PRIMARY RESEARCH PAPER

# Feeding at different plankton densities alters invasive bighead carp (*Hypophthalmichthys nobilis*) growth and zooplankton species composition

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Abstract Invasive Asian carps Hypophthalmichthys spp. are an ecological threat to non-native aquatic ecosystems throughout the world, and are poised to enter the Laurentian Great Lakes. Little is known about how these filter-feeding planktivores grow and impact zooplankton communities in mesotrophic to oligotrophic systems like the Great Lakes. Our purpose was to determine how different plankton densities affect bighead carp H. nobilis biomass and how bighead carp affect zooplankton species composition. We conducted a 37-day indoor mesocosm experiment (volume = 678 l) with high and low plankton treatments (zooplankton dry mass  $\approx$  1,900 and 700 µg  $l^{-1}$ ; chlorophyll a = 25 and 14 µg  $l^{-1}$ , respectively) in the presence and absence of juvenile bighead carp (mean = 5.0 g, 8.5 cm). Carp lost

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weight in the low plankton treatment and gained weight in the high plankton treatment, suggesting that food availability may be a limiting factor to bighead carp growth in regions of low plankton densities. In the presence of carp, zooplankton shifted from Daphnia to copepod dominance, while in the absence of carp, Daphnia remained dominant. Chydorids and ostracods increased in the presence of carp, but only in the low plankton treatment, suggesting that the impact of bighead carp on zooplankton species composition may vary with zooplankton density. Chlorophyll was higher in the absence of carp than in the presence. Chlorophyll and zooplankton densities in many Great Lakes ecosystems are substantially lower than our low treatment conditions, and thus our results suggest that Asian carp establishment in these regions may be unlikely.

**Keywords** Asian carp · Invasive species · Planktivore · *Daphnia magna* · Microcystis · Great Lakes · Mesocosm

### Introduction

Bighead *Hypophthalmichthys nobilis* and silver carp *H. molitrix*, collectively known as Asian carps, were introduced to the United States from China in the 1970s, and have since spread throughout the Mississippi River basin, becoming an ecological threat to numerous lake and river ecosystems (Chick & Pegg, 2001). Asian carps are planktivorous, large volume

filter feeders that are able to substantially reduce phytoplankton and zooplankton biomass, thus competing with larval fishes and other planktivores (Xie & Chen, 2001). Because of their generalist diet, fast growth, and high reproductive potential, bighead and silver carp populations have increased exponentially in some areas, including the Illinois River (Chick & Pegg, 2001). Recent work using radio-tagged bighead carp in the La Grange Reach of the Illinois River has shown that adults have the potential to move more than 14 km d<sup>-1</sup> (Peters et al., 2006), and thus could enter new regions relatively quickly.

An issue of particular concern is the potential invasion of the Laurentian Great Lakes by Asian carps. Lake Michigan is connected to the Illinois River via the Chicago Sanitary and Shipping Canal, and other means of possible introduction include bait bucket transfer and live fish markets (Rixon et al., 2005; Herborg et al., 2007). Bighead carp have already been reported in Lake Erie (Kolar et al., 2005), and ecological niche modeling and risk assessment suggest that silver carp could become established in the Great Lakes (Kolar & Lodge, 2002; Chen et al., 2007; Herborg et al., 2007). Recent work suggests that Asian carps in US rivers may compete with native planktivores such as bigmouth buffalo Ictiobus cyprinellus, gizzard shad Dorosoma cepedianum (Irons et al., 2007), and paddlefish Polydon spathla (Schrank et al., 2003). Thus, there is a possibility of such competitive interactions occurring among Asian carps and planktivores of Great Lakes.

However, one factor that may influence the potential invasion of the Great Lakes and similar ecosystems by Asian carp is their energy requirements. Productivity in the Great Lakes is relatively low compared to the mesotrophic to eutrophic rivers, reservoirs, and backwater lakes where Asian carp commonly thrive. For example, phytoplankton biomass in Lake Michigan is typically  $<3 \ \mu g \ l^{-1}$ chlorophyll a (Carrick, 2005), whereas chlorophyll a values in the Middle Mississippi River can reach 40  $\mu$ g l<sup>-1</sup> (Williamson & Garvey, 2005). In order to predict if successful establishment of Asian carp in the Great Lakes is likely, it is necessary to determine how their feeding, growth, and survival is affected by a less productive environment. Despite the prevalence and impact of Asian carp as invasive species throughout the world (Kolar et al., 2005), there is little or no research on how feeding and growth vary across a productivity gradient. Rather, most studies have focused on their growth in aquaculture ponds (e.g., Burke et al., 1986; Hagiwara & Mitsch, 1994; Turker et al. 2003) or other eutrophic systems (e.g. Opuszynski & Shireman, 1993a; Lu et al., 2002; Tang et al., 2002). Here, our primary objective was to determine how zooplankton and phytoplankton densities characteristic of eutrophic and oligotrophic conditions affect bighead carp growth (i.e., overall change in biomass).

