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Potential for asymmetric competition among co-inhabiting invasive Silver Carp and native shad species in the Lower Midwest

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Potential for asymmetric competition among co-inhabiting invasive Silver Carp and native shad species in the Lower Midwest

A Thesis
Presented to
The Faculty of the Department of Biological Sciences
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In Partial Fulfillment
Of the Requirements for the Degree
Masters of Science

By
Dalton D. Lebeda

Potential for competition among co-inhabiting invasive Silver Carp and native shad species in the Lower Midwest

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ABSTRACT

In the United States, Silver Carp are an invasive voracious planktivorous fish that are capable of competing with many native fish species. Until the last decade, very little was known about how Silver Carp would interact with native fish species or how quickly their populations would expand. In the early 2000's, established Silver Carp populations were reported in Kentucky Lake although they were reported in the Tennessee River much earlier (1987). Kentucky Lake is the first large flood storage reservoir that has been invaded by a reproducing population of Silver Carp in the United States. To date, control measures for Silver Carp have been relatively unsuccessful despite implementation of a commercial harvest in Kentucky Lake in which hundreds of thousands of pounds of Silver Carp are harvested annually. Due to largely unsuccessful control measures, Silver Carp are likely going to be in Kentucky Lake for the long term. Therefore, it's important to understand the ecology of Silver Carp and how they may potentially affect the native fish communities. Juvenile and adult Silver Carp and Gizzard Shad, and juvenile Threadfin Shad were collected from Kentucky Lake, Tennessee River, Ohio River, Clarks River, and Illinois River using gill netting and boat electrofishing techniques. Using stable isotope analyses, I quantified isotopic niche overlap with the goal to understand potential for competition between Silver Carp, and Gizzard Shad, and Threadfin Shad. I analyzed carbon and nitrogen ratios to calculate quantitative metrics derived from stable isotope data and to construct core isotopic niches. Results showed that, if conditions are limiting, Silver Carp are capable of competing with Gizzard Shad in Kentucky Lake, lower Tennessee River, and the Illinois River. Moreover, in Kentucky Lake, I found that juvenile Silver Carp have a higher likelihood of competing with

Gizzard Shad of all age classes than their adult counterparts. I found that Silver Carp are not exploiting the same resources as Threadfin Shad. Based on my research, I recommend managers to focus on reducing juvenile Silver Carp densities and identifying and limiting opportunities for Silver Carp reproduction.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Literature Review

Invasive species have been identified as the second leading cause of loss of species biodiversity (Walker and Steffen 1997). In addition to decreased species diversity, invasive species may also cause shifts in ecosystem function (Lovell et al. 2006). Currently, more than 50,000 terrestrial and aquatic non-native species have invaded United States lands and waters (Pimentel et al. 2005). Many aquatic invasive species have been intentionally and unintentionally introduced and spread through the release of bilge and ballast water, pet trade, biological control, and aquaculture (Keller et al. 2011, Rahel and Olden 2008). Several prominent aquatic invaders of the United States that have degraded ecosystem function through a variety of mechanisms include Sea Lamprey (*Petromyzon marinus*) that have caused drastic changes in native fish populations in the Laurentian Great Lakes (Hansen et al. 1995), dreissenids that have significantly altered water clarity through filtration and unprecedented population densities in the Great Lakes (Idrisi et al. 2001), and cyprinids, namely Common Carp (*Cyprinus carpio)* and Grass Carp (*Ctenopharyngodon idella*) that have caused drastic reductions in water quality, and shifts in ecosystem function (Kulhanek et al 2011, Bajer and Sorensen 2010, Dibble and Kovalenko 2009). Invasive species are an ever-growing threat with relatively few documented eradication stories of established populations (Anderson et al. 2004). However, with increased knowledge, technology and significant resources being employed to control these invasive species, understanding how the native community and ultimately the ecosystem respond is paramount to success (Lodge et al. 2006).

Silver Carp (*Hypophthalmichthys molitrix*) is a highly studied invasive fish species that is currently threating many aquatic ecosystems within the United States. Silver Carp were intentionally introduced into the United States in 1971 for the purpose of aquaculture and biofiltration of sewage lagoons (Xie et al. 2004, Cremer and Smitherman 1980). In January 1980, Freeze and Henderson (1982) found that Silver Carp had escaped from confinement in Arkansas during flooding events and had made their way into the Mississippi River Basin (DeGrandchamp et al. 2008, Kolar et al. 2005). Since their escape, Silver Carp have expanded into the Upper Mississippi River System (UMRS) and have established reproducing populations in the Mississippi, Missouri, Ohio, and Tennessee Rivers, as well as in Kentucky Lake (Kentucky Department of Fish and Wildlife Resources *unpublished data 2015*, Sampson et al. 2009). In 1987, Silver Carp were found in the tailwaters of Kentucky Lake and Lake Barkley and in 2004 the first Silver Carp was reported in Kentucky Lake (USGS Nonindigenous Aquatic Species List 2015). Do to their large adult size and planktivorous nature, Silver Carp have been suggested to reduce stocks of zooplankton (Sass et al. 2014) and compete with native planktivores for food resources (Tumolo and Flinn 2017, Irons et al. 2007).

Quantifying competition between native and invasive fishes is important to our understanding the interactions between them (Jackson et al. 2012, Sampson et al. 2009, Irons et al. 2007, Schleuter 2007, Fausch 1988, Sale 1974). However, measuring interspecific competition in large ecosystems is challenging, though several methodologies have been developed to investigate competition. The most common methods used in assessing the potential for competition between two or more species are: gut content analysis (Sampson et al. 2009), stable isotope analysis (Jackson et al. 2011), and body condition (Irons et al. 2007). Employing gut content analyses, Sampson and others (2009) found significant gut content overlap between Silver Carp and Gizzard Shad in backwater lakes of the Illinois and Mississippi Rivers. Additionally, Irons and others (2007) reported declining body conditions of Gizzard Shad and Bigmouth Buffalo post invasion of Silver Carp in the Illinois River. Through the use of gut contents and body conditions, Sampson and others (2009) and Irons and others (2007) suggest that direct competition may be occurring between Silver Carp and native planktivores.

