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Research Article

Elucidating the mechanism underlying the productivity-recruitment hypothesis in the invasive common carp

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Abstract

Across-ecoregion analyses showed that the recruitment of common carp, *Cyprinus carpio* (Linnaeus 1758), a globally invasive fish, is strongly influenced by lake productivity: while recruitment was frequent in hypereutrophic lakes, it was invariably absent in oligotrophic lakes. This led to a hypothesis that common carp larvae might have faster growth rates in productive lakes that allow them to outgrow native predators, whereas larvae might encounter nutritional bottlenecks in oligotrophic lakes. We shed some light on this hypothesis by documenting how zooplankton communities found in oligo-, meso-, and eutrophic lakes in Minnesota, USA affected larval carp survival, growth and diet composition. We cultured larval carp in tanks fed zooplankton at naturally occurring densities from three lakes of varying trophic states for 20 days during two consecutive springs. The growth rates were significantly higher (up to 5 times) among larvae fed zooplankton from the eutrophic lake and lowest in larvae fed zooplankton from the oligotrophic lake. Despite their small size (~6 mm), carp larvae selected large zooplankton (0.3–0.6 mm), primarily *Bosmina* spp., even on the first day of exogenous feeding. This pattern was consistent across all treatments. Rotifers were generally not found in the stomachs of larval carp, despite their high abundance, even if other food items were scarce. The densities of cladocera were highest in the productive lake, especially during one of the two years when larval carp showed very rapid growth rates. Our study shows that larval carp have well defined dietary preferences and that common carp recruitment might be especially likely to occur in productive systems with abundant cladocera populations in which carp larvae are expected to be more likely to escape gape-limited, native predators.

Key words: invasive fish, *Cyrpinus carpio*, biological invasions, lakes, zooplankton, *Bosmina*, diet

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 being introduced. While native predators have been shown to pose larval survival bottlenecks for invasive fishes in some geographic areas (Bajer et al. 2012), it is less clear whether dietary requirements might create similar bottlenecks elsewhere. Because most fish larvae are zooplanktivorous, zooplankton abundance and species composition is likely to have an effect on the 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 might their dietary preferences or their abilities to withstand starvation and escape predators. For example, the larvae of invasive carps (*Cyprinus* spp., *Hypophthalmichthys* spp.) are small (~5 mm) and might be particularly sensitive to food shortages due to low energy reserves (Dabrowski et al. 1983; Dabrowski and Bardega 1984). Further, invasive carps do not employ parental care, thus their larvae might suffer high mortality due to predation in environments where food is scarce and growth rates are slow. 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.

Across the globe, the common carp (or "carp") is a highly invasive fish whose success has been hypothesized to be linked with ecosystem productivity and zooplankton resources for its larvae. Carp tend to be most abundant in eutrophic waters (Kulhanek et al. 2011a, b) and Bajer et al. (2015a) showed that carp recruitment is generally found in productive lakes despite the fact that adults are also commonly found (although in low abundance) in meso- and oligotrophic lakes. This pattern in carp recruitment might be caused by reduced larval survival in oligotrophic lakes due to starvation or nutritional deficiencies, or increased larval predation rates as a result of reduced growth. The hypothesis that carp larvae require highly-productive environments to successfully develop and survive is supported 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 within 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 and high survival (Khadka and Rao 1986).

While rarely studied in natural systems, dietary requirements of carp larvae 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 the gape of carp larvae is large enough to consume organisms up to 0.5 mm in diameter (or even larger) during first feeding (Dabrowski et al. 1983). Rotifers have been suggested to be unimportant as an initial food of carp larvae and were even suggested to reduce growth rates in comparison with larvae fed copepods of appropriate size (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 the morphology and physiology of larval carp digestive tract and the activity of associated digestive enzymes during ontogenetic diet shifts. While much of the aquaculture work has focused on creating optimal rearing conditions for carp larvae, very little is known about the diets of carp larvae in natural environments. In particular, it is not known how naturally occurring differences in zooplankton abundance and composition in different geographic regions to which carp are being introduced might affect the diet, growth and survival of their larvae.

In this study we used a controlled laboratory experiment to test how naturally occurring zooplankton communities in eutrophic, mesotrophic, and oligotrophic lakes impact the diet, survival and growth of carp larvae. We hypothesized that carp larvae foraging on zooplankton from oligotrophic lakes would have the lowest survival and the slowest growth rate, while larvae foraging on zooplankton from eutrophic lakes would have the fastest growth and highest survival. Additionally, we examined the selectivity and plasticity of carp larvae diet when exposed to zooplankton communities from lakes of distinct trophic levels.