Because most ecological feeding studies of Asian carp have focused on plankton communities commonly used in aquaculture, it is also not well known how the impact of invasive Asian carp on plankton communities would vary with trophic condition. Unlike most other adult planktivorous fish, bighead carp feed on both phytoplankton and zooplankton, with some studies suggesting they switch mainly to phytoplankton when zooplankton abundances are low (Kolar et al., 2005). Thus, a secondary objective of this study was to measure the impact of bighead carp on plankton communities of low and high densities (that is, densities typical of oligotrophic and eutrophic systems, respectively). Specifically, we aimed to determine how much phytoplankton and zooplankton biomass and what zooplankton species are consumed by bighead carp and the resulting impact on plankton density and zooplankton species composition. In order to meet both this objective and our primary objective of measuring bighead carp growth, we conducted a controlled mesocosm experiment manipulating both plankton and carp.

### Methods

Experimental set up and maintenance

We conducted a mesocosm experiment with four treatments: high plankton densities (HP) and low plankton densities (LP) in the presence of bighead carp (+CARP) and in the absence of bighead carp (-CARP). Both zooplankton and phytoplankton were manipulated in the HP and LP treatments. There were three replicates of each treatment combination (12 mesocosms total), and the experiment was run indoors from October 3 to November 7, 2006 (37 days) at the Jake Wolf Memorial Fish Hatchery in Topeka, Illinois, USA. The facility had cool white

fluorescent light bulbs that provided diffuse illumination 24 h a day. The mesocosms were cylindrical fiberglass tanks with a center drain and standpipe and a volume of 678 l. A ring aerator was placed around each standpipe to aerate the mesocosms. Water from the taps flowing into the mesocosms came from Solar Pond, a 0.86 ha, oligotrophic (chlorophyll a = $2 \ \mu g \ l^{-1}$ ) shallow pond. Zooplankton densities in Solar Pond were very low due to the presence of fathead minnows *Pimephales promelas* and a few other small fishes. Several 10–20-m-long horizontal tows taken with a 48-µm net from multiple locations and depths yielded virtually no crustaceans or rotifers.

We desired to manipulate both phytoplankton and zooplankton so that the HP treatment would be comparable to the productive habitats where Asian carp currently thrive and the LP treatment would be comparable to peak algae and zooplankton densities observed in Lake Michigan. In order to have enough plankton for the HP treatment, we created a eutrophic "pond" in an outdoor concrete raceway-style enclosure  $(24 \times 1.5 \text{ m})$ . Several months before the experiment, the raceway was filled with Solar Pond water to a depth of 2.4 m using a fine screen filter to exclude small fishes. Nitrogen in the form of NaNO<sub>3</sub> and phosphorus in the form of Na<sub>2</sub>HPO<sub>4</sub> were added to the raceway in a single addition at concentrations of approximately 300  $\mu$ g l<sup>-1</sup> N and 50  $\mu$ g l<sup>-1</sup> P to stimulate plankton development. In the week before the experiment, chlorophyll a levels were approximately 20  $\mu$ g l<sup>-1</sup> and macrozooplankton densities were approximately 47 organisms  $l^{-1}$ , consisting mainly of Daphnia magna and unidentified species of calanoid copepods. Densities of plankton in the raceway fluctuated during the mesocosm experiment, but species composition changed little. Very few rotifers (<1 rotifer  $l^{-1}$ ) were observed in samples taken with a 48-µm net.

