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Diet of Invasive Silver Carp (*Hypophthalmichthys molitrix*) in a Mainstem Reservoir Ecosystem

Benjamin B. Tumolo^{1,2,4,*}

¹ Watershed Studies Institute, Murray State University, Murray, Kentucky 42071 USA

² Hancock Biological Station, Murray State University, Murray, Kentucky 42071 USA

and

Michael B. Flinn³

³ Department of Biological Sciences, Murray State University, 2112 Biology Building, Murray, Kentucky 42071 USA

ABSTRACT

Hypophthalmichthys molitrix (Silver Carp) is an invasive fish that threatens ecosystem function by consuming basal food web resources. In this study we quantify gut contents of 83 Silver Carp in the mainstem reservoir ecosystem of Kentucky Lake, Kentucky, Tennessee River Valley, United States. Silver Carp guts contained phytoplankton (63.5%), zooplankton (33.8%) and heterotrophic flagellates (2.7%) based on volume. Additionally, we compare existing literature on Silver Carp diet and trophic position (i.e., stable isotope information). Our study indicates that Silver Carp are planktivorous and consume organisms within multiple lower trophic levels across a range of habitats. However, we show that Silver Carp diets differ at finer taxonomic scales and suggest these differences may be driven by forage availability. To our knowledge, this is the first study to quantify diets of Silver Carp within a mainstem reservoir ecosystem designed for flood storage with a comparison to existing Silver Carp diet literature. The results of this study may be useful in predicting ecological implications of Silver Carp invasion across a diversity of habitats.

INTRODUCTION

At least 50 species of non-native fish have become established throughout the United States (Nico and Fuller 1999) presenting significant threats to biodiversity and ecosystem functions (Gido and Brown 1999; Rahel 2000; Tumolo and Flinn 2017) by altering food web structures through competition for food resources, and by predation on native species (Vander Zanden et al. 1999; Baxter et al. 2004; Strayer et al. 2010; Sagouis et al. 2015; Gallardo et al. 2016). *Hypophthalmichthys molitrix* (Valenciennes) (Silver Carp) and *H. nobilis* (Richardson) (Bighead Carp), hereafter referred collectively as Asian carp, are two such invaders that have become established throughout much of the southern and central U.S. (for a detailed summary see Kolar et al. 2005). Within invaded ranges, Asian Carp's consumption of basal resources has been

attributed to a multitude of direct and indirect effects including: suppression of ecosystem phytoplankton (Tumolo and Flinn 2017) and zooplankton biomass (Sass et al. 2014), changes in native fish communities (Irons et al. 2007; Solomon et al. 2016), and shifts in food web linkages along the aquatic-terrestrial interface (Collins and Wahl 2017). More specifically, Silver Carp pose significant threats to ecosystem function because of their high dietary overlap with native planktivorous forage fish (Sampson et al. 2009; Minder and Pyron 2017) and indiscriminate consumption of high levels of phytoplankton and zooplankton (Cremner and Smitherman 1980; Wang et al. 1989). Previous studies focusing on relationships between Silver Carp and invaded environments have increased our understanding of the potential mechanisms driving ecosystem effects. However, the scope of this study is aimed at better understanding the diets of Silver Carp in a mainstem reservoir and to recognize patterns of Silver Carp diet across a diversity of habitats.

In the early 1970's, Silver Carp were introduced to aquaculture ponds of the southern

* Corresponding author e-mail: bbtumolo@gmail.com

⁴ Present Address: Department of Ecology, Montana State University, P.O. Box 173460, Bozeman, Montana 59717-3460 USA

U.S. for biotic control of noxious algae (Freeze and Henderson 1982). Shortly after their introduction, Silver Carp escaped and subsequently have spread throughout much of the Mississippi River Basin (Freeze and Henderson 1982; Kolar et al. 2005). Research from the midwest U.S. has described key characteristics of this fish including population dynamics, reproduction, life history traits, and feeding ecology (Cremer and Smitherman 1980; Williamson and Garvey 2005; DeGrandchamp et al. 2007; Lohmeyer and Garvey 2009; Sass et al. 2010; Deters et al. 2013; Stuck et al. 2015; Minder and Pyron 2017), while others have shown how Silver Carp have affected invaded ecosystems (Irons et al. 2007; Sass et al. 2014; Solomon et al. 2016; Tumolo and Flinn 2017). Despite the growing body of literature on Silver Carp in the U.S., most research has been concentrated on large river systems including the Mississippi and Illinois and less effort has been made to synthesize and compare existing global knowledge of Silver Carp diet (however, see Kolar et al. 2005). Further, much less is known about the biology of Silver Carp in large reservoirs, such as the impoundments that occur throughout the Tennessee and Cumberland River basins. Mainstem reservoirs function along a nexus from lotic to lentic environments and often have very large lacustrine or lake-like reaches that differ limnologically from large rivers (Søballe and Kimmel 1987; Thornton et al. 1990; Wetzel 2001, Downing et al. 2006). Quantifying the diets of Silver Carp within these reservoir ecosystems may help us understand potential effects on an ecosystem that has become widespread throughout the U.S. Finally, comparing our results to existing literature may reveal general patterns for predicting Silver Carp impacts.