Methods

Study lakes

We collected zooplankton from three lakes located in the Upper Mississippi River Basin near Minneapolis, Minnesota, USA, a region where carp populations show pronounced differences in abundance and recruitment among lakes (Bajer et al. 2015a). Each year (2014 and 2015), our goal was to sample the same set of three lakes comprised of one eutrophic, one mesotrophic, and one oligotrophic lake. We defined a lake's trophic state by calculating the Trophic State Index (TSI) 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 (Carlson 1977; Minnesota Pollution Control Agency). The eutrophic lake was Lake Staring (44º84′N, 93º45′W, 60 ha, 4.9 m max depth, TSI = 70.0) located in Eden Prairie, Minnesota. The mesotrophic lake was Lake Ann (44º87′N, 93º56′W, 47 ha, 13.7 m max depth, TSI = 46.0) located in Chanhassen, Minnesota. The oligotrophic lake was represented by Courthouse Lake (44º79′N, 93º59′W, 4 ha, 17.4 m max depth, TSI = 39.8) located in Chaska, Minnesota. Total phosphorus concentrations (mean May–September epilimnetic values over the last 10 years) 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). We collected samples from the oligotrophic lake only in 2015, because our first choice oligotrophic system (Christmas Lake; 44º90′N, 93º54′W, TSI = 34.0) became infested with and treated for zebra mussels, *Dreissena polymorpha* (Pallas 1771), shortly before sampling began in 2014 and we were not able to secure permits to collect water from another oligotrophic lake during that year. For the remainder of this paper these lakes (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, we set up aquaria in a controlled indoor environment, under natural photoperiod (ambient) light conditions, which we 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); the aquaria were not set as flow-through systems to increase control over zooplankton densities.

In 2014, we established 18, 18-L aquaria in a block design to achieve six replicates per treatment: two treatment lakes (Eu 2014 and Meso 2014) and one reference (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 6/24/2014, transported to the laboratory and put in an aerated holding tank. All carp eggs were collected from a single site, because carp were not observed spawning in all treatment lakes. We stocked 18 fertilized eggs (1 egg/L) in each aquarium on 6/26/2014 (clear eggs with eyes of larvae visible). The eggs were stocked one by one on small fragments of vegetation to which they were found attached after collection. The larvae hatched the next day and were monitored (without feeding) for two more days while they continued to absorb their yolk sacs and remained resting on tank walls. The first feeding with zooplankton collected from our study lakes occurred on 6/30/2014 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; temperature and dissolved oxygen were also recorded daily. Temperature ranged between 20.9 °C and 25.6 °C (mean 22.8 °C) throughout the experiments with all treatments being exposed to the same ambient temperature. Dissolved oxygen ranged between 5.4 µg/L and 7.2 µg/L.

In 2015, we established 18 aquaria in a block design with six replicates per treatment (Eu 2015, Meso 2015, and Oligo 2015). We omitted the well-water reference in agreement with animal care protocols and also because mortality rates from the reference aquaria in 2014 were consistent with previous studies of 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 5/17/2015 and transported to the laboratory. On 5/18/2015, 24 fertilized eggs were added to each aquarium (1.27 eggs/L). We stocked an additional 6 eggs in each aquarium to collect more larval carp samples on the first and third day of feeding to increase data resolution, which is lacking in the literature and which we determined to be particularly important in light of the 2014 experiment. While these additional larvae did increase the initial larval densities in each tank, by sampling more larvae earlier in the experiment, the density of larvae in 2015 was the same as 2014 by day 6 of the experiment. One tank in the Eu 2015 treatment 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 5/19/2015 and the larvae were once again given two days to feed on their yolk reserves. The feeding began on 5/22/2015 and the experiment ran for 20 days. Daily water temperatures ranged from 18.8 °C to 29.1 °C, matching ambient conditions, with a mean temperature of 23.7 °C. The temperatures remained near the mean, except for a two-day period 5/27/2015–5/28/2015 when outdoor temperatures approached 35 °C. Dissolved oxygen in the aquaria ranged between 6.04 µg/L and 8.52 µg/L.

Zooplankton collection and feeding carp larvae

We collected the zooplankton from the littoral zone (carp spawn in the littoral) in each lake using a WILDCO® Wisconsin Plankton sampler with a 20-µm mesh. In each lake, we took four bottom-to-surface vertical zooplankton tows at three different littoral sites, which were kept consistent throughout the study, that were approximately 1 m in depth. The 12 tows per lake, which filtered 147.19 L of water, were concentrated to 1 L and transferred to the laboratory within one hour of sampling to ensure that plankton did not perish during 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 was 3.8 times more concentrated than in the lake. The previous day's water was then carefully siphoned out of each aquarium until approximately 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 we added 5 L of the concentrated zooplankton stock. By doing so, we reconstituted zooplankton density in each aquarium to match that in the lake. We chose to concentrate zooplankton from each lake and dilute it with well water rather than transport large quantities of lake water to ensure that results of this study are

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, we 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. We then fixed these 50 mL 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 × 50 grid counting well (Pyser-SGI S52 Sedgewick Rafter Counting Chamber) and counted under a microscope using 40× magnification. Rotifers were identified to phylum, 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 an "other" category, because they were rarely found in the samples. Zooplankton was also 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 (rotifers and Copepoda nauplia).

Larval sampling

In 2014, two random larvae were sacrificed from each tank on days 1, 3 and 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, we sacrificed four larvae from each aquarium on days 1 and 3. We then sacrificed two larvae per aquarium on day 6 and day 10, and all larvae on day 20. All larvae were collected one hour after feeding. Collected larvae were euthanized in MS-222 and placed in a plastic vial with 50% ethanol solution. At the completion of the experiment the larvae were measured for length to the nearest 0.01 mm using a digital micrometer, weighed to the nearest 0.1 mg (length and weight both accounting for ethanol shrinkage; supplementary Figure S1) 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, we 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 content we followed the protocol outlined in Chick and Van Den Avyle (1999). Intestines (carp lack true stomach but we will use "stomach" for simplicity) were extracted from the larvae under 40× magnification using a dissecting scope. The contents of the stomachs 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× magnification. Zooplankton lengths were transformed to dry weight using published equations [rotifers (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, we first calculated zooplankton density and composition for each treatment (i.e. lake) and sampling day. Zooplankton organisms consumed by carp larvae (by number, weight and length frequency) were also identified for each sampling day and treatment. Diet selectivity (I) was determined using Ivlev's (1961) index: $I = \frac{r_i - p_i}{r_i + p_i}$, 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 was 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 one-way ANOVA was conducted for all treatments and years combined because large differences in zooplankton abundance occurred among lakes within each trophic status, so grouping lakes by their trophic status (oligo-, meso- and eutrophic) to conduct a two-way ANOVA (trophic status and year) was not

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

biologically meaningful. The well water reference was not included in this analysis.

