day 1 and 3 in each treatment. Shown is the cumulative number of all zooplankton items consumed by all larvae sampled on each day in each treatment (count). Vertical line represents the cut off between microzooplankton (< 200 µm) and macrozooplankton (> 200 µm). Note difference in y-axes between Eu 2015 and the rest of the treatments.

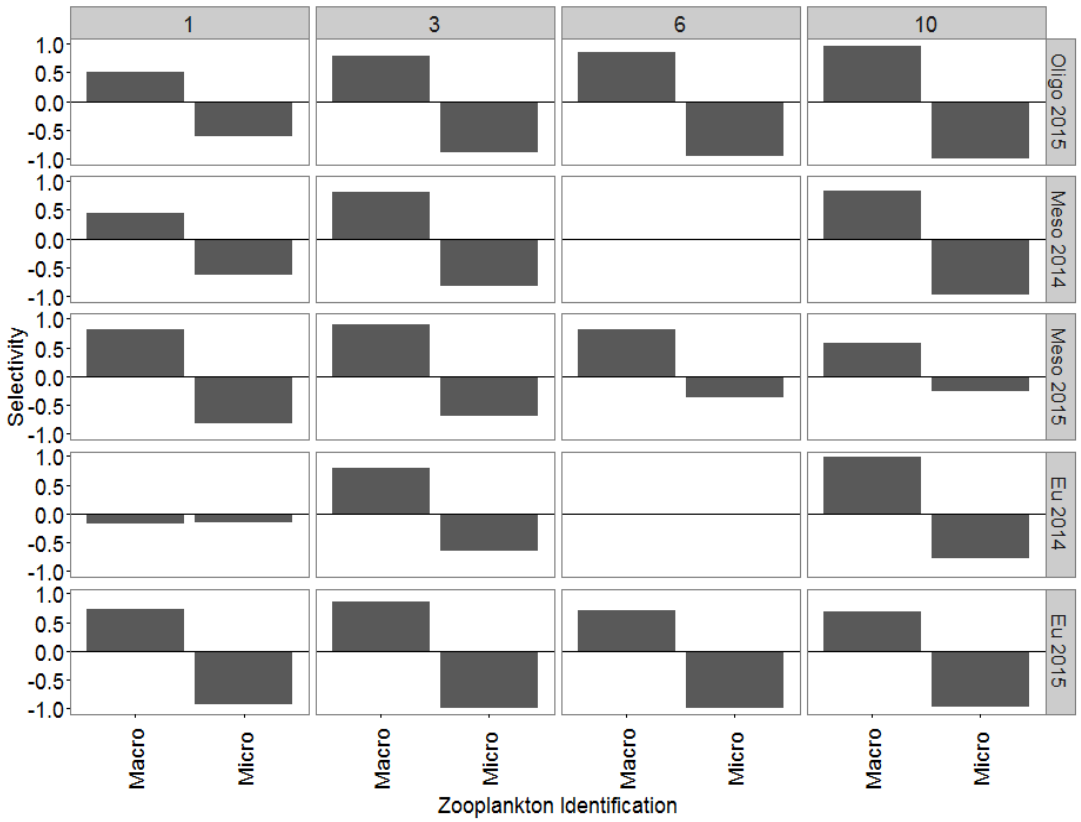

Figure 5

Ivlev's selectivity index for macrozooplankton (>200 µm) and microzooplankton (<200 µm) consumed by larval carp on day 1, 3, 6, 10 of the experiment in 2014 (no data on day 6) and 2015. Positive values show preference while negative values show avoidance. Both sizes of zooplankton were avoided in Eu 2014, because average selectivity was calculated and nearly half of the intestines were empty. The intestines that contained zooplankton were very limited in number and were not enough to elicit a positive value (Appendix 2).

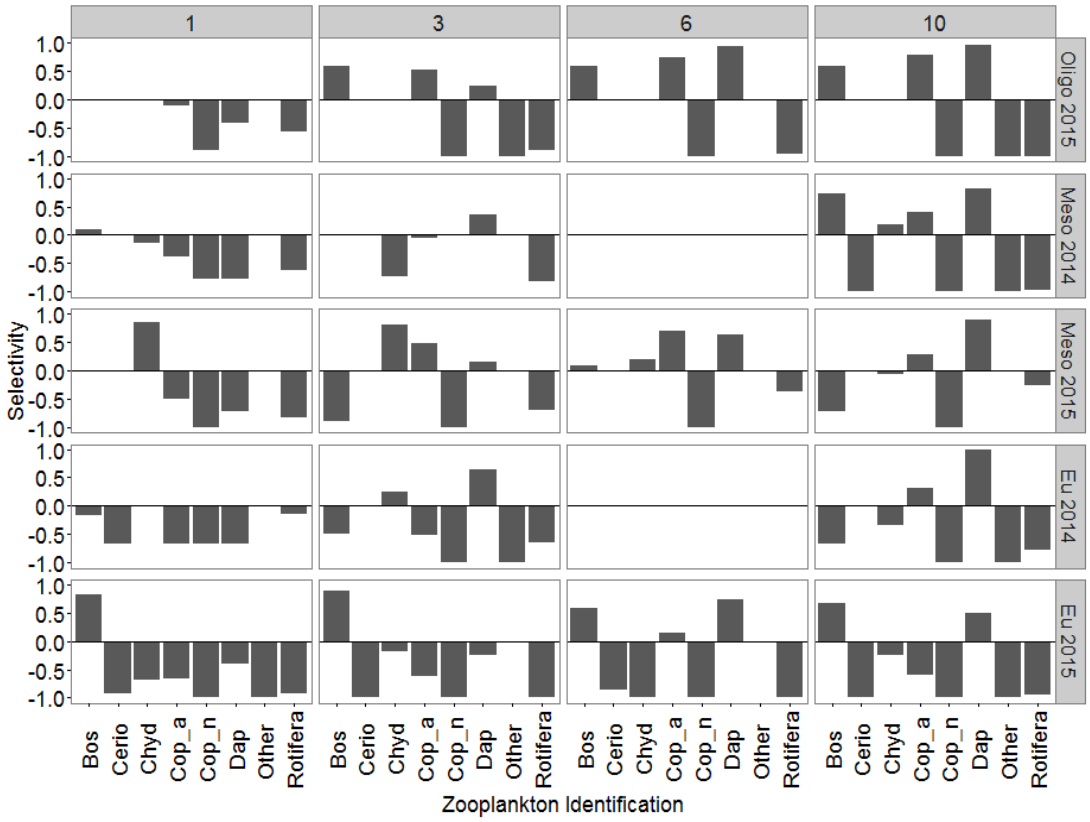

Figure 6

Ivlev's selectivity index for zooplankton consumed by larval carp on day 1, 3, 6, 10 of the experiment in 2014 (top panel; no data on day 6) and 2015 (bottom panel). Positive values show preference while negative values show avoidance. Bos = *Bosmina* spp., Cerio = *Ceriodaphnia* spp., Chyd = *Chydoridae*, Cop_a = *Copepoda* adults, Cop_n = *Copepoda* nauplii, Dap = *Daphnia* spp.

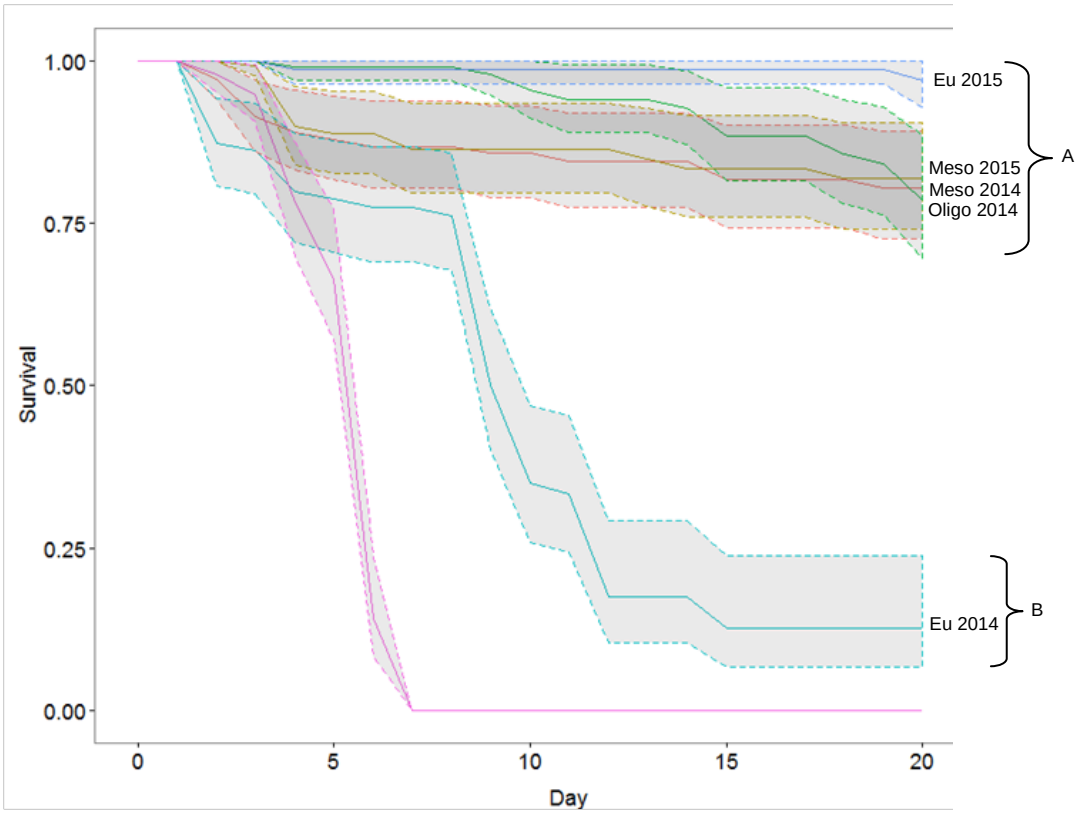

Figure 7

Mean Kaplan-Meier survival curves for common carp larvae in 2014 and 2015 treatments. The shaded areas represent the 95% confidence interval for each curve. The letters represent significant differences between final survivals (ANOVA; p = 0.05). The well water control was not used in the analysis and is only plotted for reference.