The primary objective of this study was to provide a description of Silver Carp diet in a mainstem reservoir ecosystem of the Tennessee River Valley, U.S. and compare this information with existing literature concerning Silver Carp. We predicted that Silver Carp diets would be predominantly comprised of phytoplankton, and secondarily zooplankton and that this would be consistent across a range of habitats found within the literature. To our knowledge this is the first study to quantify wild Silver Carp diets within large flood-storage reservoirs or in the Tennessee River Valley U.S.



Figure 1. The location of Kentucky Lake showing sampling sites used in the diet analysis of Silver Carp from 20 May 2014 to 28 September 2014. A total of five sites were sampled for Silver Carp in Kentucky Lake including four embayment sites (Ledbetter, Pacer, Anderson and Blood River), and one “Main Channel” site.

MATERIALS AND METHODS

Study Site

Our study took place in Kentucky Lake ($36^{\circ} 43' 56''\text{N}$, $88^{\circ} 6' 57''\text{W}$) of western Kentucky (Figure 1). Kentucky Lake is the last impoundment of the Tennessee River and is a large, shallow, well mixed, mesotrophic reservoir approximately 296 km long with a surface area of 64,874 hectares (Bukaveckas et al 2002; Yurisita et al. 2004). Phytoplankton production and community structure within Kentucky Lake have been shown to be driven by hydrology and nutrient availability (Bukaveckas et al 2002; Yurista et al. 2004). Additionally, Bukaveckas et al. (2002) found that during the early summer (May–June), nutrient availability was relatively high and the phytoplankton community was dominated by diatoms and green algae; as nutrients became more limiting (July), cyanobacteria dominated and dinoflagellates became more prevalent. We sampled five sites within Kentucky Lake that encompassed one main channel site and four embayment sites (Figure 1) weekly from 20 May 2014 to 28 Sep 2014. During the study period, the ranges of daily average values of physical variables within Kentucky Lake at 1 m deep from 1 May to

30 September 2014 were: temperature = 18.–30.3°C (mean = 26.2 ± SE 0.2°C), dissolved oxygen = 1.5–15.12 mg L⁻¹ (7.1 ± 0.1 mg L⁻¹) and pH = 7.0–8.6 (Hancock Biological Station, HBS, unpublished data).

Fish Collection and Processing

To describe Silver Carp diet, fish were collected from Kentucky Lake with mono- and multi-filament gill nets (mesh = 20.3 and 17.8 cm stretch, respectively). Gill nets were deployed over the spring and summer seasons and typically run for four day periods at embayment and channel sites (Figure 1). On a given day, nets were checked twice, allowing for approximately twelve soak hours between net checks, totaling a minimum of 72 hrs per net over a given sampling week. Captured Silver Carp were euthanized according to the Murray State University Institutional Animal Care and Use Committee (IACUC) protocol number 2014-008, and then placed on ice until further processing. Total length (TL) of individual fish was measured to nearest millimeter and weight was measured to nearest gram. Sampling sites were chosen to encompass a range of reservoir habitats (i.e., embayment, main channel) and diet information was combined across sampling sites.

Gut Content Analysis

Silver Carp diets were sampled from the foregut (from anterior of esophagus to first bend) by opening the ventral side of the fish from the anus to the base of the operculum (Gelwick and Matthews 2006). Silver Carp do not have a true stomach and previous studies have shown that prey items within the foregut are typically less digested and allow for more accurate prey identification (Sutela and Huusko 2000). Once the ventral side of the fish was opened, the start of the esophagus was located and pinched off with a binder clip (adapted from Gelwick and Matthews 2006). The esophagus/foregut was followed until the first bend and an additional binder clip was fixed to contain contents of the study section. The study section of the gut was removed from the fish and the gut contents extruded into a Whirl-Pak[®] bag, preserved with 70% ethanol, and transported to the laboratory for microscope analysis. Gut contents were shaken vigorously