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 ($p < 0.05$) to examine differences among treatments. The well water reference was not included in this analysis.

Results

The density of microzooplankton, specifically rotifers, was greater than the density of macrozooplankton in the water supplied daily to the larvae for all treatments and ranged between 692 and 4784 individuals per liter (Table 1; Figure 1). The density of rotifers was highest in Eu 2014 and Eu 2015 followed by Meso 2014, Meso 2015 and Oligo 2015 (Table 1). The mean concentration of macrozooplankton ranged between approximately 30 and 100 individuals per liter in all lakes and years, but it was markedly higher in Eu 2015 when it exceeded 200 individuals per liter (Table 1; Figure 1, 2). 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 rotifers 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 the vast majority of zooplankton in all stomachs 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, it was observed that larvae could consume prey as large as 1.00 mm on the first day and 1.25 mm on third day of exogenous feeding (Figure 4). The number of prey items and composition of prey were consistent among individual larvae within each treatment and day (supplementary Figure S2).

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 was 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 increased on days 6 and 10 (Figure 6).

Larval survival differed significantly among treatments (ANOVA, df = 4, F = 25.02, $p < 0.0001$). While survival was relatively high and not statistically different in Eu 2015, Meso 2014, 2015, and Oligo 2015 it was significantly lower in Eu 2014 due to unexpected die-offs of all larvae in four tanks on days 9 to 12 (Tukey $P < 0.05$; Figure 7). In the reference well water treatment, which was not used in statistical analyses, all larvae perished by day 7 of the experiment (Figure 7).

Final day lengths and weights were significantly different among treatments (ANOVA, df = 4, $p < 0.0001$). Final day lengths and weights in Eu 2015 and Eu 2014 were significantly higher than in other treatments (Tukey $p < 0.05$; Figure 8, 9).

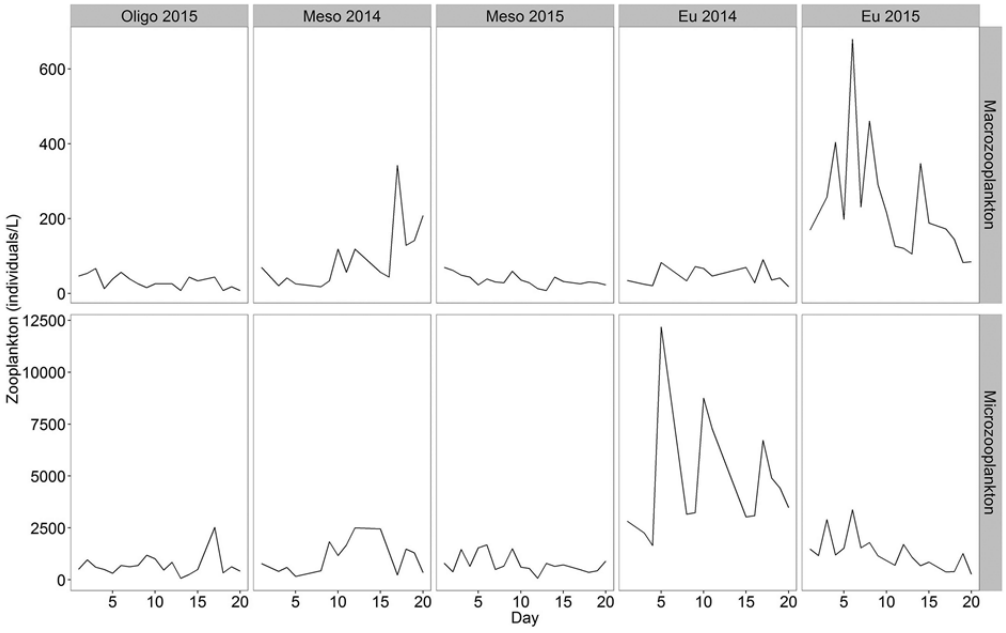

Figure 1. The daily concentration (individuals/L) of macrozooplankton (> 200 µm; top panels) and microzooplankton (< 200 µm, bottom panels) supplied to each aquarium throughout the experiment for each treatment. Note the difference in scales between panels.