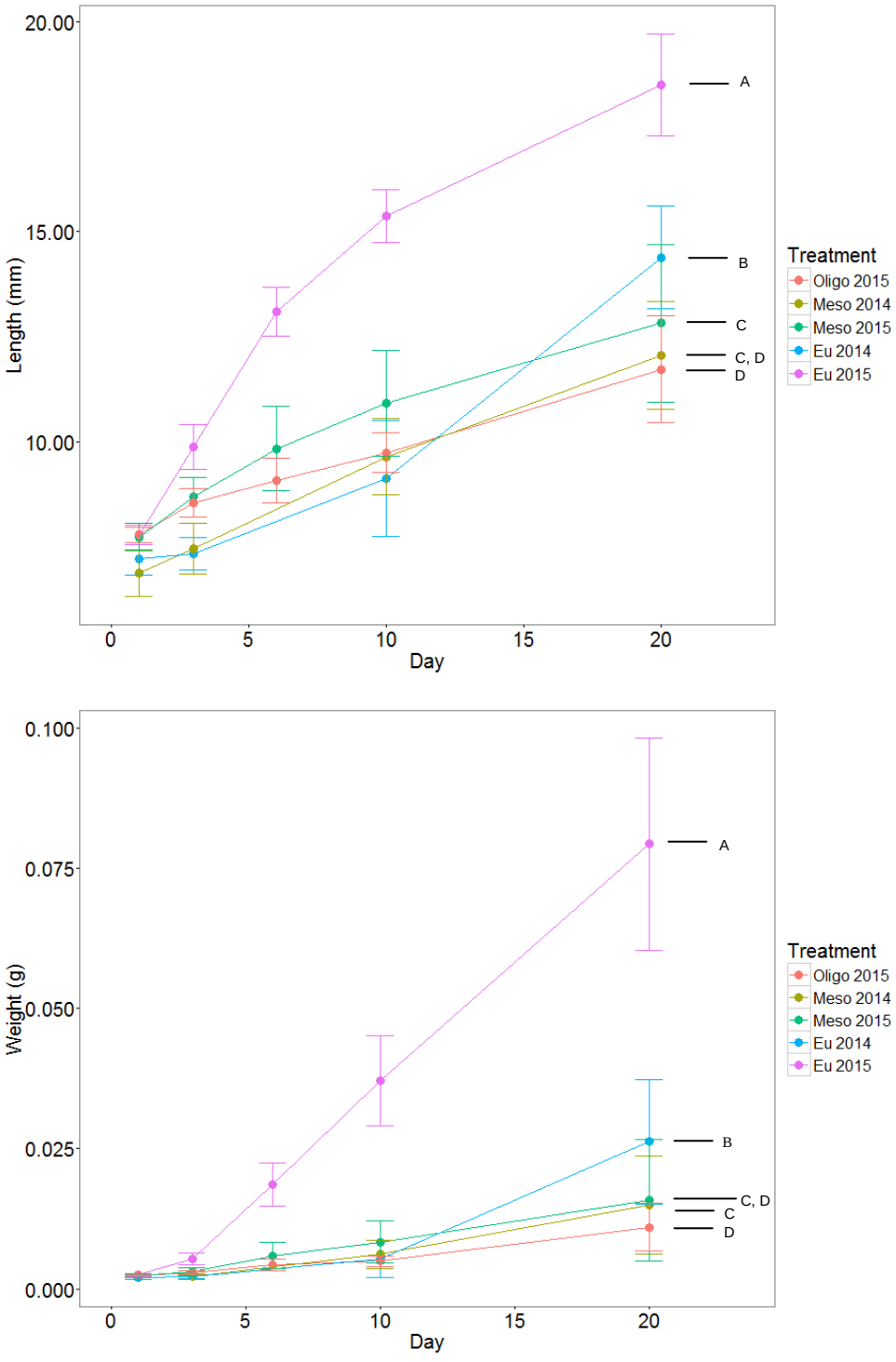

Figure 8

The mean length (top panel) in millimeters and weight (bottom panel) in grams of larval carp on days 1, 3, 6, 10, and 20 of the experiment. The error bars represent the standard deviation from the mean. Samples on day 6 were only collected for the 2015 treatments. The letters represent significant differences between final day length and weight.

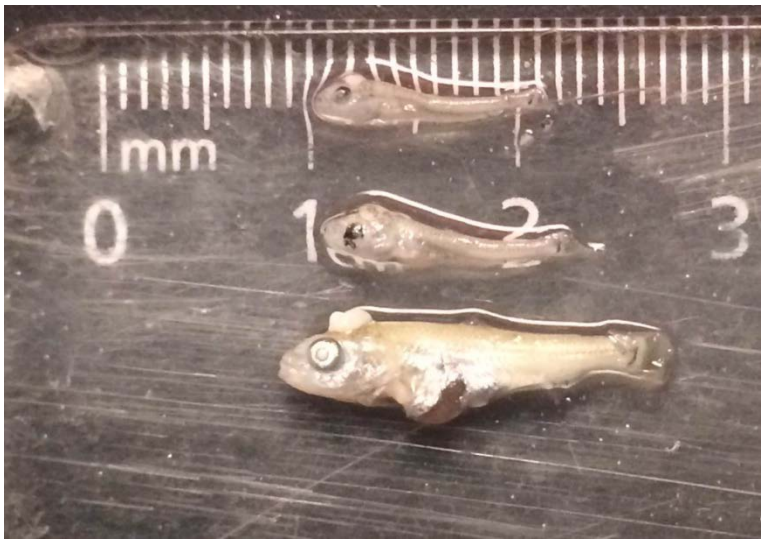

Figure 9

A photograph of carp larvae on the last day of the experiment (day 20) in 2015. The larvae represent the mean size for each treatment.

Chapter 4: Quantifying the Outmigration of Young of Year invasive Common Carp (*Cyprinus carpio*) from a Seasonally Unstable Nursery

Chapter Summary

In some populations of the invasive common carp, *Cyprinus carpio*, adults conduct spawning migrations into seasonally unstable marshes that have fewer predators and/or more food resources for the larvae. Such strategies have been shown in northern regions of the United States where winterkill-prone marshes function as carp nurseries in systems of interconnected lakes. The rates at which juveniles outmigrate from such marshes into adjacent lakes have important bearings on carp population dynamics and control, but are generally unknown. I estimated the outmigration of young of year (YOY) carp from a marsh to a downstream lake using direct and indirect approaches. I conducted trap net surveys in a lake-marsh system over a three-year period and tagged YOY carp in the marsh with passive integrated transponder (PIT) tags during two years when recruitment occurred. PIT tag antennas were placed in the stream below the marsh to record movement. Of the 468 YOY carp tagged in the marsh in 2013, the antennas detected only one, whereas 37 out of 663 were detected in 2015. Most of those fish moved in August when water level in the marsh was declining. Given these passage rates and the numbers of tagged carp in the marsh (adjusted for natural mortality), I estimated daily outmigration probability for a single YOY carp to be $4.5 \cdot 10^{-5}$ in 2013 and $1.3 \cdot 10^{-3}$ in 2015. Using ageing and mark-recapture analyses, I estimated that ~ 3,400 YOY carp moved from the marsh to the lakes in 2015, effectively doubling the lake population of carp. My results show that although only a few percent of YOY carp migrate out of the marshes in the first year, they can result in significant influxes of recruits into adjoining lakes. My estimates have important implications for common carp management in lake-marsh systems of midwestern North America.

Introduction

Many invasive fish employ spatially complex life histories in which adult individuals conduct seasonal migrations to outlying habitats to spawn. Such strategies have been shown for the common carp (*Cyprinus carpio*) in Minnesota, northern pike (*Esox lucius*) in Alaska, and the sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes (Morman et al. 1980; Bajer and Sorensen 2010; Sepulveda et al. 2013). These migrations function to exploit peripheral habitats that provide adequate spawning substrate/habitat, shelter from predators, and/or more abundant food resources for the larvae and juveniles (Clark 1950; Bajer et al. 2012). Utilization of these nursery habitats can increase recruitment success of the invader (Bajer et al. 2015b). For example, in species that employ partial migration strategies (where some but not all adults employ spawning migrations into outlying habitats), adults that migrate can disproportionally drive population abundance due to a much higher reproductive success as compared to resident individuals (Jonsson and Jonsson 1993). However, for this strategy to be successful, juveniles must outmigrate from the peripheral habitats in which they hatch to join the adult population. Juvenile outmigration rates and cues that drive them remain one of the least understood elements of population dynamics of many invasive fish that employ spatially complex life histories.

The common carp (hereafter "carp") is among the most widespread invasive fishes worldwide and it has been shown to employ partial spawning migrations in some geographic regions (Bajer and Sorensen 2010). In interconnected lake-marsh complexes of Minnesota, large numbers of adult carp migrate from lakes to outlying marshes to spawn (Bajer and Sorensen 2010). This behavior has been hypothesized to evolve in

response to heavy predation in lakes and temporary lapses in predator abundance in marshes that winterkill (Bajer et al. 2012). In those systems of lakes, winterkill-prone marshes have been suggested to be the primary source of new carp recruits (Bajer et al. 2012; Osborne 2012; Koch 2014). However, it is generally not known how many YOY carp move out of those winterkill-prone marshes and migrate to adjacent lakes, although indirect evidence (trap net surveys) suggested that outmigration rates are surprisingly low (less than 0.1%), which is lower than might be predicted from random dispersal (Bajer et al. 2015b). Verifying that YOY carp outmigration rates are low is important in developing sustainable carp management schemes that otherwise might not be possible (Lechelt and Bajer 2016). However, studies that track the movement of YOY carp out of their nurseries using direct approaches have never been conducted.

The goal of this study was to directly estimate the outmigration rate of age-0 carp from an unstable marsh to an adjacent lake from which adults initiate their spawning migrations. I used passive integrated transponders (PIT) tags and PIT antennas to directly estimate outmigration probabilities of YOY carp over a three year period, and trap net surveys to estimate relative catch and mortality rates. I also conducted ageing analysis in the recipient population to estimate the numbers of YOY carp that migrated from the marsh to the lake on an annual basis. The information from this study is important to increase the biological accuracy of existing models of carp populations in lake-marsh systems, and to inform sustainable management schemes. My results may also suggest which environmental cues drive YOY carp outmigration from marshes into lakes.

Methods

Study System

This study took place from 2013-2015 in a marsh, the Purgatory Creek Conservation Area (PCCA), and Lake Staring positioned ~1 km downstream (Figure 1). These two water bodies are located within a chain of eight lakes drained by Purgatory Creek. Purgatory Creek is a relatively small (10 m wide, 0.5 m deep) stream that experiences sudden increases in water level after storms. The stream is easily passable to YOY carp except for winters when many areas of the stream and PCCA freeze to the bottom. Because the entire chain is located within an urban area, man-made barriers, culverts and highway crossings separate Lake Staring and PCCA from the rest of the chain. PCCA (44°85' N, 93° 44' W) has a surface area of 65 ha, and a maximum depth of 1 m. It is a eutrophic system (total phosphorus > 100 µg/L) that has a history of winter hypoxia occurring ~every other year. Lake Staring (44°84' N, 93°45' W) is a 60 ha, eutrophic lake (111 µg/L total phosphorus) with a maximum depth of 4.9 m (2.5 m mean depth), and which has not winterkilled in the last ten years. At the beginning of the study (2013), Lake Staring contained ~11,000 adult carp. This population was reduced to ~3,000 individuals by 2015 using winter seining (Bajer unpublished data). Each spring, up to 90% of the adult carp migrate from Lake Staring to PCCA to spawn, before returning to Lake Staring in early summer (Bajer et al. 2015b).

Study design

This study was designed to estimate three different aspects of the outmigration of YOY carp from PCCA to Lake Staring: 1) the daily probability of a single YOY carp

outmigrating from PCCA and how it was related to abiotic conditions such as water temperature or water level, 2) the overall percentage of YOY carp that outmigrated each year, and 3) the overall number of YOY carp that outmigrated each year to Lake Staring. These analyses were conducted using a combination of trap net surveys, passive integrated transponder (PIT) tags, and ageing and mark-recapture analysis of the recipient population (Lake Staring).