inside of the Whirl-Pak[®] in an attempt to remove prey contents from gut mucilage (adapted from Sampson et al. 2009). Gut contents were then transferred to a 200 ml beaker and homogenized via manual stirring. Three, 1-ml aliquots were removed with a pipette from the homogenized gut sample, and placed into a Gridded Sedgewick Rafter cell (Wildlife Supply Company[®]). Gut contents were enumerated based on 25 randomly selected views or 1,000 cell counts (excluding colonial cyanobacteria), depending on whichever count came first. Phytoplankton were identified to genus or lowest practical taxonomic level (Wehr and Sheath 2002). Cell count exceptions were made for colonial cyanobacterium (e.g., *Microcystis* sp.) because in many instances colonies contained over 1000 cells. For the purposes of the study, we measured an approximate perimeter of cyanobacteria colonies, assigned a cell diameter of 1 µm (Wehr and Sheath 2002), and extrapolated biovolume from this estimate. Many non-colonial coccoid algae lacked identifiable features, in these cases we were unable to differentiate cyanobacteria from green algae, prompting identification as “Little Green Ball” (LGB, Rindi 2014). Phytoplankton prey were organized into one of four systematic groups: cyanobacteria (coccoid and filamentous), LGB, green algae (flagellated, non-motile coccoid, colonial, filamentous and desmids), and diatoms (chain forming centrics, colonial pennates, single celled pennates). Relative biovolume of phytoplankton was estimated based on geometric equivalents of phytoplankton taxa (Hillebrand et al. 1999). To estimate taxa specific biovolume, we used cell dimensions measured at 600X and published size ranges (Wehr and Sheath 2002). Zooplankton in stomach samples were identified to genus or lowest practical taxonomic level (Smith 2001). However, larger zooplankton prey (e.g., Copepoda and Cladocera) frequently showed signs of digestion, and features were distorted by gut mucilage (e.g., Bitterlitch and Gnaiger 1984), thus identification of these prey were often limited to Class or Order level taxonomy. Zooplankton prey items were quantified based on relative biovolume with microscope measurements and geometric equivalents. Zooplankton were placed into one of three systematic groupings: Rotifera, Copepoda (Cyclopoida/Calanoida and nauplii), and Cladocera.

Table 1. Location and sample size of Silver Carp used for diet analysis from sites within Kentucky Lake sampled from 20 May 2014 to 28 September 2014. A total of 83 Silver Carp were collected for diet analysis from embayment and channel sites using gill nets.

Site	Silver Carp (n)
Kentucky Lake	
Anderson	40
Blood River	6
Pacer	4
Ledbetter	20
Main Channel	13
Total	83

Data Analysis

For each foregut we calculated the average proportions of prey contents based on hierarchical contributions to: total foregut biovolume, trophic level (i.e., phytoplankton or zooplankton), systematic groupings, and lower taxonomy based on three replicate aliquots per fish foregut. Silver Carp diet was characterized based on all fish foreguts examined in the study.

Literature Search and Comparison

We conducted an exhaustive literature search for data and analyses focused on diet composition and trophic position (i.e., stable isotope analysis) of Silver Carp using ISI Web of Science and Google Scholar. We categorized studies based on three categories: habitat in which the study was conducted, methodology used to quantify trophic characteristics and/or diet, and the estimated proportion of phytoplankton to zooplankton consumed and/or assimilated by Silver Carp.

RESULTS

Silver Carp diet was characterized based on foregut contents of 83 fish (total length = 832 ± 6 mm, weight = 7 ± 0.2 kg [mean \pm SE]) captured from Kentucky Lake (Table 1). Silver Carp diets contained a total of 38 taxa that were divided most broadly into two major trophic groups (phytoplankton and zooplankton) and three intermediate trophic levels (bryozoans, ciliates, and dinoflagellates). Diets contained a total of seven systematic groups within broader trophic levels that included: cyanobacteria, LGB algae, green algae, diatoms, Rotifera, Copepoda, and Cladocera. A total of seven prey distinctions within system-

Table 2. Prey items identified to the generic taxonomy level within foreguts of Silver Carp (n = 83) from Kentucky Lake from 20 May 2014 to 28 September 2014. “%Total Biovolume” refers to the taxa’s average contribution to the overall foregut biovolumes, “%Class Biovolume” refers to the genera’s average contribution to its respective Class level taxonomy within foreguts. These values are based on the averaged prey biovolumes over all Silver Carp diets analyzed.

Taxa	% Total Biovolume	\pm SE	% Class Biovolume	\pm SE
Cyanophyceae				
<i>Microcystis</i> sp.	2.5	1.4	64.1	4.6
<i>Aphanocapsa</i> sp.	0.1	0.1	16.6	3.3
<i>Anabaena</i> sp.	a	a	12.9	3.3
<i>Merismopedia</i> sp.	a	a	1.5	1.2
<i>Porphyrosiphon</i> sp.	a	a	1.3	1.3
<i>Planktolyngbya</i> sp.	a	a	0.1	0.1
<i>Gloeotrichia</i> sp.	a	a	2.2	1.5
<i>Radiocystis</i> sp.	a	a	1.3	0.5
Chlorophyceae				
<i>Scenedesmus</i> sp.	a	a	10.2	2.0
<i>Eudorina</i> sp.	a	a	8.0	2.4
<i>Gonium</i> sp.	0.1	a	27.4	3.0
<i>Ankistrodesmus</i> sp.	a	a	0.1	a
<i>Pediastrum</i> sp.	0.1	a	51.4	3.6
<i>Platydorina</i> sp.	a	a	0.5	0.3
<i>Oocystidium</i> sp.	a	a	2.5	0.9
Zygnematophyceae				
<i>Staurastrum</i> sp.	a	a	90.1	4.7
<i>Euastrum</i> sp.	0.2	0.2	9.9	4.7
Bacillariophyceae				
<i>Navicula</i> sp.	a	a	80.6	4.5
<i>Gyrosigma</i> sp.	a	a	16.8	4.3
<i>Nitzschia</i> sp.	a	a	2.6	1.6
Fragilariophyceae				
<i>Fragilaria</i> sp.	a	a	2.3	1.2
<i>Synedra</i> sp.	0.3	0.1	41.6	3.8
<i>Diatoma</i> sp.	a	a	a	a
<i>Asterionella</i> sp.	0.8	0.3	56.1	4.0
Coscinodiscophyceae				
<i>Melosira</i> sp.	0.8	0.2	86.5	1.6
<i>Cyclotella</i> sp.	0.2	0.1	13.5	1.6
Rotifera				
<i>Ploima</i> sp.	a	a	1.2	0.6
<i>Keratella</i> sp.	1.5	0.5	86.7	3.7
<i>Asplanchna</i> sp.	1.4	0.6	9.1	3.5
<i>Polyarthra</i> sp.	a	a	2.9	1.5