We filled the mesocosms and added zooplankton on October 1, 2006, 2 days before the fish were added, to allow the temperature of the mesocosms to reach the temperature of the carp acclimation tanks ( $20^{\circ}$ C). The HP treatments were filled with whole water (i.e., not filtered) from the raceway, while the LP treatments were 25% raceway water and 75% Solar Pond water, both not filtered. In order to increase the densities of macrozooplankton in the mesocosms, we took horizontal zooplankton tows in the raceway with a 30 cm diameter, 153-µm net and 187

added zooplankton from those tows to each mesocosm, with the high treatment receiving twice as much as the low treatment. The addition of raceway tows yielded initial densities of approximately 68 and 27 macrozooplankters  $1^{-1}$  in the HP and LP mesocosms, respectively.

Pond-raised bighead carp, 3–15 cm in total length, were maintained in indoor aerated acclimation tanks on Hikari Middle Larval Stage Plankton food (Hikari, Hayward, CA, USA) for 2 months before the start of the experiment. From the time of harvest to the start of the experiment, the fish were healthy with no diseases and little mortality. On October 3, 2006, we added two bighead carp to each +CARP mesocosm. The dorsal fin of one fish in each tank was clipped, and biomass and total length were measured for each fish. The initial mean ( $\pm$ standard error) mass and length of the carp were 5.0  $\pm$  0.3 g and 85  $\pm$  2 mm, respectively.

In order to maintain the carps' food supply during the experiment, plankton were added to each mesocosm every 4 days. We used the 153-µm net to collect and concentrate zooplankton and colonial *Microcystis* spp. from the raceway. Periodically throughout the experiment, we quantified zooplankton densities in the raceway to determine how many tows to add to each mesocosm to maintain the initial densities. An extra plankton addition to just the HP treatments was done on November 3 because zooplankton densities were quite low in the +CARP HP treatment, despite the addition on November 1. Zooplankton samples in the mesocosms were taken both before and after this addition on November 3.

Sampling and response variables

On November 7, we measured the final biomass and total length of each fish. Percent growth of each fish was calculated as  $100 \times (\text{final mass} - \text{initial mass})/$  initial mass. Percent change in total length was calculated similarly. Each fish was sacrificed, and the foreguts (identified as the portion of the gut before the first hairpin-like bend) were immediately dissected and examined microscopically. Ammonia production by the fish was not measured and was assumed to be minimal because NH<sub>3</sub> was below detection limits in an earlier experiment using the same mesocosms and similar-sized carp (Meyer, unpublished data).

The plankton in the mesocosms were sampled every 2 days, including immediately after each addition. Each mesocosm was well mixed before sampling with a pump. In order to collect zooplankton samples, 2 l of water were filtered through a 35- $\mu$ m mesh. Zooplankton were preserved in 90% ethanol, and were later enumerated in a Bogorov chamber under a dissecting microscope. Water was collected for chlorophyll *a* analysis concurrently.

Calanoid copepod, ostracod, and chydorid densities were converted to dry biomass estimates using length-weight regressions for similar taxa (Culver et al., 1985). Mean lengths were determined for each taxon by measuring a subsample of individuals from each treatment. Because *Daphnia magna* could be easily isolated in large amounts, we measured their average dry mass by drying (60°C) to a constant weight four replicates of 20 individuals on preweighed Whatman GF/F filters.

Phytoplankton biomass was inferred from chlorophyll *a* concentration, which was determined by spectrophotometric analysis. GF/C (Whatman) filtered samples were extracted in 90% ethanol in the dark and on ice for 24 h. They were then sonicated with a probe sonicator for 30 s at 50 W and extracted for an additional 24 h before centrifugation. The absorbance of the clarified extract was measured at 750 nm and 665 nm before and after acidification. Chlorophyll *a* concentration was calculated using the equations of Sartory & Grobbelaar (1984).

Dissolved oxygen and temperature were measured in each mesocosm and the raceway every 2 to 4 days using a YSI 550A Dissolved Oxygen meter (YSI Inc., Yellow Springs, OH, USA). Temperature was also monitored continuously using HOBO temperature loggers (Onset Computer Corp., Bourne, MA, USA) placed in each mesocosm and the raceway.