Trap net surveys were conducted in PCCA and Lake Staring for three consecutive years (2013-2015) to determine the presence of YOY carp and their relative catch rates (CPUE). Trap nets were set at five locations in PCCA and in Lake Staring equidistance along the shoreline, with the exception of the western side of PCCA, which was inaccessible. Initial surveys were conducted in July. In years when YOY carp were found in PCCA (2013 and 2015), surveys were repeated at ~monthly intervals to estimate YOY carp natural mortality, which was needed to calculate daily outmigration probabilities (see below). When recruitment occurred in PCCA, additional surveys were conducted in Lake Staring to verify outmigration rates from PCCA. The trap nets had small mesh (13 mm bar), 10 m lead, 1.8 m x 0.9 m metal frame followed by three hoops. They were set in late morning and retrieved the next day. All carp were counted and measured to the nearest millimeter. YOYs were identified based on their total length (YOY carp are < 150 mm in length in the summer), which was verified by ageing using otoliths following methods in Bajer and Sorensen (2010).

All carp longer than 65 mm captured in the trap net surveys in PCCA were tagged with 12mm-HDX Passive Integrated Transponder (PIT) tags (Oregon RFID©, Portland, OR, USA) and released. Because trap net catch rates were relatively low, I conducted

supplementary beach seining and backpack electrofishing to tag additional carp in PCCA so that at least 400 were tagged each year. Tagging mortality was assessed by placing 20 tagged and untagged (control) carp in a 2 m x 2 m net pen for 48 hours. Shortly before PIT tagging began, Two PIT tag antennas were placed in Purgatory Creek 1 km downstream of PCCA (Figure 1). The antennas were placed 5 m apart to detect movement direction. The antennas were constructed of one loop of 8-gauge wire and one loop of 12-gauge wire attached to a tuning module connected to a multi-antenna HDX reader and datalogger (Oregon RFID). Detection efficiency of each antenna ranged between 85% and 100% and was assessed by tethering a tagged carp to a fishing line and allowing it to swim through the antennas twenty times both up- and downstream. Antennas were maintained from July to December. A temperature data logger (Onset® HOBO® Pendent UV-002-08) was placed near the antenna to collect water temperature data at 3 hour intervals. A meter stick was placed in the stream near the antennas to record water level at least once a week and after precipitation events.

The daily outmigration probability of YOY carp was calculated by dividing the number of PIT tagged carp detected by the antennas by the number of PIT tagged carp remaining in PCCA. These daily outmigration rates were then averaged over the entire sampling period to represent a mean for the year. The number of PIT tagged carp remaining in PCCA was calculated daily by applying a daily mortality rate, adding newly tagged carp, and subtracting carp that have moved (crossed the antennas). The daily mortality rate in PCCA was calculated by analyzing trap net catch rates (CPUE) over time. To calculate instantaneous natural mortality, Catch rates were ln(y+1) transformed (to account for zeros), a linear model was fit to the data, and the negative value of the

slope coefficient was used as the estimate (Chapman and Robson 1960). The percentage of YOY carp that outmigrated from PCCA was calculated by dividing the number of carp detected by the antennas by the number implanted with PIT tags each year.

To estimate the number of carp that recruited into the population in Lake Staring from the year class of 2013 and 2015 from PCCA, I conducted mark-recapture and ageing analyses in Lake Staring during 2014-2015. First, to estimate population abundance, 56 carp were captured using boat electrofishing, marked with fin clips and released in the summer of 2014. All of these fish were larger than 400 mm (i.e. adult carp older than the 2013 year class) thus the mark-recapture estimate is representative only of the population older than the 2013 year class. In January 2015, a winter seine was pulled in Lake Staring to collect a large sample of carp and document recapture rates. The number of adult carp in the lake was estimated using Chapman's equation (modified Lincoln-Peterson estimator). To estimate the length structure of the entire population, including year classes of 2015 and 2013, a boat electrofishing survey was conducted in October 2015. At that time, a sample of 30 was collected for ageing (3 independent readers using cross sections of asterisci otoliths; ages where at least 2 readers agreed were used; Bajer and Sorensen 2010). The results of ageing were used to develop a length-age key in 20 mm length increments. The overall number of YOY carp that moved to Lake Staring from PCCA was estimated by combining the results of the age-length analysis that estimated the proportion of YOY (year class 2015), age-2 (year class 2013) and adult carp in the population with the mark-recapture analysis which estimated the number of adult carp in the lake.

Results

Trap net surveys showed that YOY carp were present in PCCA during 2013 and 2015, but not in 2014. In 2013, mean trap net catch rates in PCCA ranged between 5.4 and 23.5 in July and August and decreased to zero in late September (Figure 2). In 2015, mean trap net catch rates were higher than in 2013, but also decreased from 79.4 in July to 0.8 in early October (Figure 2). YOY carp were not captured in Lake Staring, except in August 2015 when < 1 YOY carp were captured per net (Figure 2). The daily natural instantaneous mortality rate was 0.0412 in 2013 and 0.0437 in 2015 (Figure 3). This mortality rate was relatively high showing that the number of carp in PCCA (both PIT tagged and otherwise) declined by ~97% over a four month period (July-October). The mean length of YOY carp in the PCCA was lower in 2013 (mean = 101.9 mm; SD = 24.3) than in 2015 (mean = 131.4 mm; SD = 18.4).

A total of 468 carp were tagged in 2013 in PCCA. Tagging mortality was negligible, as 2 out of 20 (10%) carp perished for both tagged and control carp over the 48 hour period. In 2013, only one YOY carp was detected by the antennas (0.2%). This detection occurred in early August during a period of decreasing water level and when temperature was stable ~ 25°C (Figure 4). The mean daily outmigration probability for a PIT tagged carp was $4.5 \cdot 10^{-5}$.

A total of 663 carp were tagged in 2015 in PCCA, of which 37 were detected by the antennas (5.5%) (Figure 4). The majority of detections occurred in August during a period of decreasing water levels and there did not appear to be any correlation with

temperature (Figure 4). The mean daily outmigration probability for a single tagged carp was $1.3 \cdot 10^{-3}$.

Of the 56 carp marked in Lake Staring in the summer 2014, eight were recaptured in January 2015 among 834 carp that were caught and examined for marks. This suggested that in the summer of 2014 (time of marking), Lake Staring was inhabited by 5,288 adult carp ± 1,295 (400 mm to 700 mm total length). Of those fish, 2,325 were removed during the winter and summer of 2015, presumably reducing the population of adult in Lake Staring to ~2,963 individuals in the fall of 2015 (Figure 5). Electrofishing surveys in Lake Staring showed three distinct modes in fall of 2015: one comprised of carp that ranged from 150 to 310 mm, another from 370 to 460 mm, and a third from 580 to 760 mm (Figure 5). Ageing analyses showed that the first and second modes were comprised primarily of YOY and age-2 carp corresponding to recruitment events in PCCA in 2015 and 2013, respectively, while the third mode represented adult carp present in lake Staring prior to 2013 (Figure 5). Assuming equal capture probabilities across carp of various length classes, and knowing that the last mode was comprised of ~2,963 carp (above), I estimated that 3,367 YOY carp, and 1,077 age-2 carp were present in Lake Staring in fall of 2015 (Figure 5).

Discussion

The goal of this study was to estimate the outmigration rate of YOY carp from a seasonally-unstable marsh to a lake in the northern temperate region of North America. My results suggest that the outmigration rate of YOY carp is low, but can vary substantially from year to year. Between 0.2% and 5.5% of PIT tagged carp were

detected moving from the marsh for the two years when recruitment occurred. These values encompass a previous estimate from trap net catch rates, which suggested that 0.3% of YOY carp outmigrate in the first year (Bajer et al. 2015b). The mean YOY carp daily outmigration probabilities for the two years ranged between $4.5 \cdot 10^{-5}$ and $1.3 \cdot 10^{-3}$, respectively. While all existing evidence suggests that a relatively low percentage of YOY carp outmigrate in the first year, the number of migrants can still be significant given the high fecundity of carp. Using ageing and mark-recapture analyses I estimated that ~3,400 carp moved into Lake Staring in 2015, doubling the existing carp population in the lake. This suggests that reducing the rate of juvenile carp outmigration from external marshes is important to develop sustainable carp management strategies.

Low outmigration rates of YOY carp may be a result of the absence of important environmental cues in non-native habitats. In their native range, carp spawn in seasonally inundated floodplains where juveniles are forced out of by receding water levels (Balon 2004). Such cues might be subtler or not exist in marshes in Minnesota. However, the 'reluctance' of YOY carp to migrate downstream may also suggest that there is a strong evolutionary disadvantage to leaving nursery habitats. In carp's native habitat (large lowland rivers), juveniles that leave floodplain habitats where they hatch are likely to have a lower chance of survival due to predation and lack of shelter in the main river channel. YOY carp might have evolved a tendency to remain in sheltered floodplain habitat by employing positive rheotaxis to avoid downstream migration or being swept downstream into river channel. I did observe some evidence of positive rheotaxis in that YOY carp often aggregated near the inlet to PCCA and tried to jump a waterfall after significant rain events. This behavior might be important in situations where nursery

marshes are located downstream of lakes (i.e. Bajer and Sorensen 2010), in which YOY carp might show much higher tendencies to outmigrate upstream.

The majority of YOY outmigration coincided with declining water level in the summer. The largest number of YOY carp detected by the antennas occurred in August 2015 when the water level in the stream and marsh declined by nearly 0.5 m in less than two weeks. Such declines were not observed in the summer in 2013, which perhaps explains lower outmigration rates during that year. In both years there were large declines in water level in the fall (October-November) that did not coincide with outmigration events. This may have occurred because lower water temperatures decreased the activity level of YOY carp or there may not have been enough tagged carp remaining in the marsh to detect their movement due to high mortality rates. Outmigration that occurred during low water periods in the summer might have been stimulated by avian predator avoidance. During low water periods, large areas of PCCA were shallower than 20 cm and piscivorous birds such as American pelicans (*Pelecanus erythrorhynchos*), double-crested cormorants (*Phalacrocorax auritus*), egrets (*Ardea alba*), and blue herons (*Ardea herodias*) were seen foraging on juvenile fishes, which presumably included YOY carp. The threat of predation by birds has been shown to alter the distribution of some fish species; generally forcing fish to occupy deeper or more sheltered environments (Power et al. 1989; Tabor and Wurtsbaugh 1991; Gregory 1993; Allouche and Gaudin 2001). The possibility of high avian predation during low water levels is supported by the overall high mortality rates (~ 4% daily), which would have reduced YOY abundance by over 90% between July and October.

There was substantial year to year variation in the outmigration of YOY carp from PCCA. This was somewhat surprising, because even though water levels tended to fluctuate more in 2015, which may have promoted outmigration for the reasons stated above, overall the abiotic factors did not differ dramatically between years. However, the lengths of YOY carp were ~30 mm larger in 2015 than 2013, although it is not clear how that might have affected outmigration probability. Bajer et al. (2015b) showed large outmigration rates among age-2 carp, which were ~250 mm in length. They attributed that to sexual maturation, which often occurs at ~300 mm in length in carp populations in temperate regions (Sivakumaran et al. 2003; Smith and Walker 2004). Future studies should address the effects of carp length on their outmigration probability. Additionally, my estimates of outmigration probability were based on natural mortality estimates derived from trap net catch rates. I assumed that catch rates were proportional to the abundance of YOY carp. However, potential effects of hyperstability (high catch rates despite declines in abundance) or hyperdepression (low catch rates despite high abundance) might have biased my estimates.