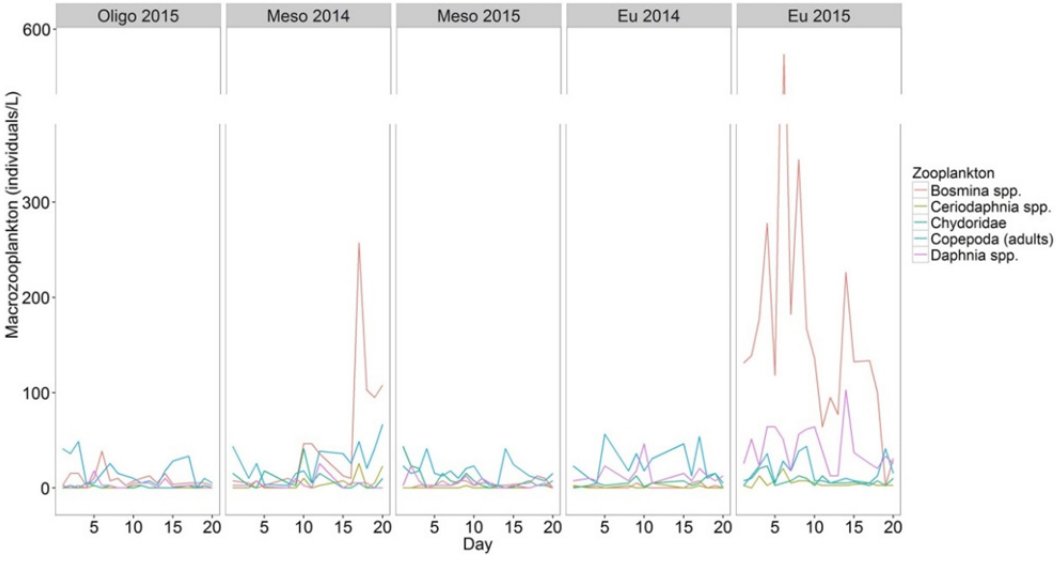

Figure 2. The concentration (individuals/L) of macrozooplankton (> 200 µm) by group in the water that was supplied to each aquarium throughout the experiment in each treatment (Note break in y-axis between 300 and 600).

Discussion

We conducted controlled laboratory experiments to shed light on processes that might explain the mechanism by which common carp recruitment occurs in eutrophic lakes but not in oligotrophic lakes (Bajer et al. 2015a). Our results suggest that common carp larvae are likely to grow much faster in productive lakes where densities of macrozooplankton that larval carp select as food are highest (Pace 1986). Faster growing carp larvae might be able to better avoid predators because reactive distance and agility to avoid predators often increases with the size of the larvae (Post and Prankevicius 1987;

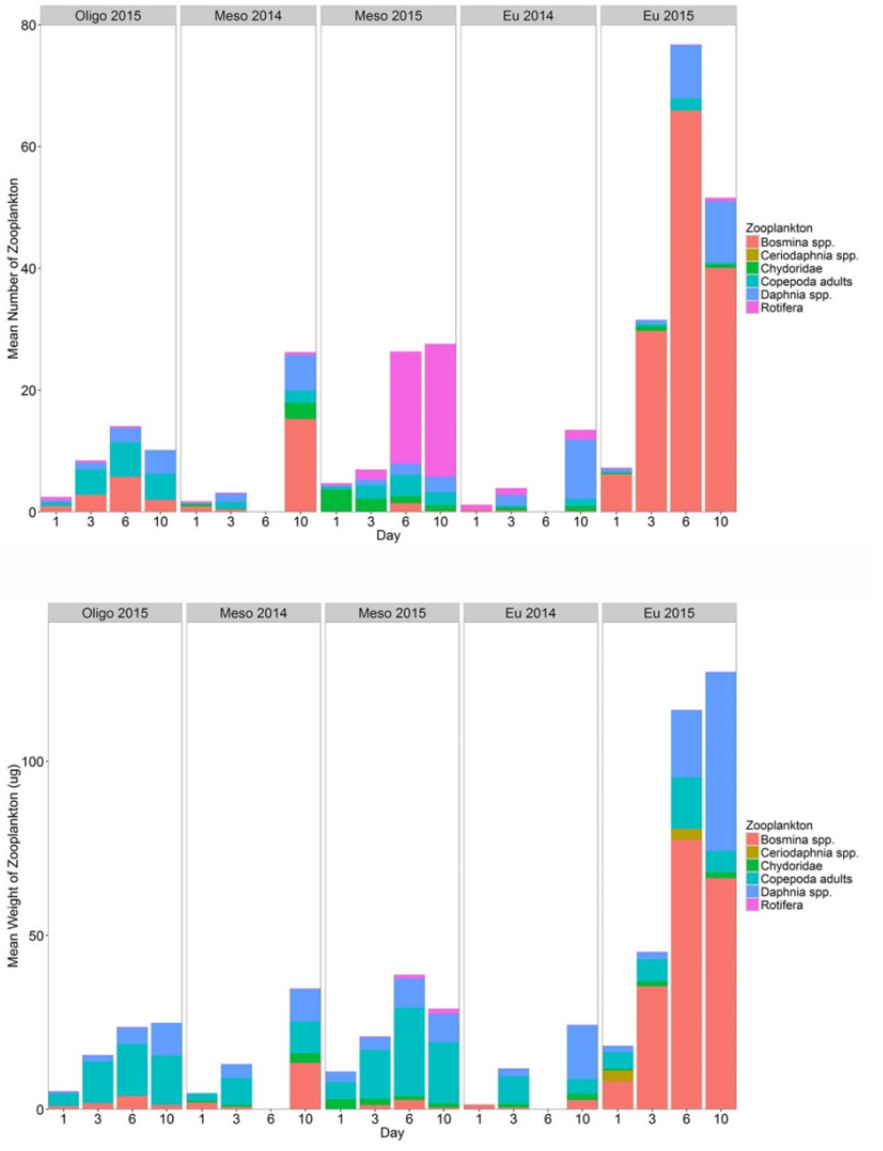

Figure 3. Mean number (top panel) and weight (µg; bottom panel) of the prey items found in the stomachs of larval carp by treatment on days 1, 3, 6 and 10 in 2014 (no samples collected on day 6) and 2015.