^a = value < 0.1%.

atic groupings were noted including: Chlorophyceae (colonial green algae), Desmidiaceae (desmid algae), Bacillariophyceae (single celled pennate diatoms), Fragilariophyceae (colonial pennate diatoms), Coscinodiscophyceae (centric diatoms), Cyclopoida/Calanoida, and nauplii. Additionally, diet analysis identified a total of 30 genera of phyto-and-zooplankton prey (Table 2).

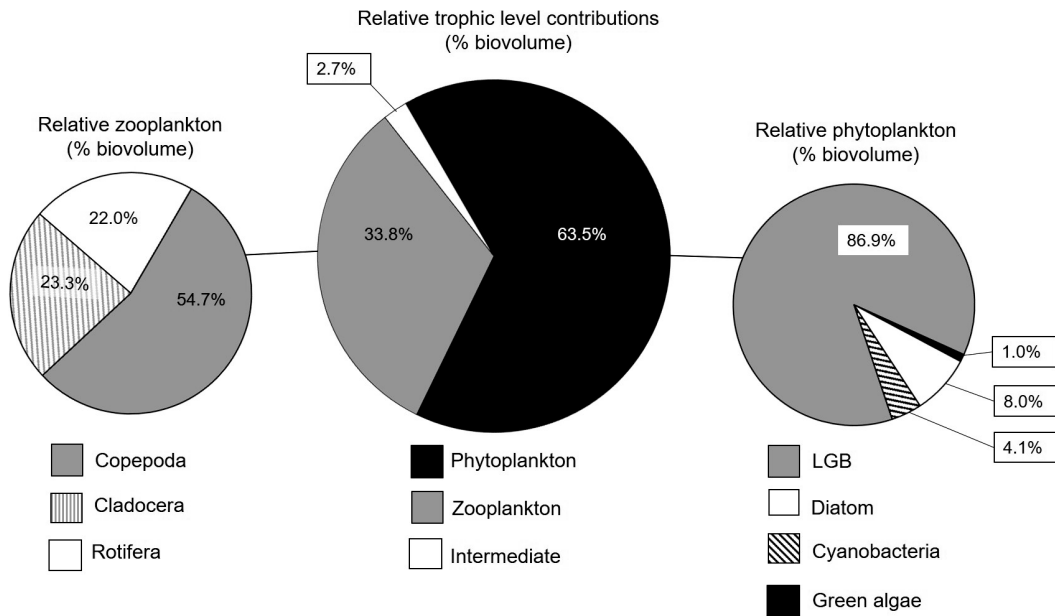


Figure 2. Overall diet composition of Silver Carp ($n = 83$) from Kentucky Lake from 20 May 2014 to 28 September 2014. Diet composition was based on the relative contribution of gut contents to foregut biovolume. The category "Other" refers to a combination of dinoflagellates, ciliates, and bryozoans. "LGB", Little Green Ball, refers to coccoid alga that cannot be distinguished as green algae or cyanobacteria.

Foregut analyses show that phytoplankton were the dominant prey comprising on average $63.5 \pm 3.8\%$ of the total prey biovolume, while zooplankton accounted for the second largest proportion ($33.8 \pm 3.8\%$, Figure 2). Dinoflagellates, contributed an average of $2.4 \pm 0.7\%$ to total foregut biovolume, while ciliates and bryozoans contributed trace amounts ($<1\%$). Within groupings, LGB algae contributed the highest average percentage to phytoplankton biovolume ($86.9 \pm 2.6\%$, Figure 2). Additionally, diatoms contributed $8.0 \pm 1.6\%$ within groups, while cyanobacteria accounted for $4.1 \pm 1.7\%$ and green algae contributed $1.0 \pm 0.3\%$ to phytoplankton (Figure 2). Centric diatoms and colonial pennates accounted for the majority of diatom biovolume, $52.7 \pm 2.6\%$ and $46.7 \pm 2.6\%$, respectively, while single celled pennates accounted for the remaining $0.5 \pm 0.2\%$. Copepoda accounted for the highest proportion of zooplankton biovolume ($54.7 \pm 4.7\%$, Figure 2). Copepoda were predominantly adult Cyclopoidia/Calanoida ($81.5 \pm 4.9\%$), and secondarily, nauplii ($18.5 \pm 4.9\%$). Cladocera comprised on average $23.3 \pm 4.1\%$ of zooplank-

ton biovolume, while Rotifera comprised $22.0 \pm 4.4\%$ (Figure 2). Our study identified and quantified the contribution of 30 phytoplankton and zooplankton prey items to generic level. The majority (26 of 30) of prey that were identified to generic level contributed $<1\%$ to total foregut biovolume and their contributions to higher trophic levels varied from 0 to 90% (Table 2).