Even low outmigration rates can result in significant fluxes of recruits into lakes. Osborne (2012) estimated that the number of YOY carp in winterkill-prone marshes in Minnesota ranged from 2,000 to 6,000 per hectare at the end of the summer. Hence, 100,000 to 500,000 YOY carp were likely present in PCCA in 2013 and 2015. Given the outmigration of 0.2% to 5.5%, ~1,000 to 27,000 YOY carp might have migrated from PCCA to Staring in each of those years. The actual numbers of YOY carp that recruited into the lake population were probably lower and more similar to my estimate of 3,400 carp in 2015 given that YOY carp will continue incurring relatively high mortality rates

once they move to the lake (due to predation). Installing technologies in lake-marsh systems to curb juvenile outmigration from marshes, such as acoustic deterrents (Zielinski and Sorensen 2015), might increase the sustainability of carp management, even if only moderately effective. Manipulations of water level might also be considered (whenever feasible) via marsh outlet modifications. Maintaining slightly higher water levels might be advantageous in the summer, since most carp moved during periods of declining water depth. Conversely, water levels could be slowly reduced during winter to induce winter freeze-outs. Marshes could also be blocked with temporary or permanent barriers to exclude spawning adults. This however would require a total elimination of adult carp from marshes, because even low densities of adults can produce strong recruitment pulses (Bajer et al. 2015b). All of these management applications require additional research on the potential impacts on native fishes that also rely on marshy habitats for spawning. Regardless of the specific strategy, recruitment from external marshes should be a focal point in developing management plans for migratory common carp populations in lake-marsh systems.

Figures

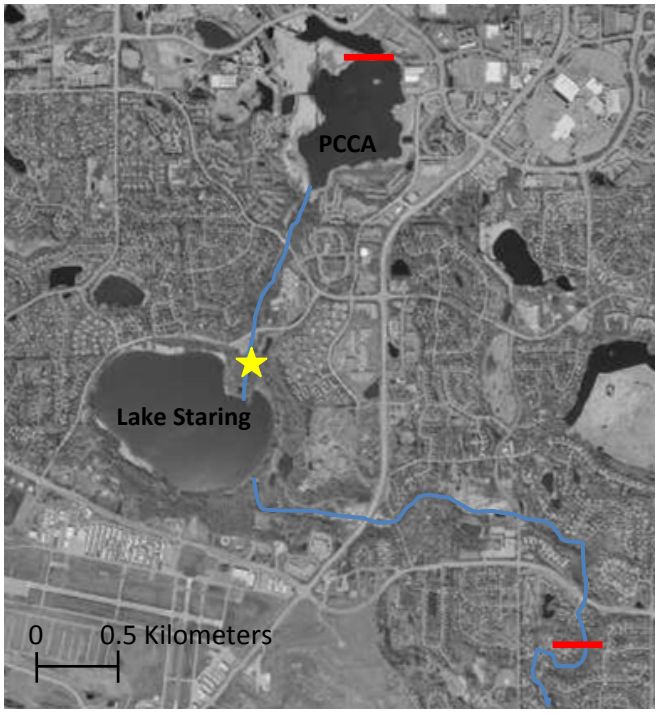

Figure 1

Map of the study area located in the Riley Purgatory Bluff Creek Watershed District. Lake Staring is connected to Purgatory Creek Conservation Area (PCCA) via Purgatory Creek (blue line). The yellow star indicates the location of the PIT tag antennas and the red lines represent the elevation barriers. The image is courtesy of (https://gis.hennepin.us/naturalresources/map/default.aspx)

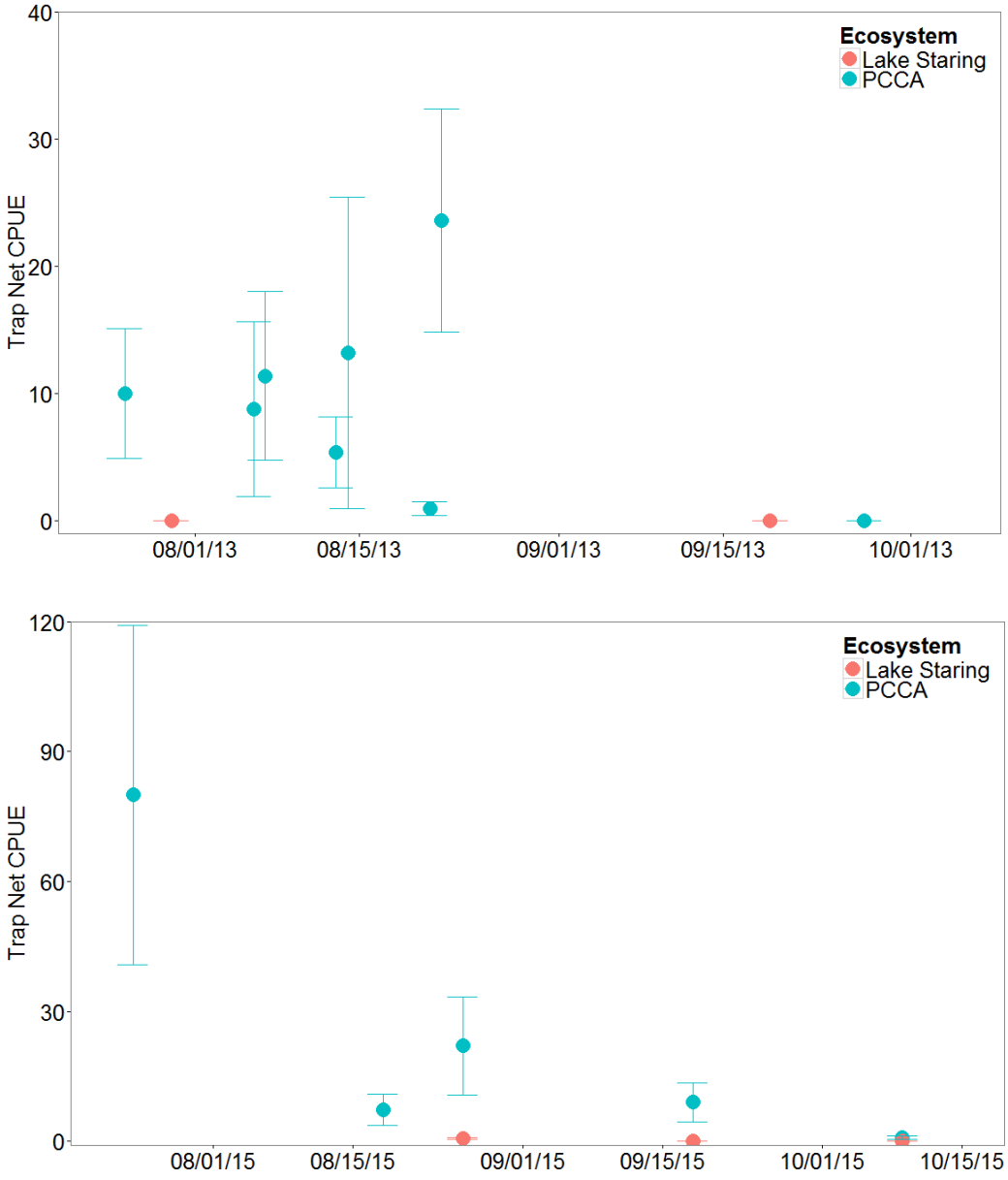

Figure 2

The mean (± SE) trap net catch rate (CPUE) of young of year common carp in the marsh (blue) and the lake (red) in 2013 (top panel) and 2015 (bottom panel). Note y-axis is different for each panel.

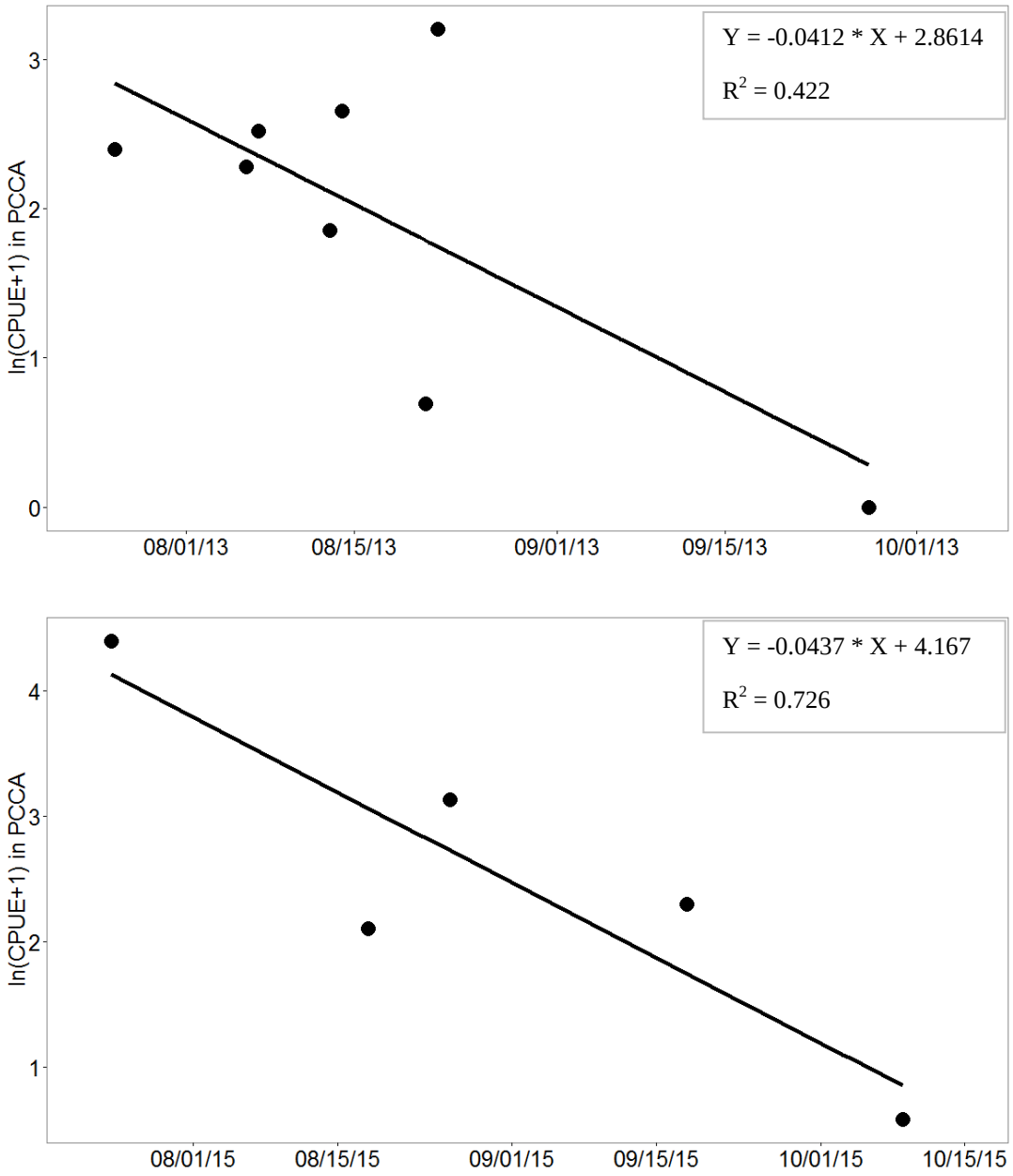

Figure 3

Trap net catch rates (CPUE) in PCCA over time in 2013 (top) and 2015 (bottom). Line fitted to the ln(y+1) data represents a linear model whose slope was used to estimate the daily mortality rate: 0.0413/day in 2013 and 0.0437/day in 2015.