Fuiman and Magurran 1994; Higgs and Fuiman 1996). Also, native predatory fish communities in lakes of the Upper Mississippi River Basin are dominated by small, gape-limited centrarchids (Rahel 1984; Bajer et al. 2012), which carp larvae might outgrow much faster in productive lakes than in oligotrophic lakes. Carp larvae might also spend less time foraging in high prey density environments in highly productive lakes, which might further decrease their vulnerability to predators (Norberg 1977; Munk 1995; Puvanendran and Brown 1999). Although our results do not support the hypothesis that larval carp perish in oligotrophic lakes due to starvation (or nutritional deficiencies), our experiments were too short to fully test that possibility. Carp larvae were visibly emaciated after 20 days in the oligotrophic treatment and we hypothesize that their mortality rates would have increased over time had the experiment run longer. It is also important to note that the oligotrophic lake used in this study borderlined mesotrophic systems in terms of its trophic state index. We suspect that the growth and survival of common carp larvae would have been even poorer in oligotrophic systems, such as those found in northern Minnesota, in which the carp has not been able to become invasive since it was introduced a century ago (Kulhanek et al. 2011a, b).

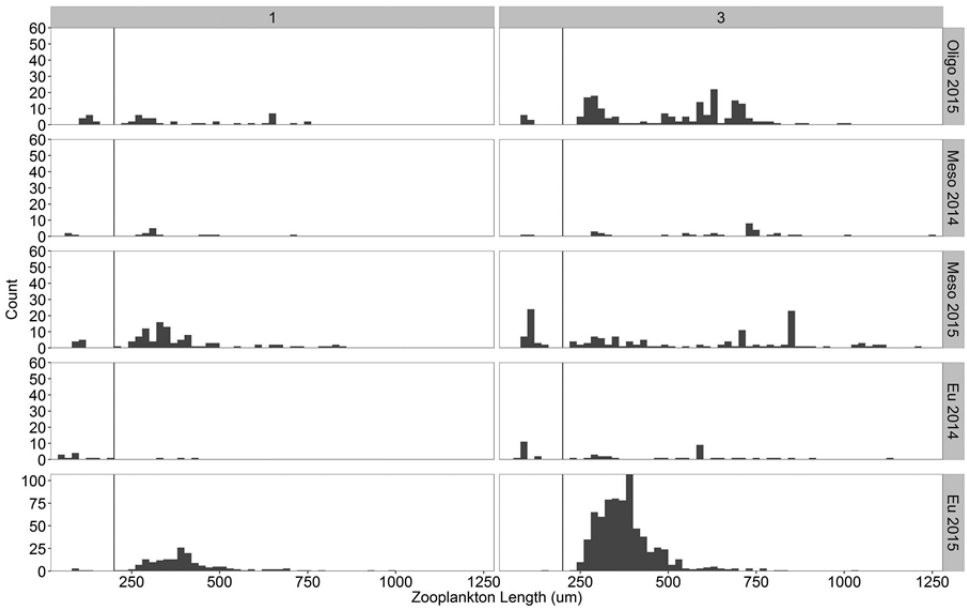

Figure 4. Length distribution of zooplankton consumed by common carp larvae on day 1 and 3 in each treatment. Shown is the cumulative number of all zooplankton items consumed by all larvae sampled on each day in each treatment (count). Vertical line represents the cut off between microzooplankton (< 200 µm) and macrozooplankton (> 200 µm). Note difference in y-axes between Eu 2015 and the rest of the treatments.