Literature Search and Comparison

Our literature search yielded a total of 12 peer reviewed studies that measured trophic characteristics (i.e., stable isotope) and/or diet components of Silver Carp (Table 3). Studies on Silver Carp diet covered four major habitat types, using two methodologies and had a range of phytoplankton: zooplankton compositions (Table 3). Habitat distinctions were characterized as large-river ($n = 3$), large-river back lakes ($n = 2$), shallow lakes ($n = 5$) and aquaculture ponds ($n = 2$). The majority of studies used some type of gut analysis ($n = 10$), while a few studies used stable isotope information ($n = 3$), and one study used a combination of the two methods. The majority ($n = 9$) of

Table 3. Studies used in the literature analysis to synthesize previous information on silver carp diet ($n = 12$) in alphabetical order. Studies covered four major habitat types including: large river ($n = 3$), large-river back lakes ($n = 2$), shallow lakes ($n = 5$), and aquaculture ponds ($n = 2$). Studies used different methods to quantify diet and/or trophic position: gut analysis ($n = 10$), stable isotope information ($n = 3$), and gut analysis combined with stable isotope determination ($n = 1$). Published phytoplankton: zooplankton ratios were assigned to one of three categories based on predominance ($>60\%$) of gut contents and/or isotopic signature: phytoplankton ($n = 9$), zooplankton ($n = 1$), and a balanced ratio ($n = 2$).

Study	Habitat type	Methodology	Phyto: Zooplankton
Calkins et al. 2012	large river	gut analysis	phytoplankton
Cremer and Smitherman 1980	aquaculture pond	gut analysis	phytoplankton
Jayasinghe et al. 2015	shallow lake	stable isotope	balanced
Ke et al. 2008	shallow lake	gut analysis	phytoplankton
Minder and Pyron 2017	large river	gut analysis	phytoplankton
Pongrakthum et al. 2010	large-river back lake	gut analysis	phytoplankton
Sampson et al. 2009	large-river back lake	gut analysis	zooplankton
Spataru 1977	aquaculture pond	gut analysis	phytoplankton
Spataru and Gophen 1985	shallow lake	gut analysis	phytoplankton
Williamson and Garvey 2005	large river	gut analysis	phytoplankton
Xu and Xie 2004	shallow lake	stable isotope	balanced
Zhou et al. 2009	shallow lake	combination	phytoplankton

studies reported predominantly ($>60\%$) phytoplankton as prey, one study reported predominantly zooplankton, and two studies reported a more balanced proportion of phytoplankton: zooplankton prey ratios (Table 3).

DISCUSSION

It is well supported that fish can exert strong top-down forces on lower trophic levels, sometimes influencing primary production, and ultimately ecosystem energy flow (Carpenter et al. 1985; Vanni and Layne 1997; Tumolo and Flinn 2017). The results of our study show that invasive Silver Carp consume predominantly phytoplankton, and secondarily zooplankton in a mainstem reservoir ecosystem. At the broadest resolution our results agree with the majority of Silver Carp diet and stable isotope analyses spanning multiple ecosystem types, however nuances in diet components suggest food availability and electivity drive finer scale differences (Sampson et al. 2009; Pongrakthum et al. 2010; Minder and Pyron 2017). Our analysis, coupled with literature review, shows strong evidence that the diet of Silver Carp is primarily phytoplankton across disparate habitat types, however the carp do show variability in diet and trophic position (i.e., proportion of assimilated phytoplankton: zooplankton) among and within habitat types.

Our analysis showed that Silver Carp diets were predominantly phytoplankton, suggesting

that planktonic algae is an important food source for invasive Silver Carp in Kentucky Lake (Figure 2). The proportion of phytoplankton to zooplankton found in our study is consistent with other studies conducted in large rivers (Williamson and Garvey 2005; Calkins et al. 2012; Minder and Pyron 2017) and large-river floodplain lakes in the U.S. (Pongrakthum et al. 2010). Additionally, these broad patterns are consistent with diet and stable isotope analyses conducted in artificial aquaculture ponds of Israel (Spataru 1977; Spataru and Gophen 1985), the southern U.S. (Cremer and Smitherman 1980), and shallow lakes across China (Ke et al. 2008; Zhou et al. 2009). Although the proportion of phytoplankton consumed by Silver Carp in our study was consistent with much of the previous literature there were key differences in the composition of phytoplankton in guts. Our study found little contribution of Cyanophyceae, consistent with previous studies (Spataru 1977; Cremer and Smitherman 1980; Pongrakthum et al. 2010), and in contrast to others (Spataru and Gophen 1985; Ke et al. 2008; Minder and Pyron 2017). Some studies examining proportion of phytoplankton in the diets of Silver Carp did not provide taxonomic resolution suitable for comparison (Williamson and Garvey 2005; Zhou et al. 2009; Calkins et al. 2012), others found that zooplankton comprised relatively higher proportions of guts (Xu and Xie 2004; Sampson et al. 2009; Jayasinghe et al. 2015). The composition of phytoplankton