My goal was to obtain information that can be used to better inform management agencies about shared resource use between Silver Carp and shad. I used stable isotope analyses to investigate the potential for competition between Silver Carp and two shad species in the lower Midwest. Compared to gut content analyses, stable isotope analyses provide longer-term information on fish diets (Vinson and Budy 2010). Furthermore, gut contents may be highly variable due to variations in digestion rates and sample collection times (Bowen 1996). For example, Bitterlich and Gnaiger (1984) reported that zooplankton are indistinguishable from detritus after being incubated with gastric juices of Silver Carp for 20 minutes. In sum, understanding the potential competition between Silver Carp and shad will further our understanding of how Silver Carp may be affecting fish communities in the lower Midwestern United States.

My primary objective was to assess the potential for interspecific competition between Silver Carp, Gizzard Shad, and Threadfin Shad in the lower Midwestern United States. I conducted spatial, temporal, and ontogenetic stable isotope analyses on Silver

Carp, Gizzard Shad, and Threadfin Shad to answer the following questions: (1) Is there a potential for competition between Silver Carp and shad?; (2) Are there temporal shifts in isotopic niches?; (3) Are there ontogenetic shifts in resource use?; (4) Do spatial shifts in resource use occur? I predicted that there would be a potential for competition between Silver Carp and Gizzard Shad due to similar feeding strategies and findings of other studies (Sampson et al. 2009, Irons et al. 2007). Furthermore, ontogenetic diet shifts are known to occur for Gizzard Shad, although to my knowledge, very little research has been conducted on ontogenetic diet shifts of Silver Carp (Zhou et al. 2009, Pilati and Vanni 2007). Lastly, I hypothesized that due to spatial differences in Gizzard Shad gill raker morphology (Walleser et al. 2014), overlap in resource use would be variable between systems. In conclusion, I predicted that overlap in resource use between Silver Carp, Gizzard Shad, and Threadfin Shad would be spatially, temporally, ontogenetically, and system dependent.

Chapter I

Stable Isotope Evidence Indicating Shared Resource Use Among Invasive Silver Carp and Two Native Planktivores in a Large Reservoir

Abstract

Biological invasions can greatly reduce native species diversity. Over 138 nonnative fish species have been introduced into the United States; some of which are known to outcompete native fish species. One such species that is currently expanding its range across the United States is the planktivorous Silver Carp, and evidence suggests, they are competing with native planktivores in the Illinois River. The objective of my study was to determine the degree of potential competition between invasive Silver Carp and native planktivores (Gizzard Shad and Threadfin Shad) in Kentucky Lake - a large reservoir located in western Kentucky. I applied relatively new methods to calculate quantitative metrics derived from stable isotope data to quantify isotopic niche overlap. My results suggest that Silver Carp and Gizzard Shad share resources and therefore have a potential to compete for limiting resources. Furthermore, I provide evidence of ontogenetic shifts in core isotopic niche area and core isotopic niche overlap between invasive and native fish species. My study demonstrates that if resources become limiting, invasive Silver Carp have the potential to compete with multiple life stages of native planktivores in Kentucky Lake.

Introduction

Biological invasions have been identified as the second leading cause of loss of species diversity in the world, with the primary cause described as change in land use (Walker and Steffen 1997). Of the estimated 50,000 nonnative species in the United States, 138 are fish species (Pimentel et al. 2005). The ecosystem effects of invasive fish species range from drastic reductions of native fish species populations (Hansen et al. 1995) to substantial losses in overall ecosystem health (Kulhanek et al 2011, Bajer and Sorensen 2010, Dibble and Kovalenko 2009). Invasive species ecologically harmful but they also cost the United States an estimated $120 billion per year in environmental damages (Pimentel et al. 2005).

One group of invasive species known to cause economic and ecological damage in the United States is commonly referred to as Asian carp (Jackson et al. 2012, Kulhanek et al 2011, Bajer and Sorensen 2010, Dibble and Kovalenko 2009, Irons et al. 2007). Asian carp collectively refers to five separate species, all of which are invasive in the United States: Common Carp, Grass Carp, Black Carp *Mylopharyngodon piceus*, Bighead Carp *Hypophthalmichthys nobilis*, and Silver Carp *H. molitrix*. Evidence suggests that invasive Silver Carp and diets of native planktivorous fish species such as Gizzard Shad *Dorosoma cepedianum* and Bigmouth Buffalo *Ictiobus cyprinellus* overlap significantly (Sampson et al. 2009, Schrank et al. 2003). Moreover, Irons and others (2007) found that post-invasion of Silver Carp in the Illinois River, the body condition and catch per unit effort of Gizzard Shad and Bigmouth Buffalo decreased. Therefore, literature suggests that interspecific competition is occurring between Silver Carp and native planktivores in the Illinois River. As Silver Carp become established throughout the United States, it’s important to understand how they influence primary producers and consumers and have the potential to shift entire food webs.

Stomach contents provide useful indications of what the fish has recently been eating, but can only provide data over a short period of time. In contrast, stable isotope samples provide longer-term indications of what a fish has eaten and assimilated and provide information on metabolically important dietary components (Vinson and Baker 2008). Stable isotope isotopic niche analysis is a relatively new method that may be used to study community trophic structure and competition between species.

Recent efforts in isotope ecology have provided statistical methods to evaluate community and individual species overlap in isotopic space (Swanson et al. 2015, Jackson et al. 2011, Turner et al. 2010, Layman et al. 2007, and Bearhop et al. 2004). Turner and others (2010) extended methods contributed by Layman et al. 2007 and Schmidt et al. 2007 to provide a framework for statistical comparison of isotopic ratios between species. Additionally, Jackson et al. 2011 built on methods presented by Layman et al. 2007 to provide a statistical procedure to plot the core isotopic niche area of individual species based on $\delta^{15}N$ and $\delta^{13}C$ signatures while also taking sample size into consideration. Importantly, the isotopic niche is shown to be tightly correlated with the trophic niche of a species (Jackson et al. 2011), which allows for the interpretation of overlap in resource use between individual species.

I conducted my study on Kentucky Lake, a flood-storage reservoir, in western Kentucky. Kentucky Lake has a long history of a locally important black bass *Micropterus salmoides and M. dolomieu* recreational fishery and a commercial fishery.