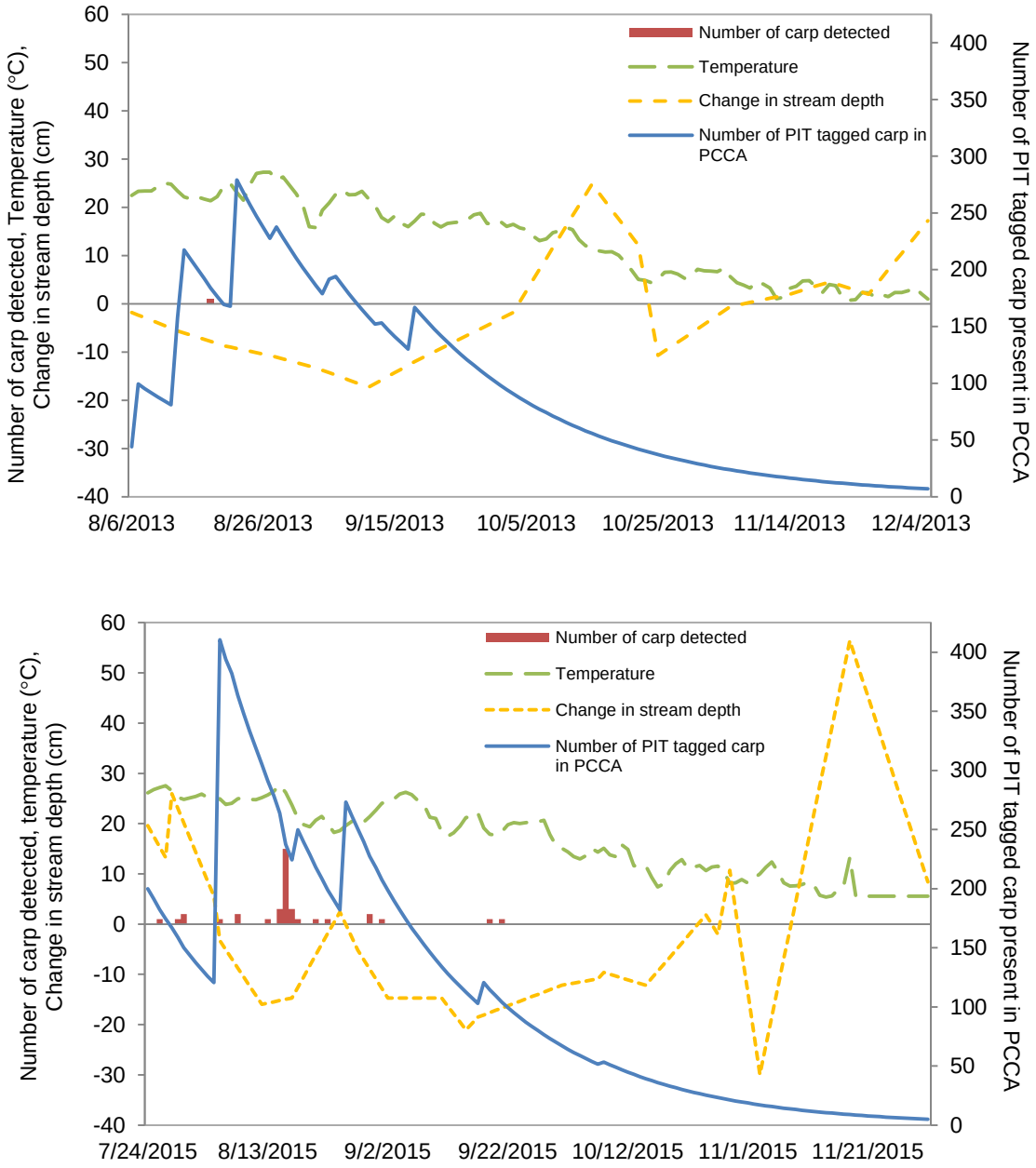

Figure 4

The number of PIT tagged carp present in PCCA (blue line; secondary y-axis) and number of carp detected by the antenna (red bars; primary y-axis) located downstream of PCCA in 2013 (top panel) and 2015 (bottom panel). The dashed lines represent change in water depth in relation to the annual mean value (yellow; short dash) and the temperature in °C (green, long dash).

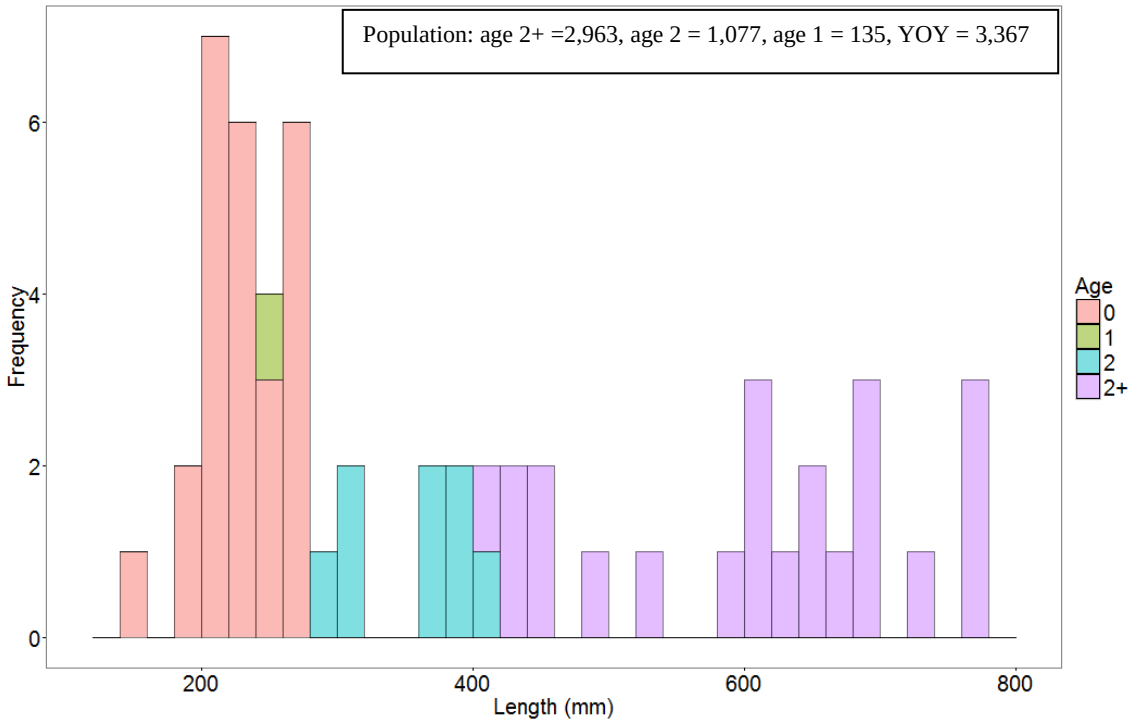

Figure 5

Length and age structure of common carp in Lake Staring in the fall 2015. Numbers in the box represent carp population estimates in each age class (see methods for details)

References

Ahmed, S.M. 2011. Note on feeding relationships of three species of cyprinid fish larvae in Al-Huwaiza marsh, Southern Iraq. Mesopotamian Journal of Marine Science. **26**(1): 35-46.

Allouche, S., and Gaudin, P. 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. Oikos. **94**(3): 481-492.

Aquiloni, L., Brusconi, S., Cecchinelli, E., Tricarico, E., Mazza, G., Paglianti, A., and Gherardi, F. 2010. Biological control of invasive populations of crayfish: the European eel (*Anguilla anguilla*) as a predator of *Procambarus clarkii*. Biological Invasions. **12**(11): 3817-3824.

Azuma, M. 1992. Ecological release in feeding behaviour: the case of bluegills in Japan. Hydrobiologia. **243**(1): 269-276.

Bajer, P.G., Chizinski, C.J., Silbernagel, J.J., and Sorensen, P.W. 2012. Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the common carp, in a naturally unstable environment. Biological Invasions. **14**(9): 1919-1929.

Bajer, P.G., Cross, T.K., Lechelt, J.D., Chizinski, C.J., Weber, M.J., and Sorensen, P.W. 2015a. Across-ecoregion analysis suggests a hierarchy of ecological filters that regulate recruitment of a globally invasive fish. Diversity and Distributions. **21**(5): 500-510.

Bajer, P.G., Parker, J.E., Cross, T.K., Venturelli, P.A., and Sorensen, P.W. 2015b. Partial migration to seasonally-unstable habitat facilitates biological invasions in a predator-dominated system. Oikos. **124**(11): 1520-1526.

Bajer, P.G., and Sorensen, P.W. 2010. Recruitment and abundance of an invasive fish, the common carp, is driven by its propensity to invade and reproduce in basins that experience winter-time hypoxia in interconnected lakes. Biological Invasions. **12**(5): 1101-1112.

Bajer, P.G., and Sorensen, P.W. 2015. Effects of common carp on phosphorus concentrations, water clarity, and vegetation density: a whole system experiment in a thermally stratified lake. Hydrobiologia. **746**(1): 303-311.

Bajer, P.G., Sullivan, G., and Sorensen, P.W. 2009. Effects of a rapidly increasing population of common carp on vegetative cover and waterfowl in a recently restored Midwestern shallow lake. Hydrobiologia. **632**(1): 235-245.

Balcombe, S.R., Bunn, S.E., McKenzie-Smith, F.J. and Davies, P.M. 2005. Variability of fish diets between dry and flood periods in an arid zone floodplain river. Journal of Fish Biology. **67**(6): 1552-1567.

Balon, E.K. 1995. Origin and domestication of the wild carp, *Cyprinus carpio*: from Roman gourmets to the swimming flowers. Aquaculture. **129**(1): 3-48.

Balon, E.K. 2004. About the oldest domesticates among fishes. Journal of Fish Biology. **65**(s1): 1-27.

Bremigan, M.T., and Stein, R.A. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences. **51**(4): 913-922.

Britton, J.R., Boar, R.R., Grey, J., Foster, J., Lugonzo, J., and Harper, D.M. 2007. From introduction to fishery dominance: the initial impacts of the invasive carp *Cyprinus carpio* in Lake Naivasha, Kenya, 1999 to 2006. Journal of Fish Biology. **71**(sd): 239-257.

Brzuska, E., and Adamek, J. 1999. Artificial spawning of European catfish, *Silurus glanis* L.: stimulation of ovulation using LHRH-a, Ovaprim and carp pituitary extract. Aquaculture Research. **30**(1): 59-64.

Carlson, R.E. 1977. A trophic state index for lakes1. Limnology and Oceanography. **22**(2): 361-369.

Carlson, R.E., and Simpson, J. 1996. A Coordinator's Guide to Volunteer Lake Monitoring Methods. North American Lake Management Society, Madison, WI. pp 96.

Carvalho, A.P., Escaffre, A.M., Teles, A.O., and Bergot, P. 1997. First feeding of common carp larvae on diets with high levels of protein hydrolysates. Aquaculture International. **5**(4): 361-367.

Chapman, D., and Robson, D.S. 1960. The analysis of a catch curve. Biometrics. **16**(3): 354-368.

Chick, J.H., and Van Den Avyle, M.J. 1999. Zooplankton variability and larval striped bass foraging: evaluating potential match/mismatch regulation. Ecological Applications. **9**(1): 320-334.