in carp guts from our study agree most closely with studies from a range of habitats and regions including: aquaculture ponds in Israel (Spataru 1977), the Southern U.S. (Cremer and Smitherman 1980), and backwater lakes of the Mississippi River (Pongruktham et al. 2010); however, despite these similarities our study found notably higher proportions of zooplankton in gut tracts.

Our study found that zooplankton composed a significant proportion of Silver Carp diets and included copepods, cladocerans, and rotifers in Kentucky Lake. Previous diet studies show zooplankton were rare in diets (Cremer and Smitherman 1980; Calkins et al. 2012; Minder and Pyron 2017) and Sampson et al. (2009) suggest that zooplankton dominated gut tracts, while stable isotope analyses (Xu and Xie 2004; Jayasinghe et al. 2015) suggest nearly even proportions of phytoplankton to zooplankton in guts. Our results suggest that large-bodied copepods and cladocerans compose the majority of zooplankton in Silver Carp diets consistent with Spataru and Gophen (1985), and Williamson and Garvey (2005). In contrast, other studies show that rotifers dominate the zooplankton prey within Silver Carp diets (Spataru 1977; Sampson et al. 2009; Pongruktham et al. 2010). Further, Sampson et al. (2009) found rotifers were selected for over larger-sized zooplankton and Pongruktham et al. (2010) suggested rotifers were the most available zooplankton prey based on system-specific zooplankton samples used in electivity indices. The previous literature suggest that the amount and types of zooplankton consumed by Silver Carp are based largely on availability and on electivity towards smaller sized taxa respectively (Sampson et al. 2009; Pongruktham et al. 2010; Minder and Pyron 2017). For example, Minder and Pyron (2017) found no zooplankton in diets from fish collected from river habitats that had very low zooplankton abundance, suggesting availability should preclude electivity and ultimately influence trophic relationships of this invasive fish. Although our study did not investigate electivity or food availability, this review of literature suggests that these are important mechanisms for food web relationships of Silver Carp within invaded ecosystems and is a consistent pattern amongst filter-feeding planktivores (Lazzaro 1987).

SUMMARY

Our diet analysis showed that invasive Silver Carp consumed multiple trophic levels within a mainstem reservoir ecosystem. Globally, studies have suggested that Silver Carp suppress plankton through predation (Starling and Rocha 1990; Starling 1993; Domaizon and Devaux 1999; Xie and Yang 2000; Guangjie et al. 2011; Lin et al. 2014; Sass et al. 2014; Tumolo and Flinn 2017) and other investigations have suggested that reductions of zooplankton negatively affected native fishes (Irons et al. 2007; Solomon et al. 2016). Our data paired with previous literature suggests Silver Carp consume a combination of phytoplankton and zooplankton across a range of habitats, however finer scale diet components are variable among and within habitats suggesting habitat specificity and food availability are factors in predicting Silver Carp diet (Sampson et al. 2009; Pongruktham et al. 2010). A recent analysis using global stable isotope data showed that invasive fish differentially altered isotopic structure of lotic and lentic ecosystems, suggesting recipient community composition may be a strong predictor of invader effects (Sagouis et al. 2015). Ultimately, our study provides descriptive information on Silver Carp gut contents from an understudied ecosystem and compares it to a range of similar analyses. This information may be useful in further measuring food web relationships and in predicting effects of Silver Carp across a geographically broad and diverse range.