Gizzard Shad and Threadfin Shad *D. petenense*, consume phytoplankton and zooplankton (Fuller and Neilson 2015, Drenner et al. 1982, Holanov and Tash 1978) and represent important prey fish species in Kentucky Lake (Yako et al. 1996, Dettmers and Stein 1992). Additionally, adult Gizzard Shad are capable of supplementing their diets with sediment detritus (Vanni et al. 2005, Yako et al. 1996, Mundahl and Wissing 1988, Drenner et al. 1982). An established Silver Carp population was first officially reported in Kentucky Lake in 2004 (USGS 2015) although they were believed to be in the reservoir since 1979 (*David White, May 2016, personal communication*). The first documented juvenile Silver Carp were captured in Kentucky Lake in 2015 via cast nets (*unpublished data*), which suggests an established population. Similar to the diets of native shad species, Silver Carp are known to consume phytoplankton, zooplankton, and sediment detritus (Williamson and Garvey 2005, Bitterlich 1985, Spataru and Gophen 1985).

Due to evidence of competition in published studies and the importance of shad species as prey sources for piscivorous fishes in Kentucky Lake, I evaluated the potential for direct competition between Silver Carp, Gizzard Shad, and Threadfin Shad. Additionally, I evaluated the potential for direct competition among different life stages of Silver Carp and Gizzard Shad across the spring and summer seasons. I hypothesized that Silver Carp, Gizzard Shad, and Threadfin Shad would show core isotopic niche overlap and therefore overlap in resource use. Additionally, I expected a greater potential for competition among Silver Carp and Gizzard Shad in the summer due to the typical patterns of low productivity in the reservoir during this time period (Yurista et al. 2001). Lastly, I expected juvenile Silver Carp and juvenile Gizzard Shad to have a greater potential for direct competition based on the assumption that juvenile Silver Carp and juvenile Gizzard Shad have less variability in their diets than adults due to limitations in gill raker morphology (gill raker pore size; Walleser et al. 2014).

Methods

Study Area

Kentucky Lake is the last impoundment of the Tennessee River (White et al. 2010, Yurista et al. 2001) and was constructed by the Tennessee Valley Authority (TVA) in 1944 to reduce flooding in the Ohio and Mississippi River basins, increase navigation, and provide hydroelectric power. At full pool, the reservoir has a surface area of 64,870 ha and extends 296 km, thus making it the largest impoundment east of the Mississippi River (Kerns et al. 2009). Kentucky Lake is considered a large mesotrophic freshwater reservoir (White 2014), and provides habitat to several native planktivorous fish species including Gizzard Shad, Threadfin Shad, Paddlefish *Polyodon spathula*, and Bigmouth Buffalo.

I established three study sites centrally located in Kentucky Lake near Hancock Biological Station. The study areas included two relatively shallow embayment sites, Turkey Bay and Anderson Bay, and one deeper channel site. Across all three sites during the spring and summer, secchi depths ranged from 0.6 m to 1.4 m and 0.8 m to 1.4 m, respectively.

Sampling Methods

Fish – All specimens were handled and euthanized according to the Murray State University Institutional Animal Care and Use Committee (IACUC) protocol number 2014-008. Fish used for stable isotope analysis were sampled by cast netting, gill netting, and boat electrofishing during spring and summer of 2015 and 2016. Monofilament cast nets were actively fished by locating a school of shad and tossing the net over the school. Additionally, monofilament gill nets 68.5 m long and 3.6 m deep with 10.1 cm bar mesh were passively fished for Silver Carp. Variable size mesh gill nets ranging from 1.27 cm to 6.35 cm bar mesh were employed to sample Gizzard Shad, Threadfin Shad and top end members (e.g. Skipjack Herring, *Alosa chrysochloris*; Flathead Catfish *Pylodictis olivaris*, etc.). Gill nets were fished between 10 and 14 hours per set depending on water temperatures, weather, and fish saturation. Boat electrofishing was conducted using a gas powered generator, twin booms with matching steel umbrella array droppers, and a Midwest Lake Electrofishing System (MLES) infinity control box rigged to a jon-boat. While electrofishing, various settings were experimented with; voltage ranged from 225-475, pulses/sec ranged from 25-80, and duty cycle ranged from 25-50. The electrofishing runs occurred during the day with an average run time of 15 minutes.

Silver Carp, shad species, and top end members sampled were weighed to the nearest gram, measured to the nearest millimeter (total length), sexed, a small sample of dorsal muscle tissue was removed, and an aging structure was collected. For age analysis, the first pectoral fin ray was removed from Silver Carp and sagittal otoliths were extracted for shad species. All stable isotope muscle samples were immediately placed on ice and frozen for later processing. By-catch was immediately released after being identified to species and measuring total length to the nearest millimeter.

Plankton and Detritus – Zooplankton and phytoplankton samples were taken at dawn or dusk via horizontal tows with a 63 µm mesh Wisconsin net. Tows were 10 to 15 minutes long at a depth of approximately 1 m. After the tows were completed, the samples were filtered through a 256 µm mesh sieve to separate zooplankton from phytoplankton. Following the splitting of the sample, zooplankton and phytoplankton were placed into separate Whirl-Pak® bags and frozen for later analysis. Three plankton samples were taken at each site from March through August. One to two detritus samples were collected at each site from March through August using ponar grabs. Detritus samples were filtered through 256 µm mesh to dispose of silt and inorganic material. The remaining material was stored in Whirl-Pak® bags and frozen for later processing.

Stable Isotope Preparation

Stable isotope samples were oven dried at 50˚C for a minimum of 48 hours and then ground into a fine powder with a mortar and pestle (Mazumder 2013). After grinding, the samples were returned to the drying oven for an additional 48 hours to ensure that the sample was thoroughly dried. Once dry, the powder was evenly mixed and 0.31- 0.34 milligrams of fish tissue, 0.41-0.44 mg of zooplankton, 1-1.2 mg of phytoplankton, or 1.3-1.5 mg of detritus was loaded into Costech® pressed 3.5x5 mm tin capsules. Ground samples were analyzed using a Costech Elemental Combustion System 4010 along with a Thermo Delta V Plus Isotope Ratio Mass Spectrometer to obtain isotopic ratios of the samples (Mazumder 2013). The analytical precision of δ^{13}C and

$\delta^{15}N$ was ±0.06 per mil relative to the standards Vienna Pee Dee Belemnite (VPDB) and air (AIR) for carbon and nitrogen, respectively.