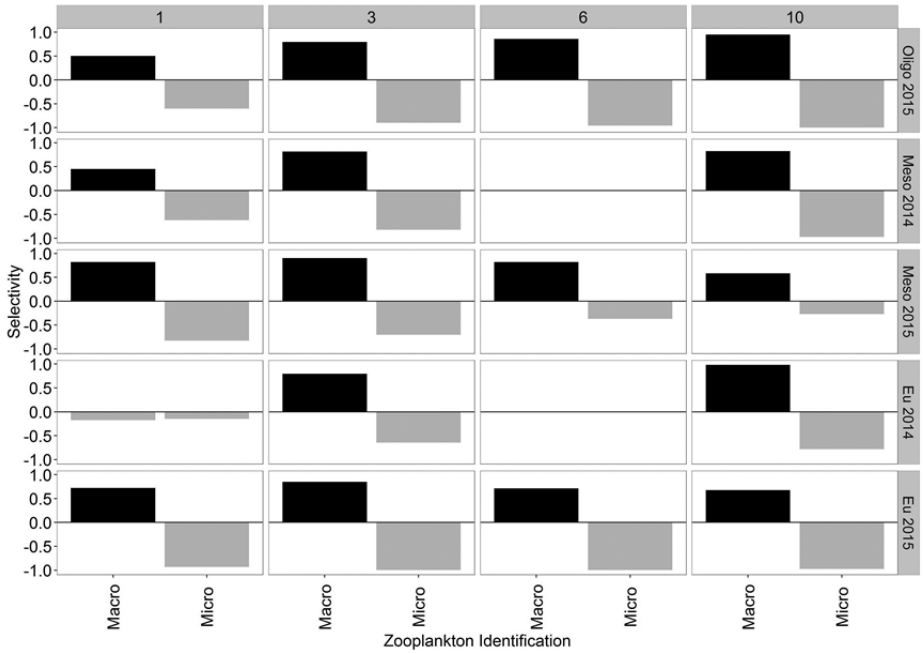

Figure 5. Ivlev's selectivity index for macrozooplankton (>200 µm) and microzooplankton (<200 µm) consumed by larval carp on day 1, 3, 6, 10 of the experiment in 2014 (no data on day 6) and 2015. Positive values (black) show preference while negative values (grey) show avoidance. The mean selectivity values for both sizes of zooplankton in Eu 2014 were negative due to predominance of larvae with empty stomachs (larvae with empty stomach have selectivity value of -1 for all food categories and cause the mean to be negative when averaged across all individuals including those that consumed some food).

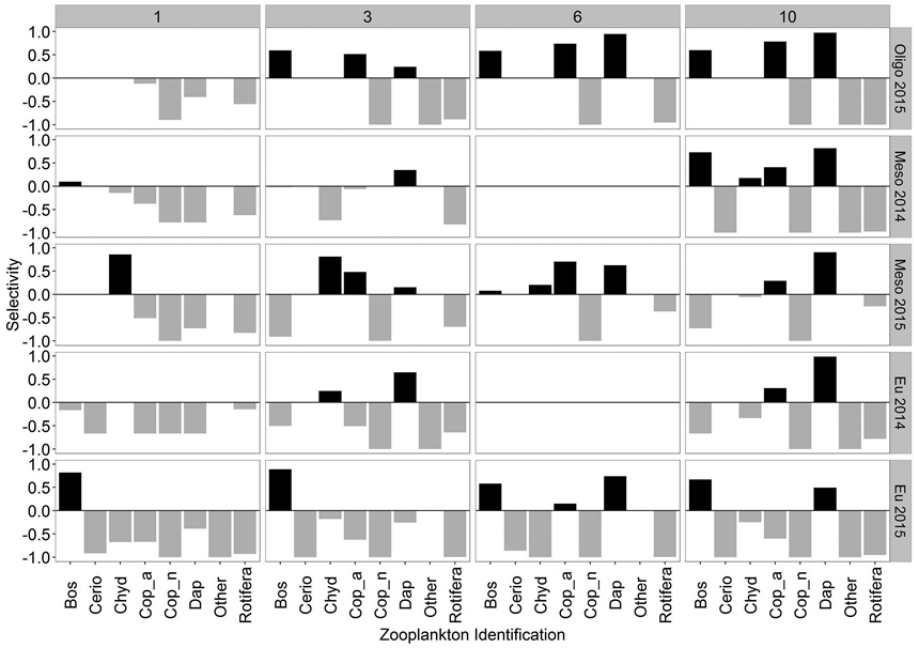

Figure 6. Ivlev's selectivity index for zooplankton consumed by larval carp on day 1, 3, 6, 10 of the experiment in 2014 (no data on day 6) and 2015. Positive values (black) show preference while negative values (grey) show avoidance. Bos = *Bosmina* spp., Cerio = *Ceriodaphnia* spp., Chyd = Chydoridae,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

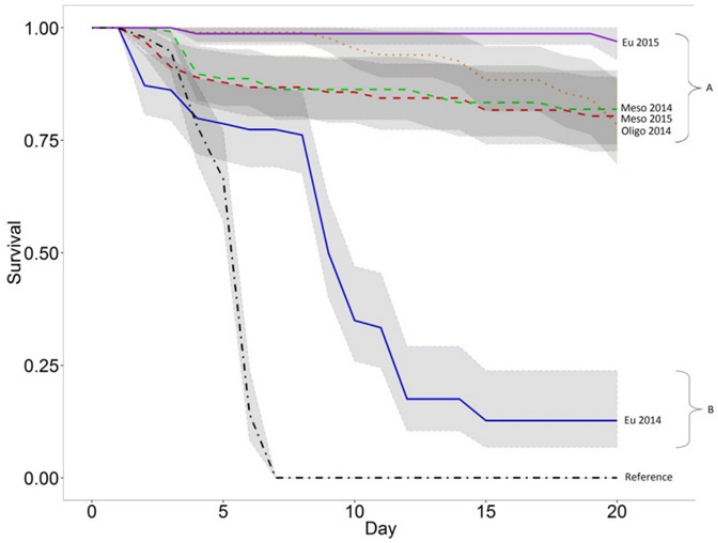

Figure 7. Mean Kaplan-Meier survival curves for common carp larvae in 2014 and 2015 treatments. The shaded areas represent the 95% confidence interval for each curve. Solid lines are used for eutrophic treatments (Eu 2014, 2015), dashed lines for mesotrophic treatments (Meso 2014, 2015) and dotted lines for oligotrophic treatments (Oligo 2015). Different letters represent significant differences in larval survival among treatments on the last day of the experiment (Tukey; $p = 0.05$). The well water treatment (dot-dashed line) was not used in the analysis and is only plotted for reference.