#### Data analysis

We performed two-way repeated measures analysis of variance (RMANOVA) on chlorophyll, *Daphnia magna*, calanoids, chydorids, and ostracods to test the hypothesis that bighead carp influence plankton differently in the HP and LP treatments over time. We expected plankton density to be a significant factor because we were adding plankton over time to maintain the treatment conditions. We also expected carp to be a significant main effect on plankton, as they are voracious planktivores. Hence, our main interest in the RMANOVA was the interaction of carp and plankton density over time. Our study has a large number of levels of within-subject effects (20 levels corresponding to the 20 sampling timepoints), which can lead to inflated *F* statistics (Von Ende, 2001). To account for this, we used the more conservative Greenhouse-Geisser  $\varepsilon$ -adjusted *F* statistic for testing the hypotheses of within-subject effects (i.e., time by treatment interactions). We used a Bonferroni corrected significance level of  $\alpha = 0.01$  because of the five different RMANOVA tests (chlorophyll and four zooplankton groups).

In order to test if changes in fish biomass differed between HP and LP treatments, we conducted a Wilcoxon Rank Sum test because of the low replication. We computed mean fish biomass per mesocosm. We used a one-tailed *z* statistic because we were testing the directional hypothesis that growth would be higher in the HP treatment than in the LP treatment. In order to avoid a Type II error with such a small sample size (n = 3 for each treatment), we set our significance level at  $\alpha = 0.10$ . SAS 9.1 (SAS Institute, Inc. © 2002–2003) was used for all statistical analyses.

## Results

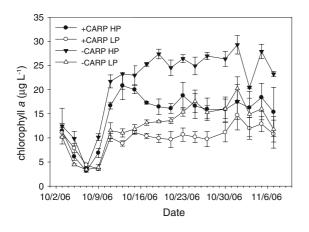
There was one fish mortality near the end of the experiment in a high replicate and in a low replicate; so one mesocosm of each treatment only had one fish instead of two (five total fish in each treatment). Over the 37 days mean bighead carp growth (percent change in mass) increased by 2.3% in the HP treatment and decreased by 2.8% in the LP, a significant treatment difference (z = 1.53; P = 0.06). Four of the five fish increased in total length in the HP treatment, whereas only one fish increased in length in the LP treatment (Table 1).

Overall, the high and low phytoplankton and zooplankton treatment conditions were maintained during the experiment. Phytoplankton biomass, as measured by chlorophyll *a* (chl *a*) concentrations, was higher in the HP treatments compared to the LP (Fig. 1, Table 2). *Daphnia magna* and calanoid copepod biomasses were also higher in the HP treatment than in the LP (Fig. 2a, b, Table 2). These were the two dominant zooplankton groups at the start of the experiment (~90% of total zooplankton biomass).

| Treatment &<br>Tank replicate | Initial<br>mass (g) | Initial total<br>length (cm) | Growth (%) | Change in total<br>length (%) |
|-------------------------------|---------------------|------------------------------|------------|-------------------------------|
| HP                            |                     |                              |            |                               |
| А                             | 3.7                 | 7.6                          | +5.4       | +2.6                          |
| А                             | 5.7                 | 8.8                          | +1.8       | +1.1                          |
| В                             | 6.5                 | 9.5                          | -1.5       | +5.3                          |
| С                             | 4.2                 | 7.8                          | +7.1       | +2.6                          |
| С                             | 7.1                 | 10.0                         | -1.4       | 0                             |
| LP                            |                     |                              |            |                               |
| А                             | 4.0                 | 7.7                          | -2.5       | 0                             |
| А                             | 5.8                 | 9.3                          | -6.9       | -3.2                          |
| В                             | 4.1                 | 7.8                          | 0          | +2.6                          |
| С                             | 4.1                 | 7.9                          | -2.4       | 0                             |
| С                             | 6.3                 | 9.5                          | -1.6       | 0                             |

**Table 1** Initial mass (g), initial total length (cm), percent change in mass (i.e., growth), and percent change in total length of each bighead carp over the course of the 37-day experiment in the high (HP) and low (LP) plankton treatments

The letters indicate to which replicate tank each carp was assigned (replicate B of both treatments lost one fish). Percent growth is  $100 \times (\text{final mass} - \text{initial mass})/\text{initial mass}$ , and percent change in total length was calculated similarly



**Fig. 1** Chlorophyll *a* concentrations over the 37-day experiment. Each symbol is the mean of the three replicate mesocosms in each treatment, and error bars represent the standard error (SE). *Closed circles* +CARP high plankton (HP) treatment, *open circles* +CARP low plankton (LP) treatment, *closed triangles* –CARP HP treatment, *open triangles* –CARP LP treatment