Clark, C.F. 1950. Observations on the spawning habits of the northern pike, *Esox lucius*, in northwestern Ohio. Copeia. **1950**(4): 285-288.

Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M., and Chaney, K. 2002. Influence of beetle banks on cereal aphid predation in winter wheat. Agriculture, Ecosystems and Environment. **93**(1): 337-350.

Cole, L.J. 1905. German carp in the United States (No. 592). US Government Printing Office, Washington D.C.

Cooper, G.P., and Washburn, G.N. 1949. Relation of dissolved oxygen to winter mortality of fish in Michigan lakes. Transactions of the American Fisheries Society. **76**(1): 23-33.

Crivelli, A.J. 1981. The biology of the common carp, *Cyprinus carpio* L. in the Camargue, southern France. Journal of Fish Biology. **18**(3): 271-290.

Crivelli, A.J. 1983. The destruction of aquatic vegetation by carp. Hydrobiologia. **106**(1): 37-41.

Crossman, E.J. 1991. Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. Canadian Journal of Fisheries and Aquatic Sciences. **48**(s1): 46-57.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology. **26**: 249-293.

Czesny, S., Dabrowski, K., and Frankiewicz, P. 2001. Foraging patterns of juvenile walleye (*Stizostedion vitreum*) in a system consisting of a single predator and two prey species: testing model predictions. Canadian Journal of Zoology. **79**(8): 1394-1400.

Dabrowska, H., Grudniewski, C., and Dabrowski, K. 1979. Artificial diets for common carp: effect of the addition of enzyme extracts. The Progressive Fish-Culturist. **41**(4): 196-200.

Dabrowski, K. (1984). The feeding of fish larvae: present «state of the art» and perspectives. Reproduction Nutrition Développement. **24**(6): 807-833.

Dabrowski, K., Bardega, R., and Przedwojski, R. 1983. Dry diet formulation study with common carp (*Cyprinus carpio* L.) larvae. Zeitschrift für Tierphysiologie Tierernährung und Futtermittelkunde. **50**(1-5): 40-52.

Davis, J.M., Rosemond, A.D., Eggert, S.L., Cross, W.F. and Wallace, J.B. 2010. Long-term nutrient enrichment decouples predator and prey production. Proceedings of the National Academy of Sciences. **107**(1): 121-126.

De Moor, I.J., and Bruton, M.N. 1988. Atlas of alien and translocated indigenous aquatic animals in southern Africa. National Scientific Programmes Unit: CSIR, SANSP Report 144. pp 103-110.

DeMott, W.R., and Kerfoot, W.C. 1982. Competition among cladocerans: nature of the interaction between Bosmina and Daphnia. Ecology. **63**(6): 1949-1966.

Devries, D.R., Stein, R.A., and Bremigan, M.T. 1998. Prey selection by larval fishes as influenced by available zooplankton and gape limitation. Transactions of the American Fisheries Society. **127**(6): 1040-1050.

Diggle, J., Patil, J., and Wisniewski, C. 2012. A manual for carp control: The Tasmanian model. PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia. pp 1-28.

Donkers, P., Patil, J.G., Wisniewski, C., and Diggle, J.E. 2012. Validation of mark-recapture population estimates for invasive common carp, *Cyprinus carpio*, in Lake Crescent, Tasmania. Journal of Applied Ichthyology. **28**(1): 7-14.

Drenner, R.W., Strickler, J.R. and O'Brien, W.J. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. Journal of the Fisheries Board of Canada. **35**(10): 1370-1373.

Dumont, H.J., Van de Velde, I., and Dumont, S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia. **19**(1): 75-97.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology. **58**(1): 46-59.

Ehlinger, T.J., and Wilson, D.S. 1988. Complex foraging polymorphism in bluegill sunfish. Proceedings of the National Academy of Sciences. **85**(6): 1878-1882.

Eilenberg, J., Hajek, A., and Lomer, C. 2001. Suggestions for unifying the terminology in biological control. BioControl. **46**(4): 387-400.

Ferry-Graham, L.A., Wainwright, P.C., and Lauder, G.V. 2003. Quantification of flow during suction feeding in bluegill sunfish. Zoology. **106**(2): 159-168.

Fontagne, S., Pruszynski, T., Corraze, G., and Bergot, P. 1999. Effect of coconut oil and tricaprylin vs. triolein on survival, growth and fatty acid composition of common carp (*Cyprinus carpio* L.) larvae. Aquaculture. **179**(1): 241-251.

Gabelhouse Jr, D.W. 1984. A length-categorization system to assess fish stocks. North American Journal of Fisheries Management. **4**(3): 273-285.

Geurden, I., Bergot, P., Van Ryckeghem, K., and Sorgeloos, P. 1999. Phospholipid composition of common carp (*Cyprinus carpio*) larvae starved or fed different phospholipid classes. Aquaculture. **171**(1): 93-107.

Geurden, I., Marion, D., Charlon, N., Coutteau, P., and Bergot, P. 1998. Comparison of different soybean phospholipidic fractions as dietary supplements for common carp, *Cyprinus carpio*, larvae. Aquaculture. **161**(1): 225-235.

Geurden, I., Radünz-Neto, J., and Bergot, P. 1995. Essentiality of dietary phospholipids for carp (*Cyprinus carpio* L.) larvae. Aquaculture. **131**(3): 303-314.

Gosch, N.J.C., Phelps, Q.E., and Willis, D.W. 2006. Habitat characteristics at bluegill spawning colonies in a South Dakota glacial lake. Ecology of Freshwater Fish. **15**(4): 464-469.

Gotceitas, V. 1990. Variation in plant stem density and its effects on foraging success of juvenile bluegill sunfish. Environmental Biology of Fishes. **27**(1): 63-70.

Gotceitas, V., Puvanendran, V., Leader, L.L., and Brown, J.A. 1996. An experimental investigation of the match/mismatch hypothesis using larval Atlantic cod. Oceanographic Literature Review. **8**(43): 29-37.

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences. **50**(2): 241-246.

Hawryshyn, C.W., Arnold, M.G., McFarland, W.N., and Loew, E.R. 1988. Aspects of color vision in bluegill sunfish (*Lepomis macrochirus*): ecological and evolutionary relevance. Journal of Comparative Physiology A. **164**(1): 107-116.

Hein, C.L., Roth, B.M., Ives, A.R., and Vander Zanden, M.J. 2006. Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. Canadian Journal of Fisheries and Aquatic Sciences. **63**(2): 383-393.

Herborg, L.M., Mandrak, N.E., Cudmore, B.C., and MacIsaac, H.J. 2007. Comparative distribution and invasion risk of snakehead (*Channidae*) and Asian carp (*Cyprinidae*) species in North America. Canadian Journal of Fisheries and Aquatic Sciences. **64**(12): 1723-1735.

Hepher, B., Milstein, A., Leventer, H., and Teltsch, B. 1989. The effect of fish density and species combination on growth and utilization of natural food in ponds. Aquaculture Research. **20**(1): 59-71.

Hickley, P., Muchiri, S.M., Britton, J.R., and Boar, R.R. 2004. Discovery of carp, *Cyprinus carpio*, in the already stressed fishery of Lake Naivasha, Kenya. Fisheries Management and Ecology. **11**(2): 139-142.

Hinojosa-Garro, D., and Zambrano, L. 2004. Interactions of common carp (*Cyprinus carpio*) with benthic crayfish decapods in shallow ponds. Hydrobiologia. **515**(1-3): 115-122.

Howarth, F.G. 1991. Environmental impacts of classical biological control. Annual Review of Entomology. **36**(1): 485-509.

Hunter, J.R. 1972. Swimming and feeding behavior of larval anchovy (*Engraulis mordax*). Fishery Bulletin. **70**(82): 82l-838.

Iguchi, K.I. and Yodo, T. 2004. Impact of indigenous egg eaters on the early survival of exotic smallmouth bass. Ecological Research. **19**(5): 469-474.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Jhingran, V.G. and Pullin, R.S.V. 1985. A hatchery manual for the common, Chinese and Indian major carps. ICLARM Studies and Review, Asian Development Bank and ICLARM Publication, Manila, Philippines. pp 191.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries. **3**(4): 348-365.

Jonsson, M., Wratten, S D., Landis, D.A., and Gurr, G.M. 2008. Recent advances in conservation biological control of arthropods by arthropods. Biological Control. **45**(2): 172-175.

Keast, A. 1978. Feeding interrelations between age-groups of pumpkinseed (Lepomis gibbosus) and comparisons with bluegill (*L. macrochirus*). Journal of the Fisheries Board of Canada. **35**(1): 12-27.

Khadka, R.B., and Rao, T. R. 1986. Prey size selection by common carp (*Cyprinus carpio var. communis*) larvae in relation to age and prey density. Aquaculture. **54**(1): 89-96.

King, A.J., Humphries, P., and Lake, P.S. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. Canadian Journal of Fisheries and Aquatic Sciences. **60**(7): 773-786.

Koch, J.D. 2014. Source-sink population structure of invasive common carp in a model Midwestern watershed: empirical evidence and notes on management. Master's thesis. University of Minnesota, St. Paul, MN.

Koehn, J.D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. Freshwater Biology. **49**(7): 882-894.

Koehn, J.D., Brumley, A.R., and Gehrke, P.C. 2000. Managing the Impacts of Carp. Bureau of Resource Sciences, Canberra, Australia.

Kogan, M. 1998. Integrated pest management: historical perspectives and contemporary developments. Annual Review of Entomology. **43**(1): 243-270.

Kolar, C.S., and Wahl, D.H. 1998. Daphnid morphology deters fish predators. Oecologia. **116**(4): 556-564.

Köprücü, K., and Aydin, R. 2004. The toxic effects of pyrethroid deltamethrin on the common carp (*Cyprinus carpio* L.) embryos and larvae. Pesticide Biochemistry and Physiology. **80**(1): 47-53.

Kulhanek, S.A., Leung, B., and Ricciardi, A. 2011a. Using ecological niche models to predict the abundance and impact of invasive species: application to the common carp. Ecological Applications. **21**(1): 203-213.

Kulhanek, S.A., Ricciardi, A., and Leung, B. 2011b. Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species?. Ecological Applications. **21**(1): 189-202.

Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. Hydrobiologia. **146**(2): 97-167.

Lechelt, J.D., and Bajer, P.G. 2016. Modeling the potential for managing invasive common carp in temperate lakes by targeting their winter aggregations. Biological Invasions. **18**(3): 831-839.

Lehtonen, H. 2002. Alien freshwater fishes of Europe. In: Leppäkoski, E., Gollasch, S., Olenin, S. eds. Invasive Aquatic Species of Europe: distribution, impacts and management. Kluwer Academic Publisher, Dordrecht, Netherlands. pp 153-161.

Lemke, A.M., and Benke, A.C. 2004. Growth, reproduction, and production dynamics of a littoral microcrustacean, *Eurycercus vernalis* (*Chydoridae*), from a southeastern wetland, USA. Journal of the North American Benthological Society. **23**(4): 806-823.

Lougheed, V.L., Crosbie, B., and Chow-Fraser, P. 1998. Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. Canadian Journal of Fisheries and Aquatic Sciences. **55**(5): 1189-1197.

Lowe, S., Browne, M., Boudjelas, S., and De Poorter, M. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand.