Nitrogen-15 ratios were used to determine the trophic position of Silver Carp and shad species within Kentucky Lake. An increase of 3-4‰ in $\delta^{15}N$ has been shown to represent an increase in one trophic level (Weber and Brown 2013). In contrast, $\delta^{13}C$ were used to determine the source of carbon flow to consumers. A depleted $\delta^{13}C$ signature indicates a pelagic diet whereas more enriched signatures indicate a littoral or benthic based diet (Weber and Brown 2013, Nerot et al. 2012).

Analyses

For all analyses, fish captured in the following months were grouped together and analyzed as “spring” fish: March, April, and May; fish captured in June, July, and August were considered “summer” fish (Table 1). Silver Carp and Gizzard Shad were further divided based on total length and age. Silver Carp and Gizzard Shad less than 250 mm and 200 mm, respectively, and younger than one year of age were considered juvenile (Table 1). Silver Carp and Gizzard Shad older than one year of age and greater than the minimum length requirements were considered adults (Table 1). All Threadfin Shad captured were younger than one year of age and therefore considered juveniles. No juvenile Silver Carp or juvenile Gizzard Shad were captured during the summer months (Table 1).

Statistical Analyses – Isotopic ratios from adult Silver Carp and Gizzard Shad and juvenile Threadfin Shad were used for the following analysis. Following methods developed by Turner et al. 2010, I tested for differences in centroid location (MD), mean distance to centroid (CD), and mean nearest neighbor distance (NND) among species and seasons, using Euclidean distances. Additionally, I tested for differences in path length. Quantifying CDs and NNDs allowed us to compare trophic structure between individual species between seasons. All test statistics were contrasted with null distributions produced by a non-parametric residual permutation procedure (RPP; Permutations 9,999: Turner et al. 2010).

Stable Isotope Metrics – Before completing statistical testing, I tested for multivariate normality using Henze-Zirkler's normality test. I found that all groups in the spring and summer met the multivariate normality assumption with one exception; juvenile Gizzard Shad in the spring did not meet the normality assumption (HZ = 0.72, P = 0.02). Due to the high variability in juvenile Gizzard Shad data, smaller sample size, and the same interpretation (with or without outliers), I decided to continue the analysis without removing outliers or transforming the data.

Following assumption testing, I constructed isotopic niches for Silver Carp and Gizzard Shad to determine isotopic niche width and overlap in isotopic space. Quantitative population metrics were calculated using δ^{15}N and δ^{13}C to estimate isotopic niche overlap of Silver Carp, Gizzard Shad, and Threadfin Shad (Jackson et al. 2012). Nitrogen δ^{15} and δ^{13}C used to calculate quantitative population metrics were bootstrapped to 10,000 iterations (Jackson et al. 2012). Standard ellipse area (SEA) was calculated using the variance and covariance from bivariate isotope data. The SEA ellipses contain approximately 40% of the bivariate data that serves as a focus for the isotopic niche of each species (Guzzo et al. 2013, Jackson et al. 2012). SEA is less sensitive to sample sizes than convex hull area (TA) which is why SEA was used in this study (Jackson et al.

2011). Standard ellipse areas controlling for small sample size (SEA_c) were derived from SEA using the following equation, where n represents sample size (Jackson et al. 2011):

$$\boldsymbol{SEAc} = \boldsymbol{SEA} \times [(\boldsymbol{n}-\mathbf{1}) \div (\boldsymbol{n}-\mathbf{2})]$$

SEA_c are influenced even less than SEA by small sample size and were used to calculate isotopic niche overlap, which is a quantitative measure of similarity between the diets of two or more populations (Jackson et al. 2011). The greater the niche width of a species, the more generalized the diet for that species (Guzzo et al. 2013, Mills and Marchant-Forde 2010).

Results

I found that centroid locations of adult Silver Carp and adult Gizzard Shad differed in bivariate space during both the spring and summer seasons (Table 1). Results from the RPP demonstrate that, in the spring, the distance between centroids differed significantly from zero for all pairwise comparisons between adult fish (Table 2). Similarly, in the summer, the distances between centroids of adult fish differed significantly from zero (Table 2). Adult Silver Carp and Gizzard Shad trophic positions are statistically different in both the spring and summer seasons. Furthermore, results from pairwise comparisons of mean distance to centroids (CD) and mean nearest neighbor distances (NND) revealed comparable isotopic niche structures between adult Silver Carp and adult Gizzard Shad (Table 2).

Overlap in core isotopic niche area may be used to demonstrate similarities in resource use. The core isotopic niche area of adult Silver Carp overlapped with that of adult Gizzard Shad in the spring and summer by 7.76% and 7.34%, respectively (Figure

1). Interestingly, adult Gizzard Shad had a larger SEAc than adult Silver Carp in the spring while a smaller SEAc in the summer (Table 3). Adult Gizzard Shad used a wider variety of resources than adult Silver Carp in the spring and a narrower range of resources than adult Silver Carp in the summer.

In contrast to the patterns of adult Silver Carp and adult Gizzard Shad, the distance between centroids of juvenile fish of the same species, was statistically similar (distance = 0.79, P = 0.1236; Table 2), which suggests that juveniles share trophic positions. In contrast, during both the spring and summer seasons, the distances between centroids of juvenile Threadfin Shad and all other groups were statistically different from zero (Table 2). Additionally, I found statistical differences between the mean distance to centroids (NND) between groups. The NND differed significantly from zero for pairwise comparisons between juvenile Gizzard Shad and adult Silver Carp (distance = 0.85, P = 0.0152) and juvenile Gizzard Shad and juvenile Silver Carp (distance = 0.89, P = 0.0031). Furthermore, NND differed significantly between juvenile Silver Carp and adult Gizzard Shad (distance = 0.29, P = 0.0384), and juvenile Gizzard Shad and juvenile Silver Carp (distance = 0.78, P = 0.0480; Table 2). Although these results do not demonstrate shared resource use, they do illustrate differences in trophic structure between juvenile fish, and juvenile and adult fish.