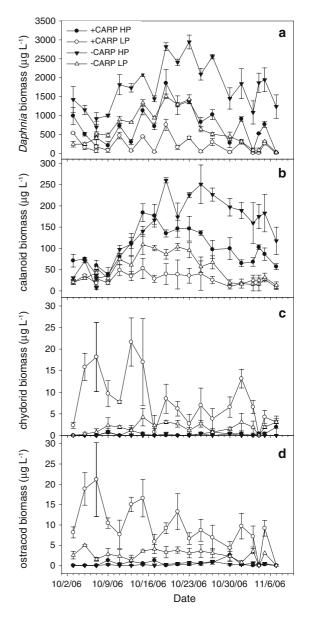
There was more chl *a* in the –CARP compared to +CARP, indicating that carp may have consumed phytoplankton, although with P = 0.0148 this was not quite significant at the Bonferroni corrected level of 0.01 (Fig. 1, Table 2). During most of the experiment, the phytoplankton community was dominated by *Microcystis* spp. colonies. *Microcystis* comprised approximately 80% of the carp foregut contents by volume at the end of the experiment.

Daphnia magna individuals in this experiment were quite large, with a mean ( $\pm$ standard error) dry mass of 20.2  $\pm$  0.3 µg. *Daphnia* biomass was higher in the -CARP than in the +CARP (Fig. 2a, Table 2). There appeared to be a plankton  $\times$  carp interaction for Daphnia, especially near the end of the experiment when biomass was higher in the -CARP HP compared to +CARP HP, indicating consumption of Daphnia in the HP, but biomass was no different between the -CARP LP and +CARP LP, indicating little consumption in the LP (Fig. 2a). However, this effect was not statistically significant (Table 2). Likewise, for calanoid copepod biomass, the time  $\times$  carp  $\times$  plankton interaction was not significant at the  $\alpha = 0.01$  level (Table 2). However, it appeared that on several later dates (October 19, 23, 27; November 1), the carp in the HP treatment may have been consuming copepods during the last couple weeks of the experiment (Fig. 2b).

Chydorids and ostracods increased during the first 2 weeks in the +CARP LP treatment and remained greater than in the HP treatment throughout the experiment (Fig. 2c, d; Table 2). Ostracods and chydorids were also elevated in the -CARP LP treatment. However, initial chydorid densities, while quite low in all treatments (0–1 1<sup>-1</sup>), were significantly higher in the +CARP LP treatment ( $F_{1,8} = 12.00$ , P = 0.0085). Likewise, initial ostracod densities (0–5 1<sup>-1</sup>) were higher in the +CARP LP and -CARP LP

| Dependent variable Between-subject effects | Between   | -subject eff | fects     |        |              |        | Within-s     | Within-subject effects | cts           |        |                    |        |              |                     |
|--|-----------|--------------|-----------|--------|--------------|--------|--------------|------------------------|---------------|--------|--------------------|--------|--------------|---------------------|
|  | plnkn     |              | carp      |        | plnkn × carp | carp   | time         |                        | time × plnkn  | olnkn  | time $\times$ carp | arp    | time × pl    | time × plnkn × carp |
|  | $F_{1,6}$ | Ρ            | $F_{1,6}$ | Ρ      | $F_{1,6}$    | Ρ      | $F_{19,114}$ | Р                      | $F_{19,1114}$ | Ρ      | $F_{19,114}$       | Ρ      | $F_{19,114}$ | Ρ                   |
| Chlorophyll <i>a</i>                       | 28.24     | 28.24 0.0018 | 11.43     | 0.0148 | 2.26         | 0.1835 | 22.78        | 0.0001                 | 3.31          | 0.0596 | 2.90               | 0.0808 | 0.69         | 0.5394              |
| Daphnia                                    | 158.16    | 0.0001       | 122.71    | 0.0001 | 11.19        | 0.0155 | 71.47        | 0.0001                 | 13.83         | 0.0001 | 9.38               | 0.0009 | 4.22         | 0.0233              |
| Calanoids                                  | 51.22     | 0.0004       | 4.78      | 0.0713 | 0.28         | 0.6136 | 17.79        | 0.0001                 | 6.97          | 0.0010 | 3.47               | 0.0257 | 3.47         | 0.0258              |
| Chydorids                                  | 33.99     | 0.0004       | 17.15     | 0.0032 | 14.81        | 0.0049 | 2.75         | 0.0951                 | 2.71          | 0.0976 | 2.61               | 0.1054 | 2.62         | 0.1046              |
| Ostracods                                  | 29.77     | 29.77 0.0006 | 13.11     | 0.0068 | 11.69        | 0.0091 | 3.65         | 0.0617                 | 3.98          | 0.0510 | 2.89               | 0.0984 | 3.06         | 0.0884              |