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LITERATURE CITED

- Baxter, C.V., K.D. Fausch, M. Murakami, and P.L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85: 2656–2663.
- Bitterlich, G., and E. Gnaiger. 1984. Phytoplanktivorous or omnivorous fish? Digestibility of zooplankton by silver carp, *Hypophthalmichthys molitrix* (Val.). *Aquaculture* 40: 261–263.
- Bukaveckas, P.A., J.J. Williams, and S.P. Hendricks. 2002. Factors regulating autotrophy and heterotrophy in the main channel and an embayment of a large river impoundment. *Aquatic Ecology* 36: 355–369.
- Calkins, H.A., S.J. Tripp, and J.E. Garvey. 2012. Linking silver carp habitat selection to flow and phytoplankton in the Mississippi River. *Biological Invasions* 14: 949–958.
- Carpenter, S.R., J.F. Kittell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.
- Collins, S. F., and D.H. Wahl. 2017. Invasive planktivores as mediators of organic matter exchanges within and across ecosystems. *Oecologia* 184: 521–530.
- Cremer, M.C., and R.O. Smitherman. 1980. Food habits and growth of silver and bighead carp in cages and ponds. *Aquaculture* 20:57–64.
- DeGrandchamp, K.L., J.E. Garvey, and L.A. Csoboth. 2007. Linking adult reproduction and larval density of invasive carp in a large river. *Transactions of the American Fisheries Society* 136: 1327–1334.
- Deters, J.E., D.C. Chapman, and B. McElroy. 2013. Location and timing of Asian carp spawning in the lower Missouri River. *Environmental Biology of Fishes* 96:617–629.
- Domaizon, I., and J. Devaux. 1999. Experimental study of the impacts of Silver Carp on plankton communities of eutrophic Villere reservoir (France). *Aquatic Ecology* 33:193–204.
- Downing, J. A., Y.T. Prairie, J.J. Cole, C.M. Duarte, L.J. Tranvik, R.G. Striegl, W.H. McDowell, P. Kortelainen, N.F. Caraco, J.M. Melack, and J.J. Middelburg. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography* 51: 2388–2397.
- Freeze, M., and S. Henderson. 1982. Distribution and status of the bighead carp and Silver Carp in Arkansas. *North American Journal of Fisheries Management* 2:197–200.
- Gallardo B, Clavero M, Sánchez MI, and Vilà M. 2016. Global ecological impacts of invasive species in aquatic ecosystems. *Glob Change Biol* 22:151–163.
- Guangjie, Z.H.O.U., Z.H.A.O. Xuemin, B.I. Yonghong, and H.U. Zhengyu. 2011. Effects of Silver Carp (*Hypophthalmichthys molitrix*) on spring phytoplankton community structure of Three-Gorges Reservoir (China): Results from an enclosure experiment. *Journal of Limnology* 70: 26–32.
- Gelwick, F.P., and W.J. Matthews. 2006. Trophic relations of stream fishes. Pp.611–635, In F.R. Hauer, G.A. Lamberti (Eds.). *Methods in Stream Ecology*. Vol. 1. Academic Press. New York, USA. 877 pp.
- Gido, K.B., and J.H. Brown. 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* 42:387–399.
- Hancock Biological Station (HBS). 2017. Unpublished data. <http://www.murraystate.edu/qacd/cos/hbs/hbs.htm>. Accessed 16 October 2017.
- Hillebrand, H., C.D. Dürselen, D. Kirschtel, U. Pollinger, and T. Zohary. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35:403–424.
- Irons, K.S., G.G. Sass, M.A. McClelland, and J.D. Stafford. 2007. Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, USA Is this evidence for competition and reduced fitness?. *Journal of Fish Biology* 71: 258–273.
- Jayasinghe, U.A.D., E. García-Berthou, Z. Li, W. Li, T. Zhang, and J. Liu. 2015. Co occurring bighead and silver carps show similar food preference but different isotopic niche overlap in different lakes. *Environ Biol Fishes*. 98: 1185–1199.
- Ke Z, P. Xie, and L. Guo. 2008. In situ study on effect of food competition on diet shifts and growth of silver and bighead carps in large biomanipulation fish pens in Meiliang Bay, Lake Taihu. *Journal of Applied Ichthyology* 24: 263–268.
- Kolar, C.S., D.C. Chapman, W.R. Courtenay Jr, C.M. Housel, J.D. Williams, and D.P. Jennings. 2005. Asian carps of the genus *Hypophthalmichthys* (Pisces, Cyprinidae) a biological synopsis and environmental risk assessment. Report to the U.S. Fish and Wildlife Service, 183 pp.
- Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146: 97–167.
- Lin, Q., X. Jiang, B.P. Han, and E. Jeppesen. 2014. Does stocking of filter-feeding fish for production have a cascading effect on zooplankton and ecological state? a study of fourteen (sub) tropical Chinese reservoirs with contrasting nutrient concentrations. *Hydrobiologia* 736:115–125.
- Lohmeyer, A.M., and J.E. Garvey. 2009. Placing the North American invasion of Asian carp in a spatially explicit context. *Biological Invasions* 11:905–916.
- Minder, M., and M. Pyron. 2017. Dietary overlap and selectivity among silver carp and two native filter feeders