Comparisons of core isotopic niche areas revealed contrasting patterns between native shad and invasive Silver Carp. I found that the isotopic niche of juvenile Silver Carp overlapped that of juvenile Gizzard Shad (10.82%; Figure 1). Even though there was a 10.82% overlap between juvenile Silver Carp and juvenile Gizzard Shad, the core isotopic niche area of juvenile Silver Carp fell completely within that of juvenile Gizzard

Shad (Figure 1). Additionally, I found that the core isotopic niche of adult Silver Carp overlapped with juvenile Gizzard Shad by 8.68% (Figure 1). Conversely, the core isotopic niche area of juvenile Threadfin Shad never overlapped with another group (Figure 2). Notably, juvenile Silver Carp had the smallest core isotopic niche area, while juvenile Gizzard Shad had the largest isotopic niche area (Table 3). Overall, these results suggest that juvenile Silver Carp utilize fewer resources than juvenile Gizzard Shad.

Quantifying differences in absolute path length revealed dissimilarities between Threadfin Shad, Gizzard Shad and Silver Carp. Differences in the absolute value of path length may be used to indicate discrepancies between shifts in trophic position over time between two species. The trophic position of adult Silver Carp and adult Gizzard Shad shifted similarly between spring and summer seasons (difference = 0.13, P = 0.70; Figure 2). In contrast, I found that the difference in absolute value of path lengths between adult Silver Carp and juvenile Threadfin Shad (difference = 2.53, P = 0.0001) was significantly different than 0. Further, adult Silver Carp and adult Gizzard Shad became more enriched in nitrogen-15 during the summer while juvenile Threadfin Shad became more depleted in nitrogen-15 (Table 1; Figure 2). Additionally, adult Silver Carp, adult Gizzard Shad, and juvenile Threadfin Shad were all more enriched in carbon-13 during the summer than during the spring.

Lastly, important patterns emerged when I compared centroid locations for each group in the spring and summer (Figure 2). Adult Gizzard Shad appeared to follow a similar path direction as zooplankton while adult Silver Carp appeared to follow a path direction analogous to phytoplankton. Interestingly, juvenile Threadfin Shad had an inverse path direction when compared to zooplankton suggesting a switch in resource use between the spring and summer seasons (Figure 2).

Discussion

I tested for differences in dispersion metrics (MD, CD, and NND), plotted core isotopic niche areas, and calculated core isotopic niche overlap values to illustrate patterns in trophic structure and resource use between invasive Silver Carp and shad species in Kentucky Lake. I found that adult Silver Carp and adult Gizzard Shad had relatively similar trophic positions, although adult Gizzard Shad were slightly more enriched in nitrogen – 15 during both spring and summer seasons. Additionally, I found similarities in trophic structure (e.g. CD, NND, SEAc) suggesting similar ranges in diets and densities of individuals within isotopic space (Table 3; Figure 1). Not surprisingly, core isotopic niche estimates revealed overlap between adult Silver Carp and adult Gizzard Shad (Figure 1). This suggests, that adult Silver Carp and adult Gizzard Shad do share some of the same resources, even though the overlap value was not exceedingly high. Therefore, due to similar trophic structures and overlapping core isotopic niche areas of adult Silver Carp and adult Gizzard Shad, it is possible that competition may increase if resources become limiting in Kentucky Lake. Furthermore, if adult Gizzard Shad and adult Silver Carp share resources, it is possible that Silver Carp may outcompete Gizzard Shad due to drastic differences in body sizes (Jackson et al. 2012 and Young 2004).

In addition to reporting a potential for competition between adult Silver Carp and adult Gizzard Shad I also found ontogenetic differences in core isotopic niche overlap, SEAc, and dispersion metrics (Table 2 and Table 3). To my knowledge, ontogenetic differences in core isotopic niche overlap has never been documented in Silver Carp and Gizzard Shad. My results demonstrate significantly more overlap between juvenile Gizzard Shad and juvenile Silver Carp than adult Gizzard Shad and adult Silver Carp (Figure 1). The core isotopic niche area of juvenile Gizzard Shad was overlapped by both adult and juvenile Silver Carp. Therefore, I suggest that the potential for competition is highest between Silver Carp and juvenile Gizzard Shad. Many studies have shown that interspecific competition has negative impacts on the growth and health of native planktivores. For example, Schrank and others (2011) provided evidence of Bighead Carp reducing growth rates of juvenile Paddlefish when interspecific competition occurred in a mesocosm experiment. Furthermore, Irons et al. (2007) reported decreased body condition of native planktivores after Silver Carp invaded the Illinois River. Consequently, if interspecific competition occurs between Silver Carp and Gizzard Shad, Gizzard Shad growth rates and fecundity may decrease. Additionally, due to slower growth, predation on Gizzard Shad may occur over an extended period of time, therefore increasing natural mortality rates.

Seasonal differences in trophic position may indicate variation in resource use (Figure 2). Results showed little variability in the trophic position of adult Silver Carp and adult Gizzard Shad, suggesting minimal variation in diet between spring and summer seasons. (Figure 2). Studies have shown that Silver Carp and Gizzard Shad are obligate filter feeders known to feed on phytoplankton, zooplankton, and detritus (Vanni et al. 2005, Williamson and Garvey 2005, and Spataru and Gophen 1985) and if available resources do not vary then shifts in trophic position is unexpected. In contrast, my results support the findings of Holanov and Tash (1978), where Threadfin Shad are capable of employing two feeding methods, particulate and filter feeding. I found that juvenile Threadfin Shad exhibit a distinct trophic position shift between the spring and summer seasons. In the spring, juvenile Threadfin Shad are approximately 4‰ more enriched in $\delta^{15}N$ than in the summer, which suggests a sudden and distinct switch in resource use. In conclusion, I believe that juvenile Threadfin Shad are particulate feeding on zooplankton in the spring and therefore have a higher trophic position than in the summer when they may be filter feeding phytoplankton.