190



**Fig. 2** Daphnia magna (**a**), calanoid copepod (**b**), chydorid (**c**), and ostracod (**d**) dry mass over the 37-day experiment. Each symbol is the mean of the three replicate mesocosms in each treatment. Symbols are the same as Fig. 1. Error bars represent SE

treatments compared to the HP treatment  $(F_{1,8} = 34.61, P = 0.0004)$ .

Throughout most of the experiment, *Daphnia* was the dominant zooplankton species. However, toward the end of the trial, *Daphnia* was depleted at a higher rate than other species in the +CARP treatments, but remained dominant in the -CARP treatments

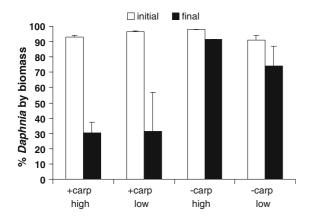


Fig. 3 Percentage of the zooplankton biomass that was *Daphnia magna* in each treatment at the beginning (white bars) and end (black bars) of the experiment. Each bar is the mean of the three replicate mesocosms in each treatment. Error bars represent SE

(Fig. 3). The final total biomasses were 84  $\mu$ g l<sup>-1</sup> in the +CARP HP, 11  $\mu$ g l<sup>-1</sup> in the +CARP LP, 1,355  $\mu$ g l<sup>-1</sup> in the -CARP HP, and 37  $\mu$ g l<sup>-1</sup> in the -CARP LP treatments.

Microscopic examination of carp foreguts confirmed that along with *Microcystis* spp., the fish had consumed zooplankton and other materials, at least at the end of the experiment. In the HP treatment, pieces of *Daphnia* and copepods could be seen in two of the five fish, and in one fish, at least 15 whole *Daphnia* and several copepods could be discerned. In the LP treatment, four of the five fish guts had ostracod shells. Ephippia and bryozoan statoblasts were observed in gut samples from both treatments.

Dissolved oxygen was slightly but significantly lower in the +CARP compared to -CARP  $(F_{1,8} = 16.66, P = 0.0035)$ . Oxygen levels averaged 97.6% and 98.2% saturation in the +CARP and -CARP treatments, respectively. Oxygen saturation never dropped below 94%. The average temperature over the course of the experiment was 17.1°C, and the range was from 15.4 to 21.8°C. This range is comparable to summer surface temperatures in Lake Michigan and other northern temperate lakes.

## Discussion

Bighead carp are known to have broad, adaptable feeding habits (Jennings, 1988), but these growth

results suggest that food availability may limit their establishment in regions of low plankton density. Weight loss in the LP treatment indicates that there was not enough food to support basic metabolic requirements, while weight gain in the HP treatment indicates that food sources and general conditions within the mesocosms were favorable.

The two biggest carp in the HP treatment were the only ones that experienced weight loss (Table 1). The fact that one of these carp increased in length by the highest percentage indicates that it may have experienced weight gain during the experiment, but lost mass as zooplankton became depleted toward the end. The other carp with negative growth, the largest (initial mass of 7.1 g), was the only carp in the high treatment that did not increase in length. In the LP treatment, no fish gained weight and only one fish increased in length. This fish was in replicate B, where the second fish was lost about a week before the experiment ended; so the lower fish to plankton ratio during this time may have been responsible for the positive growth of this fish. We initially had trouble maintaining treatment conditions, which may have compromised carp growth and fitness during the first week, especially in the HP treatment. However, for the majority of the experimental trial we were able to maintain adequate plankton biomass.

Maximum feeding of bighead carp is generally observed in the range of 20 to 30°C (Jennings, 1988), but the mean temperature during this experiment was 17.1°C, with the maximum reaching 21.8°C. Growth may have been higher in both treatments if we had conducted the experiment at a higher temperature, but our objective was to mimic the thermal conditions of potential north temperate invasion sites such as the Great Lakes.