Invasive fish are likely to be more successful in regions where their larvae can find abundant food resources that match their specific dietary preferences. This hypothesis, however, has received little attention. This study provides one of the first accounts of prey organisms that larval common carp consume as first exogenous food in natural lakes. Larval common 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 common carp can consume particles sizes of 0.5 mm as first food, although we documented that even larger prey items

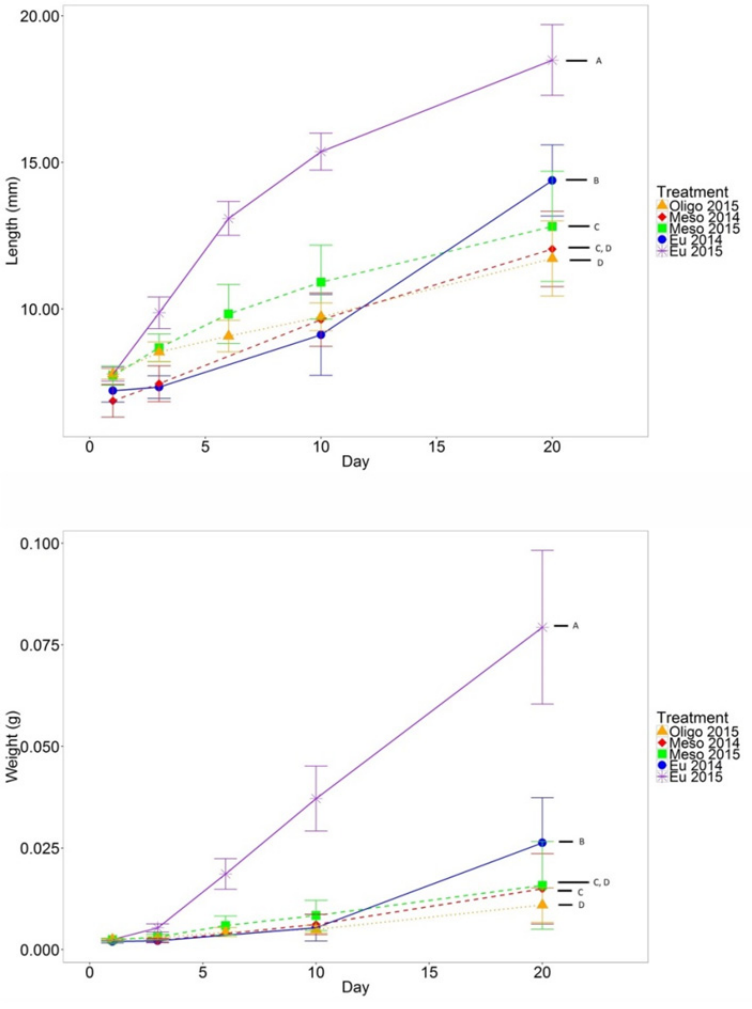

Figure 8. The mean length (top panel) in millimeters and weight (bottom panel) in grams of larval carp on days 1, 3, 6, 10, and 20 of the experiment. The error bars represent the standard deviation from the mean. Solid lines are used for eutrophic treatments (Eu 2014, 2015), dashed lines for mesotrophic treatments (Meso 2014, 2015) and dotted lines for the oligotrophic treatment (Oligo 2015). Samples on day 6 were only collected for the 2015 treatments. Different letters represent significant differences in larval lengths and weights among treatments on the last day of the experiment (Tukey; $p = 0.05$).

could 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 1.25 mm. A similar pattern was shown in an experiment where the sizes of available prey items were artificially manipulated (Khadka and Rao 1986). Rotifers were generally not observed in the stomachs of larval carp in our experiments, even in treatments where macrozooplankton were scarce, supporting earlier observations by Dabrowski et al. (1983). However, our results may convey a somewhat inaccurate representation of the role of rotifers in the diet of common carp larvae. First, the number of rotifers in larval carp stomachs might have been underestimated due to their rapid digestion rates (Williamson 1987; Sutela and Huusko 2000). Further, rotifers represent a very diverse phylum and might play a larger role in the diet of common carp larvae

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.

in systems where larger taxa are more abundant. Nevertheless, despite these caveats, our results suggest that rotifers may not be important in explaining the success of common carp across different geographic areas and ecosystem types. It is also worth noting

that dietary preferences of common carp larvae appear to be different than those of other invasive carps, such as the bigheaded carps (*Hypophthalmichthys* spp.), which forage primarily on rotifers (Dabrowski and Bardega 1984; Sampson et al. 2009; Chick et al. 2010). This suggests that larvae of multiple species of invasive carps might recruit sympatrically due to low diet overlap, at least in the initial stages of development.

Even in lakes that have relatively consistent records of common 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 and the occurrence of carp spawning might not always synchronize with zooplankton blooms (McCauley and Murdoch 1987). This might be illustrated by observed differences in larval growth rates between Eu 2014 and Eu 2015. Although growth rates were always highest in the eutrophic treatment, the larvae reached much smaller final lengths and weights in Eu 2014 than in Eu 2015. The concentration of macrozooplankton in our eutrophic lake was much lower in 2014 than in 2015, possibly due to the seasonal patterns of large macrozooplankton 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 lake was already dominated by algal blooms, while the experiment in 2015 was conducted at the beginning of the spawning season, in May, during the clear-water phase when the densities of large zooplankton are often highest. The synchronization of carp spawning with the spring blooms of large-bodied zooplankton is likely important in this species' life history. Khadka and Rao (1986) have also demonstrated the importance of synchronizing larval carp stocking with plankton blooms in aquaculture ponds. Similar patterns have been shown in marine species, such as Atlantic cod (*Gadus morhua*), where a mismatch between the timing of reproduction and plankton production might decrease the survival in young of the year (Cushing 1990; Gotceitas et al. 1996).