Although stable isotope analysis limits interpretation of feeding habits compared to gut content analysis, stable isotope analysis does provide indications of what fish have been feeding on and assimilating over time. I found that Gizzard Shad generally had a wider $\delta^{13}C$ range suggesting utilization of a broader range of resources than Silver Carp (Table 1 and Figure 1). Multiple studies have reported that Gizzard Shad are capable of switching to sediment detritus in times of low resource availability (Yako et al. 1996, Stein et al. 1995). I suggest that because Silver Carp and Gizzard Shad are both obligate filter feeders, Gizzard Shad may be consuming more detrital material than Silver Carp, therefore widening their niche. My results provide evidence that Gizzard Shad utilize more resources than Silver Carp and therefore, may be able to mitigate the severity of competition that may occur with Silver Carp.

In conclusion, I have provided evidence supporting a potential for direct competition between Silver Carp and Gizzard Shad in Kentucky Lake. More importantly, I have found evidence of increased potential for competition between juvenile Gizzard Shad and both juvenile and adult Silver Carp. Irons and others (2007) reported evidence of competition between Silver Carp and native planktivores in the Illinois River. My results compliment those of Irons et al. (2007) in that I provide evidence of direct competition between Silver Carp and Gizzard Shad at different life stages. I believe that future studies should take into consideration the ontogenetic shifts of Silver Carp and the implications of Silver Carp occupying different positions in isotopic space on food web dynamics. In sum, my findings have provided evidence and supported previous studies, suggesting direct interspecific competition occurs among invasive Silver Carp and native planktivores.

Acknowledgements

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Tables

Table 2-1: Mean $\delta^{13}C$ and $\delta^{15}N$ values, (Stdv.), and sample sizes for adult (43) and juvenile (13) Silver Carp and adult (50) and juvenile (10) Gizzard Shad, juvenile Threadfin Shad (23), zooplankton (19), phytoplankton (17), and detritus (19) collected from Kentucky Lake during the spring and summer of 2015 and 2016. Adult fish are represented by (A) and juvenile fish are symbolized by (J).

Species	**n**	**Season**	**$\delta^{13}C$**	**Stdv. $\delta^{13}C$**	**$\delta^{15}N$**	**Stdv. $\delta^{15}N$**
(a) Silver Carp	15	Spring	-28.20	1.14	12.37	0.36
	28	Summer	-27.81	0.72	12.68	0.74
(j) Silver Carp	13	Spring	-28.22	0.68	11.16	0.58
	0	Summer	-	-	-	-
(a) Gizzard Shad	22	Spring	-27.33	1.10	12.94	0.75
	28	Summer	-27.61	1.08	13.50	0.52
(j) Gizzard Shad	10	Spring	-27.46	1.86	11.38	1.11
	0	Summer	-	-	-	-
(j) Threadfin Shad	14	Spring	-29.87	0.65	14.31	0.68
	9	Summer	-28.63	0.29	11.54	1.19
Zooplankton	1	Spring	-29.10	-	8.20	-
	13	Summer	-30.77	1.20	10.81	0.77
Phytoplankton	5	Spring	-31.26	4.63	6.16	1.43
	12	Summer	-29.46	1.06	9.04	0.43
Detritus	7	Spring	-29.26	0.50	0.82	1.80
	12	Summer	-29.21	0.60	3.66	2.96

Table 2-2: Dispersion metrics calculated using a residual permutation procedure for adult (43) and juvenile (13) Silver Carp, adult (50) and juvenile (10) Gizzard Shad, and juvenile Threadfin Shad (23) captured in Kentucky Lake during the spring and summer of 2015 and 2016. Two numbers are given for every comparison. The top number is the difference between measurements for the pairwise comparison and the bottom number is the p-value testing the null hypothesis for the specific pairwise comparison. All p-values in bold were considered of significant importance to the study. Adult fish are represented by an (A) and juvenile fish are symbolized by a (J).

Comparisons	Season	MD	CD	NND
(A) Gizzard Shad - (A) Silver Carp	Spring	1.04	0.28	0.05
		0.0021	0.24	0.72
	Summer	0.85	0.18	0.03
		0.0009	0.23	0.71
(A) Silver Carp - (J) Threadfin Shad	Spring	2.56	0.02	0.08
		0.0001	0.92	0.66
	Summer	1.41	0.13	0.23
		0.0004	0.56	0.46
(J) Silver Carp - (A) Gizzard Shad	Spring	1.99	0.31	0.29
		0.0001	0.1066	**0.0384**
(J) Gizzard Shad - (A) Silver Carp	Spring	1.23	0.85	0.54
		0.0110	**0.0152**	0.0989
(J) Gizzard Shad - (J) Silver Carp	Spring	0.79	0.89	0.78
		0.1236	**0.0031**	**0.0480**
(J) Silver Carp - (J) Threadfin Shad	Spring	3.55	0.06	0.16
		0.0001	0.8676	0.6283

Table 2-3: Core isotopic niche area estimates of adult (43) and juvenile (13) Silver Carp, adult (50) and juvenile (10) Gizzard Shad, and juvenile Threadfin Shad (23) in Kentucky Lake in the spring and summer (2015 and 2016). The following metrics are represented in the table below, standard ellipse area controlling for small sample size (SEAc), standard ellipse area (SEA), and convex hull area (TA).