- in the Wabash River. *Ecology of Freshwater Fish*. DOI: 10.1111/eff.12365.
- Nico, L.G., and P.L. Fuller. 1999. Spatial and temporal patterns of nonindigenous fish introductions in the United States. *Fisheries* 24:16–27.
- Pongruktham, O., C. Ochs, and J.J. Hoover. 2010. Observations of silver carp (*Hypophthalmichthys molitrix*) planktivory in a floodplain lake of the lower Mississippi River basin. *Journal of Freshwater Ecology* 25:85–93.
- Rahel, F.J. 2000. Homogenization of fish faunas across the United States. *Science* 288:854–856.
- Rindi, F. 2014. Bringing order to little green balls: new insights from the Chlorophyceae order Sphaeropleales. *Journal of Phycology* 50:11–13.
- Sagouis, A., J. Cucherousset, S. Villéger, F. Santoul, and S. Boulétreau. 2015. Non-native species modify the isotopic structure of freshwater fish communities across the globe. *Ecography* 38:979–985.
- Sampson, S.J., J.H. Chick, and M.A. Pegg. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. *Biological Invasions* 11:483–496.
- Sass, G.G., T.R. Cook, K.S. Irons, M.A. McClelland, N.N. Michaels, T.M. O'Hara, and M.R. Stroub. 2010. A mark-recapture population estimate for invasive Silver Carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. *Biological Invasions* 12:433–436.
- Sass, G.G., C. Hinz, A.C. Erickson, N.N. McClelland, M.A. McClelland, and J.M. Epifanio. 2014. Invasive bighead and Silver Carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research* 40: 911–921.
- Smith, D. G. 2001. Pennak's Freshwater Invertebrates of the United States: Porifera to Crustacea. John Wiley and Sons. New York, NY. 617 pp.
- Søballe, D.M., and B.L. Kimmel. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. *Ecology* 68:1943–1954.
- Solomon, L.E., R.M. Pendleton, J.H. Chick, and A.F. Casper. 2016. Long-term changes in fish community structure in relation to the establishment of Asian carps in a large floodplain river. *Biological Invasions* 1–13.
- Spataru, P. (1977). Gut contents of Silver Carp—*Hypophthalmichthys molitrix* (Val.)—and some trophic relations to other fish species in a polyculture system. *Aquaculture* 11, 137–146.
- Spataru, P., and M. Gophen. 1985. Feeding behaviour of silver carp *Hypophthalmichthys molitrix* Val. and its impact on the food web in Lake Kinneret, Israel. *Hydrobiologia* 120, 53–61.
- Starling, F.L.D.R.M. 1993. Control of eutrophication by Silver Carp (*Hypophthalmichthys molitrix*) in the tropical Paranoa Reservoir (Brasilia, Brazil): a mesocosm experiment. *Hydrobiologia* 257:143–152.
- Starling, F.L., and A.J. Rocha. 1990. Experimental study of the impacts of planktivorous fishes on plankton community and eutrophication of a tropical Brazilian reservoir. *Hydrobiologia* 200:581–591.
- Strayer, D.L. 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55:152–174.
- Stuck, J.G., A.P. Porreca, D.H. Wahl, and R.E. Colombo. 2015. Contrasting Population Demographics of Invasive Silver Carp between an Impounded and Free-Flowing River. *North American Journal of Fisheries Management* 35:114–122.
- Sutela, T. and A. Huusko. 2000. Varying resistance of zooplankton prey to digestion: implications for quantifying larval fish diets. *Transactions American Fisheries Society* 129:545–551.
- Thornton, K.W., B.L. Kimmel, and F.E. Payne. 1990. *Reservoir Limnology: Ecological Perspectives*. John Wiley and Sons. New York, NY. 246 pp.
- Tumolo B.B., and M.B. Flinn. 2017. Top-down effects of an invasive omnivore: detection in long-term monitoring of large-river reservoir chlorophyll-*a*. *Oecologia*. 185: 293–303.
- Vander Zanden, M.J., J.M. Casselman, and J.B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–467.
- Vanni, M.J., and C.D. Layne. 1997. Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. *Ecology* 78:21–40.
- Wang, J.Q., S.A. Flickinger, K. Be, Y.A.O. Liu, and H. Xu. 1989. Daily food consumption and feeding rhythm of Silver Carp (*Hypophthalmichthys molitrix*) during fry to fingerling period. *Aquaculture* 83:73–79.
- Wehr, J. D., and R.G. Sheath. 2002. *Freshwater Algae of North America: Ecology and Classification*. Academic Press, San Diego, CA. 918 pp.
- Wetzel, R.G. 2001. *Limnology: Lake and River Ecosystems*. Academic Press, San Diego, CA. 1006 pp.
- Williamson, C.J., and J.E. Garvey. 2005. Growth, fecundity, and diets of newly established Silver Carp in the middle Mississippi River. *Transactions of the American Fisheries Society* 134:1423–1430.
- Xie, P., and Y. Yang. 2000. Long-term changes of Copepoda community (1957–1996) in a subtropical Chinese lake stocked densely with planktivorous filter-feeding silver and bighead carp. *Journal of Plankton Research* 22:1757–1778.
- Xu, J., and P. Xie. 2004. Studies on the food web structure of Lake Donghu using stable carbon and nitrogen isotope ratios. *Journal of Freshwater Ecology* 19: 645–650.
- Yurista, P.M., D.S. White, G.W. Kipphut, K. Johnston, G. Rice, and S.P. Hendricks. 2004. Nutrient patterns in a mainstem reservoir, Kentucky Lake, USA, over a 10-year period. *Lake and Reservoir Management* 20:148–163.
- Zhou, Q., P. Xie, J. Xu, Z. Ke, and L. Guo. 2009. Growth and food availability of silver and bighead carps: evidence from stable isotope and gut content analysis. *Aquaculture Research*, 40: 1616–1625.