A secondary goal of this study was to evaluate the effects of bighead carp on zooplankton community composition and phytoplankton density. There was a community shift from *Daphnia* to calanoids in the +CARP but not in the –CARP, indicating differential consumption of *Daphnia* over calanoids. This shift was robust: it occurred despite our repeated plankton additions. Although the bighead carp consumed calanoids toward the middle and end of the trial, they consumed *Daphnia* at a higher rate throughout the trial. This apparent feeding selection for *Daphnia* over calanoids, as suggested by Williamson & Garvey

(2005). We also observed an increase in small bodied chydorids and ostracods in the +CARP LP but not in the +CARP HP, an effect that may be due to competitive release from Daphnia and calanoids. Chydorids and ostracods may not have experienced competitive release in the HP treatment because Daphnia and calanoid densities were still relatively high despite some consumption by the carp. Also, initial chydorid and ostracod densities were lower in the HP treatment compared to LP treatment, indicating that these taxa may have entered the mesocosms with the unfiltered Solar Pond water rather than raceway water. Nevertheless, the higher ostracod and chydorid densities in the +CARP LP compared to -CARP LP treatment suggests that differential feeding of bighead carp can indirectly benefit certain zooplankton species, at least on a short-term time scale. A final consumption result we observed was the abundance of Microcystis in the carps' guts. Bighead carp have been shown to graze upon and substantially reduce Microcystis and other blue-green algae (Opuszynski & Shireman, 1993a; Datta & Jana, 1998), although other studies suggest that the digestibility and assimilation of blue-green algae by Asian carp can be poor (Burke et al., 1986; Kolar et al., 2005). Because of the experimental nature of our study, the plankton communities in the mesocosms did not precisely replicate those in the Great Lakes. Nonetheless, the results of our experiments still provide general information on bighead carp feeding characteristics and trophic effects.

It is possible to estimate carp consumption rates during the experiment by assuming that consumption was the major factor accounting for plankton differences between mesocosms with and without carp. If this were the case, then rough estimates based on the zooplankton biomass differences between the +CARP and -CARP over time indicate the carp consumed about 7-14% of their body mass per day, which is similar to other estimates for bighead carp (Opuszynski & Shireman, 1993b). However, zooplankton differences between the +CARP and -CARP may have also been due to other factors, such as higher Microcystis spp. in the -CARP treatments, as this algae is often toxic to Daphnia magna (Trubetskova & Haney, 2006).

Our study focused on one size class of bighead carp at a relatively narrow temperature range, and thus, extrapolation of our growth and consumption results to the full range of biological and environmental conditions that affect Asian carps should be done cautiously. Nevertheless, our growth results suggest that the threat of invasion by filter-feeding carp will be limited to particular times of year and regions within ecosystems. Certain littoral zones, bays, harbors, and backwater regions are likely to have higher plankton levels than pelagic zones. Within Lake Erie, phytoplankton biomass is more than 40 times higher at sampling sites in the western and central basins than in the eastern (Barbiero & Tuchman, 2001), and macrozooplankton densities range from about 15 to 21 l<sup>-1</sup> in the western and central basins compared to 9  $l^{-1}$  in the eastern basin (Barbiero et al., 2001). Thus, establishment by invading Asian carps may be more likely in the western and central basins of Lake Erie where there are more adequate food resources. It should be reiterated, however, that bighead carp are generalist feeders, and are known to switch to feeding on detritus and sediments when plankton are low (Kolar et al., 2005). Thus, it is possible that sediment resuspension events, such as the 1998 coastal plume in Lake Michigan (Schwab et al., 2000), could provide additional food resources in oligotrophic pelagic regions, although the quality of detritus and sediment compared to plankton is probably low.

Our results also have important implications for regions that are subject to both anthropogenic changes and the establishment of Asian carps. Asian carps are global invaders with reproducing populations in non-native ecosystems throughout the world. Invasive bighead carp is considered "established" or "probably established" in 24 countries and is listed as present but "probably not established" in 10 countries (Kolar et al., 2005). Ecological changes such as eutrophication could potentially facilitate the expansion of Asian carps in ecosystems where they are present but have not yet established large reproducing populations. We suggest that changes in potential food resources in these ecosystems be assessed, and that further evaluation of Asian carp feeding characteristics is warranted.

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