Species	Season	SEAc	SEA	TA
(A) Silver Carp	Spring	1.34	1.25	3.06
	Summer	1.53	1.47	5.91
(J) Silver Carp	Spring	0.77	0.71	1.16
	Summer	-	-	-
(A) Gizzard Shad	Spring	2.25	2.14	6.84
	Summer	1.36	1.31	4.00
(J) Gizzard Shad	Spring	7.17	6.37	11.98
	Summer	-	-	-
(J) Threadfin Shad	Spring	1.27	1.17	2.43
	Summer	1.20	1.05	1.74

Figures

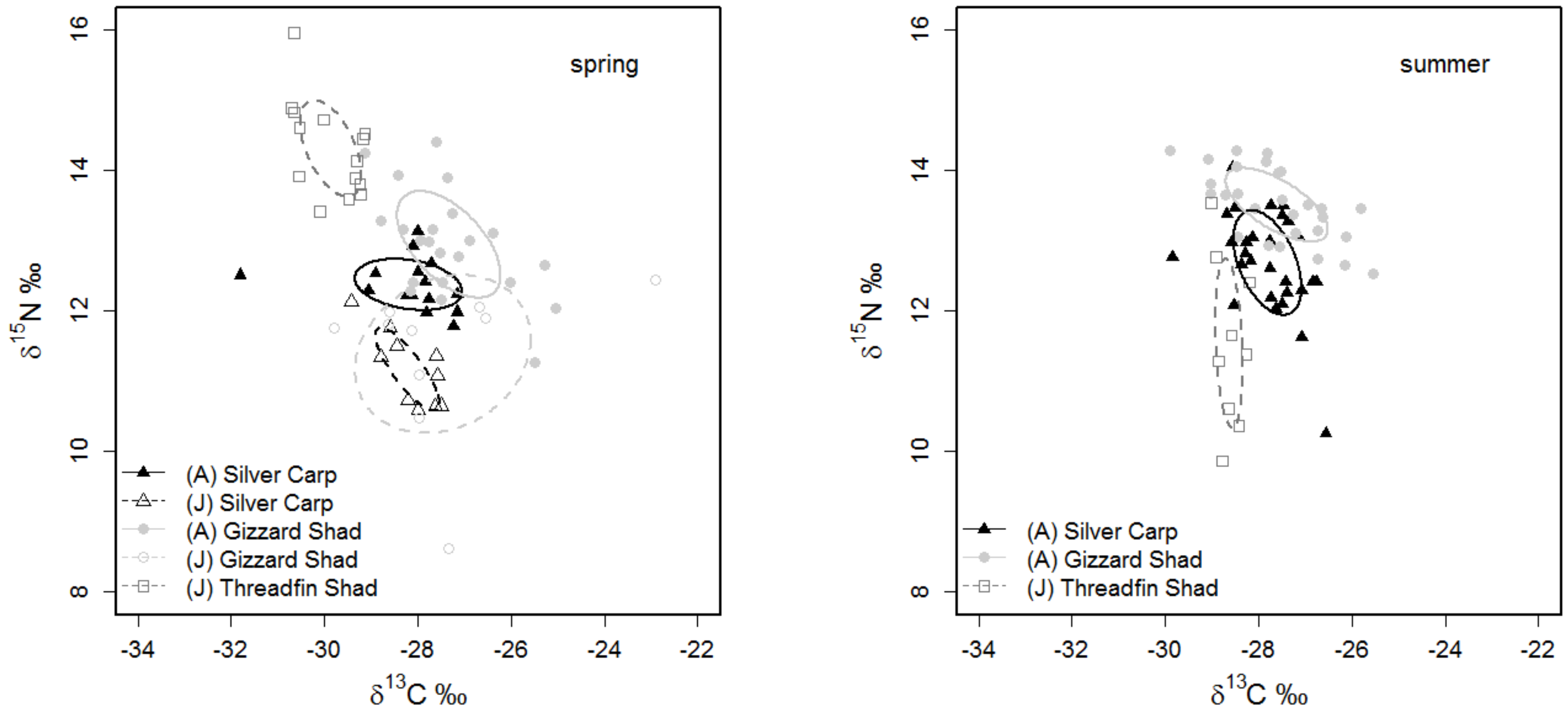

Figure 2-1: Core isotopic niche areas represented by standard ellipse areas controlling for small sample size for adult (43) and juvenile (13) Silver Carp and adult (50) and juvenile (10) Gizzard Shad, and juvenile Threadfin Shad (23) collected in the spring and summers of 2015 and 2016. Adult fish are represented by (A) and juvenile fish are represented by (J).

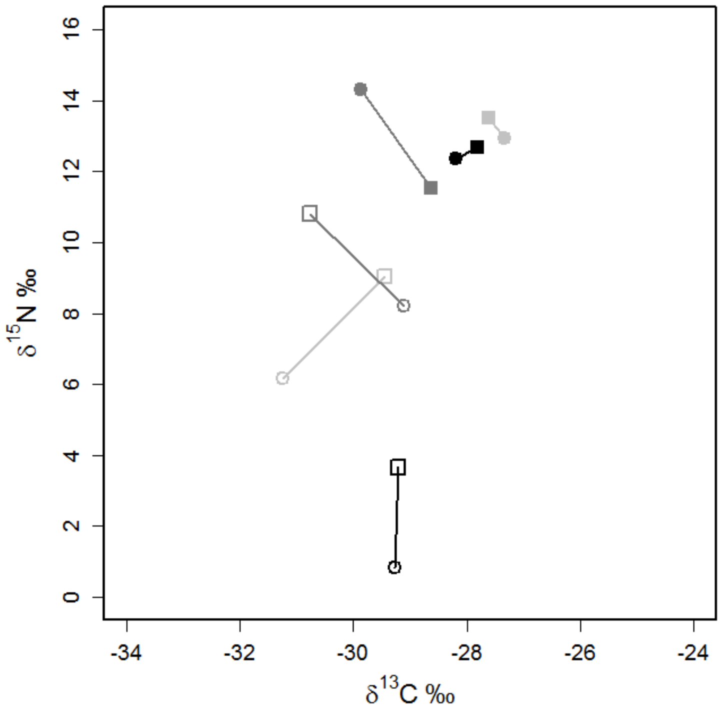

Figure 2-2: Path distance and direction among adult Silver Carp (43), adult Gizzard Shad (50), juvenile Threadfin Shad (23), zooplankton (19), phytoplankton (17), and detritus (19) between the 2015 and 2016 spring and summer seasons. Path distance is illustrated with lines connecting the centroids. The centroids are expressed using different shapes for spring (circle) and summer (square). Adult Silver Carp and detritus are depicted by black, solid and hollow shapes, respectively. Adult Gizzard Shad and phytoplankton are illustrated with light gray, solid and hollow shapes, respectively. Lastly, juvenile Threadfin Shad and zooplankton are represented by dark gray, solid and hollow shapes, respectively.