We 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 are unclear. However, complete die-offs in some tanks but not in others suggest oxygen deficits possibly due to insufficient air supply in some tanks. Although we did not detect oxygen deficits during the experiment, we did not measure oxygen before daybreak when daily minima occur. Such deficits might have been more likely in this particular treatment due to heavy algal concentration in Eu 2014, which increases demand for oxygen at night. In addition, 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. Interestingly, the concentration of macrozooplankton in Eu 2014 was similar to other treatments (e.g. Meso 2014 and Meso 2015), suggesting that larval carp had difficulties capturing their prey. High densities of algae in the Eu 2014 might have obstructed the visual acuity of carp larvae (Lazzaro 1987) or caused them to strike at wrong targets, increasing their metabolic demand ("confusion effect"; Czesny et al. 2001). Larval carp were observed to strike at particles and reject them in Eu 2014, thus it is plausible that poor diet along with exhaustion contributed to lower survival of carp larvae in this treatment. Future studies should examine the effect of algal density on the ability of common 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.

Our study adds an important piece of evidence to explain the complexity of processes that regulate the success (recruitment) of an invasive fish, such as the common carp in various types of environments. Empirical evidence shows that carp recruitment is most frequent and robust in systems that are both productive (in which larvae can find plenty of food) and which also have few predators, such as the bluegill (*Lepomis macrochirus*), that forage on carp eggs and larvae (Bajer et al. 2012; Bajer et al. 2015a). It is also relatively clear that carp recruit very infrequently (if ever) in systems that are oligotrophic (slow larval growth rates) and which also have abundant populations of predators (Bajer et al. 2015a). However, the frequency and strength of carp recruitment are likely to vary among ecosystems where larval food availability and predator abundance interact at different levels. Intermediate levels of recruitment might occur in system where high cladocera densities coincide with high predator abundance, in which fast growth rates might allow some larvae to escape gape-limited predators. In support of this argument, Bajer et al. (2015a) showed that carp recruited with 0.17 probability in hypereutrophic lakes (Secchi depth < 30 cm) in which bluegill catch rates exceeded 1.6 per net, but this probability increased to 0.75 if bluegill densities fell below that threshold. Further, even in predator-dominated productive lakes, carp can escape predation by spawning in peripheral shallow habitats in which predator populations are unstable due to,

for example, winter hypoxia (Bajer et al. 2015b). Carp's longevity (often > 30 years) and fecundity allows them to become invasive even if such patches of productive, predator-free habitat become available only once every several years (Bajer et al. 2015b). This illustrates that recruitment of invasive fish might often be driven by complex interactions between ecosystem productivity, abundance of predators, natural instability events, and migratory behaviors of the adults.

Introductions of invasive fish offer unique opportunities to examine the effectiveness of life history strategies employed by invader and native species in different types of environments. Many species that are native to our study region are able to recruit successfully in oligotrophic systems, albeit at lower rates (Downing et al. 1990). This suggests that they possess physiological or behavioral adaptations that allow their larvae to survive better in environments where food is scarce and/or predators are abundant. For example, to protect their eggs and larvae from predators, most of the native species that dominate fish communities in lakes of the Upper Mississippi River Basin develop nest guarding strategies or spawn in early spring when water temperatures (often as low as 2 °C–10 °C) are below optima for native predators. The first strategy is used by native centrarchids and ictalurids (Gross 1991; Novomeská and Kováč 2009), while the latter is used by esocids, percids, and some suckers (Hokanson 1977). Common carp is somewhat unique among fishes of the region because it spawns during the warm part of the season (May and June), when water temperatures approach thermal optima for native centrarchids (dominant predators), but does not employ parental care. Notably, fish communities of Eastern Europe (carp's native range) are dominated by cyprinids and have relatively few predators, which might explain carp's poor adaptations to recruit in predator-rich communities of North America. Common carp larvae also follow a faster growth trajectory than larvae of most native species (e.g. common carp typically approach 150 mm in length five months after spawning; Phelps et al. 2008; Lechelt 2016), however it is not clear how the steepness of the growth trajectory might influence larval survival in environments where food is limiting (Miller et al. 1988).

Our study has important management implications. First, it suggests possible limits for the use of biocontrol for common carp recruitment. Specifically, while it appears that abundant populations of bluegills (and likely also other egg and larval predators) can control carp recruitment in eutrophic lakes (Bajer et al. 2015a), it is not known if predatory control might also extend into hypereutrophic lakes where the growth rates of larval carp might be even higher. Secondarily, lake eutrophication due to human activities, which is a global problem (Smith 2003), is likely to enhance carp recruitment and increase the number of ecosystems in which this species can become invasive (Kulhanek et al. 2011a, b). Conversely, watershed and lake restoration efforts that result in reduced nutrient levels (and likely also reduced zooplankton abundance) in lakes might have an indirect positive effect on carp control by lowering available food resources for larval growth and reducing carp recruitment rates. We suggest that the effects of ecosystem productivity and zooplankton abundance on the invasiveness of common carp and other species of invasive carps be addressed by future studies.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Length and weight of larval carp pre and post ethanol shrinkage

Figure S2. Total number of the prey items found in the stomachs of larval carp.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2016/Supplements/AI_2016_Lechelt_Bajer_Supplement.xls