Marchetti, M.P., Light, T., Moyle, P.B., and Viers, J.H. 2004. Fish invasions in California watersheds: testing hypotheses using landscape patterns. Ecological Applications. **14**(5): 1507-1525.

Matsuzaki, S.I.S., Usio, N., Takamura, N., and Washitani, I. 2007. Effects of common carp on nutrient dynamics and littoral community composition: roles of excretion and bioturbation. Fundamental and Applied Limnology. **168**(1): 27-38.

Matthews, S., and Brand, K. 2004. Africa invaded: the growing danger of invasive alien species. Global Invasive Species Programme, Cape Town, South Africa. pp 28-29.

McCauley, E., and Murdoch, W.W. 1987. Cyclic and stable populations: plankton as paradigm. American Naturalist. **129**(1): 97-121.

McPhail, J.D. 2007. Freshwater Fishes of British Columbia (The) (Vol. 6). University of Alberta, Alberta, Canada.

Merz, J.E., Setka, J.D., Pasternack, G.B., and Wheaton, J.M. 2004. Predicting benefits of spawning-habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production in a regulated California river. Canadian Journal of Fisheries and Aquatic Sciences. **61**(8): 1433-1446.

Miller, S.A., and Crowl, T.A. 2006. Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. Freshwater Biology. **51**(1): 85-94.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1994. Exotic species and the integrity of the Great Lakes. BioScience. **44**(10): 666-676.

Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology. **62**(5): 1370-1386.

Moav, R., Hulata, G., and Wohlfarth, G. 1975. Genetic differences between the Chinese and European races of the common carp. Heredity. **34**(3): 323-340.

Moreau, J., and Costa-Pierce, B. 1997. Introduction and present status of exotic carp in Africa. Aquaculture Research. **28**(9): 717-732.

Morgan, D.L., Gill, H.S., Maddern, M.G., and Beatty, S.J. 2004. Distribution and impacts of introduced freshwater fishes in Western Australia. New Zealand Journal of Marine and Freshwater Research. **38**(3): 511-523.

Morman, R.H., Cuddy, D.W., and Rugen, P.C. 1980. Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences. **37**(11): 1811-1826.

Munk, P. 1995. Foraging behaviour of larval cod (*Gadus morhua*) influenced by prey density and hunger. Marine Biology. **122**(2): 205-212.

Nandini, S. and Sarma, S.S.S. 2000. Zooplankton preference of two species of freshwater ornamental fish larvae. Journal of Applied Ichthyology. **16**(6): 273-275.

Naranjo, S.E., Ellsworth, P.C., and Frisvold, G.B. 2015. Economic value of biological control in integrated pest management of managed plant systems. Annual Review of Entomology. **60**(2015): 621-645.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C., Clay, J., Folk, C., Lubchenco, J., Mooney, H., and Troell, M. 2000. Effect of aquaculture on world fish supplies. Nature. **405**(6790): 1017-1024.

Nico, L.G., and Fuller, P.L. 1999. Spatial and temporal patterns of nonindigenous fish introductions in the United States. Fisheries. **24**(1): 16-27.

Norberg, R.A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. The Journal of Animal Ecology. **46**(2): 511-529.

Ogutu-Ohwayo, R., Hecky, R.E., Cohen, A.S., and Kaufman, L. 1997. Human impacts on the African Great Lakes. Environmental Biology of Fishes. **50**(2): 117-131.

Oliver, J.D., Holeton, G.F., and Chua, K.E. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society. **108**(2): 130-136.

Osborne, J.B. 2012. Distribution, abundance and overwinter survival of young-of-the-year common carp in a Midwestern watershed. Master's Thesis. University of Minnesota, St. Paul, MN.

Pace, M.L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. Limnology and Oceanography. **31**(1): 45-55.

Panek, F.M. 1987. Biology and ecology of carp. In: Cooper, E.L. eds. Carp in North America. American Fisheries Society, Bethesda, Maryland. pp 1–15.

Parameswaran, S., Alikunhi, K.H., and Sukumaran, K.K. 1972. Observations on the maturation, fecundity and breeding of the common carp, *Cyprinus carpio* Linnaeus. Indian Journal of Fisheries. **19**(1, 2): 110-124.

Parkos III, J.J., Santucci, Jr, V.J., and Wahl, D.H. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. Canadian Journal of Fisheries and Aquatic Sciences. **60**(2): 182-192.

Petrosky, B.R., and Magnuson, J.J. 1973. Behavioral responses of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winterkill conditions. Copeia. **1973**(1): 124-133.

Phelps, Q.E. 2006. Population dynamics of common carp in eastern South Dakota glacial lakes. Master's thesis. South Dakota State University, Brookings, South Dakota.

Phelps, Q.E., Graeb, B.D.S., and Willis, D.W. 2008a. First year growth and survival of common carp in two glacial lakes. Fisheries Management and Ecology. **15**(2): 85-91.

Phelps, Q.E., Graeb, B.D.S., and Willis, D.W. 2008b. Influence of the Moran effect on spatiotemporal synchrony in common carp recruitment. Transactions of the American Fisheries Society. **137**(6): 1701-1708.

Post, J.R., and Prankevicius, A.B. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences. **44**(11): 1840-1847.

Power, M.E., Dudley, T.L., and Cooper, S.D. 1989. Grazing catfish, fishing birds, and attached algae in a Panamanian stream. Environmental Biology of Fishes. **26**(4): 285-294.

Power, M.E., Parker, M.S. and Dietrich, W.E. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. Ecological Monographs. **78**(2): 263-282.

Puvanendran, V., and Brown, J.A. 1999. Foraging, growth and survival of Atlantic cod larvae reared in different prey concentrations. Aquaculture. **175**(1): 77-92.

R Development Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 3-900051-07-0 (URL http://www.R-project.org/).

Radunz-Neto, J., Corraze, G., Bergot, P., and Kaushik, S.J. 1996. Estimation of essential fatty acid requirements of common carp larvae using semi-purified artificial diets. Archives of Animal Nutrition. **49**(1): 41-48.

Rahel, F.J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology. **65**(4): 1276-1289.

Raina, H. S. (1987). Biological note on the introduced common carp in the temperate waters of Kashmir. Indian Journal of Fisheries. **34**(1): 114-119.

Reshetnikov, A.N., and Ficetola, G.F. 2011. Potential range of the invasive fish rotan (*Perccottus glenii*) in the Holarctic. Biological Invasions. **13**(12): 2967-2980.

Schael, D.M., Rudstam, L.G., and Post, J.R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens),* freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). Canadian Journal of Fisheries and Aquatic Sciences. **48**(10): 1919-1925.

Sepulveda, A.J., Rutz, D.S., Ivey, S.S., Dunker, K.J., and Gross, J.A. 2013. Introduced northern pike predation on salmonids in southcentral Alaska. Ecology of Freshwater Fish. **22**(2): 268-279.

Shearer, K.D., and Mulley, J.C. 1978. The introduction and distribution of the carp, *Cyprinus carpio* Linnaeus, in Australia. Marine and Freshwater Research. **29**(5): 551-563.

Silbernagel, J.J. 2011. Field and laboratory studies suggest that recruitment of the invasive common carp is controlled by native fish in stable lakes of the Upper Mississippi Basin. Master's thesis. University of Minnesota, St. Paul, MN.

Silbernagel, J.J., and Sorensen, P.W. 2013. Direct field and laboratory evidence that a combination of egg and larval predation controls recruitment of invasive common carp in many lakes of the Upper Mississippi River Basin. Transactions of the American Fisheries Society. **142**(4): 1134-1140.

Simberloff, D., and Stiling, P. 1996. Risks of species introduced for biological control. Biological Conservation. **78**(1): 185-192.

Singh, A.K., Pathak, A.K., and Lakra, W.S. 2010. Invasion of an exotic fish—common carp, *cyprinus carpio* L. (*actinopterygii: cypriniformes: cyprinidae*) in the Ganga River, India and its impacts. Acta Ichthyologica et Piscatorial. **40**(1): 11-19.

Sivakumaran, K.P., Brown, P., Stoessel, D. and Giles, A. 2003. Maturation and reproductive biology of female wild carp, *Cyprinus carpio*, in Victoria, Australia. Environmental Biology of Fishes. **68**(3): 321-332.

Smallwood, W.M., and Smallwood, M.L. 1931. The development of the carp, *Cyprinus carpio*. I. The larval life of the carp, with special reference to the development of the intestinal canal. Journal of Morphology. **52**(1): 217-231.

Smith, B.B. and Walker, K.F., 2004. Spawning dynamics of common carp in the River Murray, South Australia, shown by macroscopic and histological staging of gonads. Journal of Fish Biology. **64**(2): 336-354.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science. **60**(3): 1129-1157.

Stern, V.M., Smith, R.F., Van den Bosch, R., and Hagen, K.S. 1959. The integration of chemical and biological control of the spotted alfalfa aphid. The integrated control concept. Hilgardia. **29**(2): 81-101.

Stickney, R. R. 1996. Aquaculture of the United States: A Historical Survey. John Wiley and Sons, New York, New York.

Stuart, I.G., and Jones, M. 2006. Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (*Cyprinus carpio* L.). Marine and Freshwater Research. **57**(3): 333-347.

Swaffar, S.M., and O'Brien, W.J. 1996. Spines of *Daphnia lumholtzi* create feeding difficulties for juvenile bluegill sunfish (*Lepomis macrochirus*). Journal of Plankton Research. **18**(6): 1055-1061.

Swee, U.B., and McCrimmon, H.R. 1966. Reproductive biology of the carp, *Cyprinus carpio* L., in Lake St. Lawrence, Ontario. Transactions of the American Fisheries Society. **95**(4): 372-380.

Tabor, R.A., and Wurtsbaugh, W.A. 1991. Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. Transactions of the American Fisheries Society. **120**(6): 728-738.

Tapia, M., and Zambrano, L. 2003. From aquaculture goals to real social and ecological impacts: carp introduction in rural central Mexico. Ambio. **32**(4): 252-257.

Tetzlaff, J.C., Roth, B.M., Weidel, B.C., and Kitchell, J.F. 2011. Predation by native sunfishes (*Centrarchidae*) on the invasive crayfish *Orconectes rusticus* in four northern Wisconsin lakes. Ecology of Freshwater Fish. **20**(1): 133-143.

Therneau, T. 2015. A Package for Survival Analysis in S. version 2.38, http://CRAN.R-project.org/package=survival.

Thompson, W.R. 1930. The principles of biological control. Annals of Applied Biology. **17**(2): 306-338.

Threlkeld, S.T. 1979. The midsummer dynamics of two Daphnia species in Wintergreen Lake, Michigan. Ecology. **60**(1): 165-179.

Thresher, R.E., Hayes, K., Bax, N.J., Teem, J., Benfey, T.J., and Gould, F. 2014. Genetic control of invasive fish: technological options and its role in integrated pest management. Biological Invasions. **16**(6): 1201-1216.

Vilizzi, L. 2012. The common carp, *Cyprinus carpio*, in the Mediterranean region: origin, distribution, economic benefits, impacts and management. Fisheries Management and Ecology. **19**(2): 93-110.

Vilizzi, L., Tarkan, A.S., and Copp, G.H. 2015. Experimental evidence from causal criteria analysis for the effects of common carp *Cyprinus carpio* on freshwater

ecosystems: a global perspective. Reviews in Fisheries Science and Aquaculture. **23**(3): 253-290.

Vilizzi, L., and Walker, K.F. 1998. The onset of the juvenile period in carp, *Cyprinus carpio*: a literature survey. Environmental Biology of Fishes. **56**(1): 93-102.

Wahab, M.A., Ahmed, Z.F., Islam, M.A., Haq, M.S., and Rahmatullah, S.M. 1995. Effects of introduction of common carp, *Cyprinus carpio* (L.), on the pond ecology and growth of fish in polyculture. Aquaculture Research. **26**(9): 619-628.

Wainwright, P.C., and Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. Environmental Biology of Fishes. **44**(1): 97-113.

Wainwright, P.C., Carroll, A.M., Collar, D.C., Day, S. W., Higham, T.E., and Holzman, R.A. 2007. Suction feeding mechanics, performance, and diversity in fishes. Integrative and Comparative Biology. **47**(1): 96-106.

Watkins, J., Rudstam, L., and Holeck, K. 2011. Length-weight regressions for zooplankton biomass calculations–A review and a suggestion for standard equations. Available at https://ecommons.cornell.edu/handle/1813/24566

Weber, M.J., and Brown, M.L. 2009. Effects of common carp on aquatic ecosystems 80 years after "carp as a dominant": ecological insights for fisheries management. Reviews in Fisheries Science. **17**(4): 524-537.

Weber, M.J., and Brown, M.L. 2011. Relationships among invasive common carp, native fishes and physicochemical characteristics in upper Midwest (USA) lakes. Ecology of Freshwater Fish. **20**(2): 270-278.

Weber, M.J., and Brown, M.L. 2013. Density-dependence and environmental conditions regulate recruitment and first-year growth of common carp in shallow lakes. Transactions of the American Fisheries Society. **142**(2): 471-482.

Weber, M.J., Hennen, M.J., and Brown, M.L. 2011. Simulated population responses of common carp to commercial exploitation. North American Journal of Fisheries Management. **31**(2): 269-279.

Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. Journal of the Fisheries Board of Canada. **31**(9): 1531-1536.

Werner, E.E., and Hall, D.J. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology. **55**(5): 1042-1052.

Werner, E.E. and Hall, D.J. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology. **69**(5): 1352-1366.

Zambrano, L., Scheffer, M., and Martínez-Ramos, M. 2001. Catastrophic response of lakes to benthivorous fish introduction. Oikos. **94**(2): 344-350.

Zambrano, L., Martínez-Meyer, E., Menezes, N., and Peterson, A.T. 2006. Invasive potential of common carp (*Cyprinus carpio*) and Nile tilapia (*Oreochromis niloticus*) in American freshwater systems. Canadian Journal of Fisheries and Aquatic Sciences. **63**(9): 1903-1910.

Zehnder, G., Gurr, G.M., Kühne, S., Wade, M.R., Wratten, S.D., and Wyss, E. 2007. Arthropod pest management in organic crops. Annual Review of Entomology. **52**: 57-80.

Zielinski, D.P., and Sorensen, P.W. 2015. Field test of a bubble curtain deterrent system for common carp. Fisheries Management and Ecology. **22(**2): 181-184.

Appendix 1

In 2015, in order to compensate for ethanol shrinkage larvae were euthanized using MS222 (concentration 1.5 g/L). These larvae were weighed and measured immediately following euthanization and then preserved in 50% ethanol and reweighed and measured two months later to establish a correction factor for 2014.

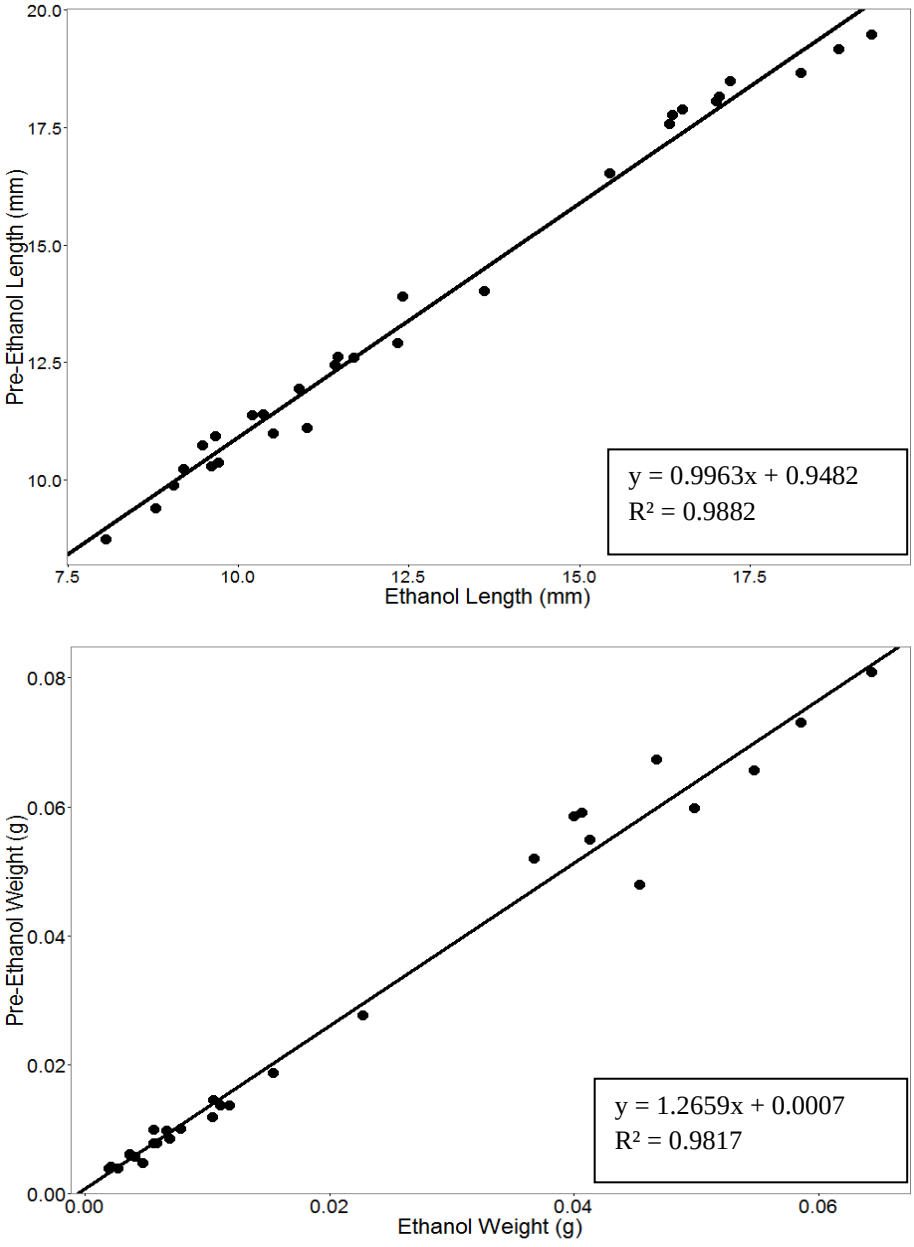

Figure A1: The top figure shows the pre-ethanol length (mm) on the y-axis and the length of the same larvae following two months in 50% ethanol on the x-axis. The bottom figure shows the pre-ethanol weight (g) on the y-axis and the weight of the same larvae following two months in 50% ethanol on the x-axis.

Appendix 2

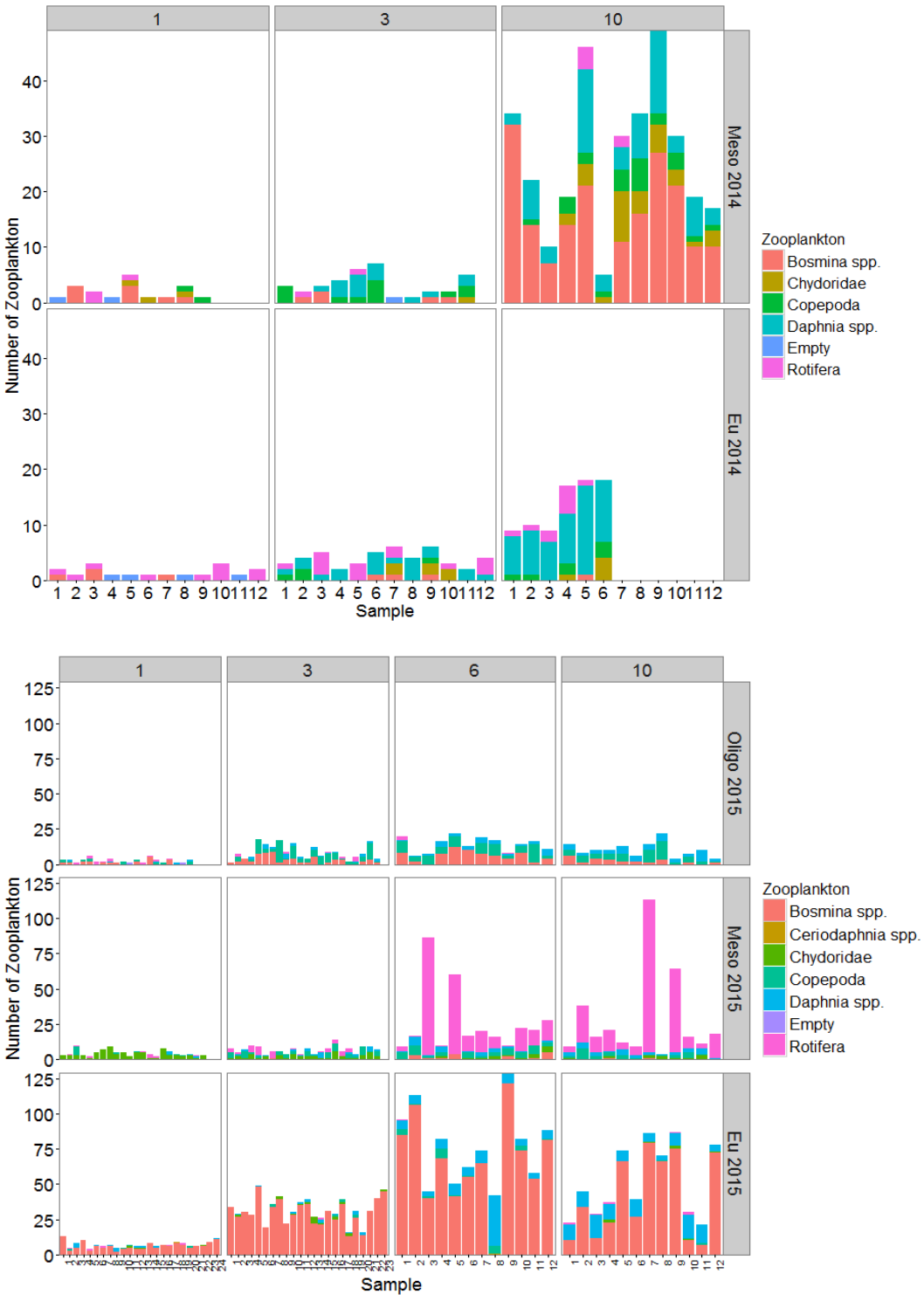

Figure A2: Total number of the prey items found in the intestines of larval carp on days 1, 3, 6 and 10 in 2014 (top panel, no samples collected on day 6) and 2015 in each treatment (bottom panel).