Chapter II

Potential for Competition between Invasive Silver Carp and Native Gizzard Shad in Four Lower Midwestern River Systems

Abstract

Silver Carp and Gizzard Shad have the potential to compete for resources due to similar feeding mechanisms and diets. However, resource availability can flux over time and space, especially in large dynamic river systems. To completely understand interactions between invasive Silver Carp and native planktivores, it is important to understand how they interact in diverse systems. I studied Silver Carp and Gizzard Shad resource use in five large-river systems using stable isotope techniques. I found variable core isotopic niche area overlap and trophic structure among Silver Carp and Gizzard Shad across five sites where the two species co-occur. My data suggest that Silver Carp and Gizzard Shad in the Illinois River, lower Tennessee River, and Kentucky Lake share planktonic resources across space and time, and therefore, have the potential to compete. In contrast, Silver Carp and Gizzard Shad in the Ohio River and Clarks River do not appear to be sharing resources, which suggests niche partitioning may be occurring in these systems. In conclusion, my results suggest that Silver Carp may not be utilizing the same resources as Gizzard Shad in all of the systems where they co-occur; therefore, direct competition should be studied across small spatial scales and may be context dependent.

Introduction

Invasive species have the potential to outcompete and displace native species (Peterson et al. 2004, Solomon et al. 2016). Consequently**,** scientists are concerned over the rapidly growing number of invasive species in the United States. Although competition is difficult to quantify, the effects of competition between invasive and native species are well documented (Simon and Townsend 2003, Irons et al. 2007). Currently, an invasive species of concern is the planktivorous Silver Carp *Hypophthalmichthys molitrix*. Silver Carp were introduced into Arkansas in the United States in 1971 for biofiltration and aquaculture purposes (Xie et al. 2004, Cremer and Smitherman 1980). Currently, Silver Carp have invaded much of the Mississippi River Basin (Kolar et al. 2005). Evidence suggests, that within some of their invaded environments, such as the Illinois River, Silver Carp have facilitated decreases in body condition and reduced native planktivore populations (Irons et al. 2007). Irons and others (2007) found that post Silver Carp invasion in the Illinois River, the body condition and catch-per-unit-effort of Gizzard Shad *Dorosoma cepedianum* and Bigmouth Buffalo *Ictiobus cyprinellus* declined. Furthermore, Silver Carp can cause shifts in zooplankton species composition (Lu et al. 2002) and reductions in zooplankton densities (Radke and Kahl 2002). Moreover, the potential for competition and negative effects of Silver Carp on native planktivorous fish communities and zooplankton communities has been well documented in multiple riverine environments.

Research has been focused on both direct and indirect competition between Silver Carp and native planktivores in riverine systems (Irons et al. 2007, Lu et al. 2002, Radke and Kahl 2002, Domaizon and Devaux 1999, Kajak 1977). It is well established that

Silver Carp are capable of directly competing with native planktivores due to similarities in feeding mechanisms and habitat preferences (Sampson et al. 2009). Like most native planktivores, Silver Carp are filter feeders and are capable of filtering organisms ranging from 8 µm to 100 µm. (Sampson et al. 2009, Yako et al. 1996, Drenner et al. 1982, Cremer and Smitherman 1980). Accordingly, Silver Carp are capable of indirectly competing with native planktivores by depleting resources at the bottom of the food web (Xie and Yang 2000, Spataru and Gophen 1985). Reductions in fish diversity and condition have alarmed managers and scientists studying various aquatic ecosystems. For example, Great Lakes biologists are focused on stopping the invasion of Silver Carp, and predicting the effects that Silver Carp may have on Great Lakes ecosystems (Zhang and et al. 2016, Cooke and Hill 2010). In conclusion, Silver Carp are capable of competing with native planktivores, but the intensity of competition and degree of effects are still unknown and unpredictable within a given system.

To date, most of the studies focused on competition have estimated the effect of Silver Carp on native planktivores using gut contents and body condition measurements (Sampson et al. 2009, Irons et al. 2007, Williamson and Garvey 2005). Although gut content studies have been successfully used to illustrate shared feeding habits between Silver Carp and native planktivores, several complications arise. First, gut contents reflect the diet of a short period of time before they were captured. For example, Bitterlich and Gaigner (1984) reported that Silver Carp are capable of digesting zooplankton within 20 minutes of consumption. Second, identification of plankton in gut contents is difficult due to their size (Hanif 2013), thus reducing the quality of comparisons between gut contents of Silver Carp across systems. Third, gut contents are relatively expensive and time consuming to process (Vinson and Budy 2010). In conclusion, gut contents are a useful tool for demonstrating similar feeding habits between two species but caution should be used when using gut contents to quantify patterns of biologically important resources (Evans-White et al. 2001).

In contrast to gut content analyses, stable isotope analyses give long-term indications of what resources a fish has been utilizing and assimilating for biological processes (e.g. growth; Vinson and Baker 2008). Furthermore, stable isotopes are relatively inexpensive to process and analyze when compared to gut contents (Vinson and Budy 2010). Methods of stable isotope analysis have been developed and refined over the past 15 years (Swanson et al. 2015, Jackson et al. 2011, Turner et al. 2010, Layman et al. 2007, and Bearhop et al. 2004). Recently, analyses have been developed to determine isotopic niche in bivariate space (Jackson et al. 2011). Using isotopic niche analysis, it is possible to compare resource use spatially, temporally, and across multiple species (Jackson et al. 2012).

I conducted my study using stable isotope analyses to compare resource use between invasive Silver Carp and native Gizzard Shad at five sites in the Midwestern United States. Understanding factors that influence competition between Silver Carp and native planktivores is important to help better predict the effects of Silver Carp on invaded systems and systems that may be invaded (e.g. Laurentian Great Lakes). I hypothesized that Silver Carp and Gizzard Shad may not compete in all aquatic systems due to differences in gill raker morphology and resource availability. Walleser and others (2014) reported that the structure of gill rakers in Silver Carp and Gizzard Shad may be influenced by ontogenetic shifts. Additionally, the morphology of Gizzard Shad gill rakers may be influenced by their habitat. Furthermore, niche overlap between Silver Carp and Gizzard Shad may by spatially variable (Walleser et al. 2014). Therefore, the interactions and the potential for competition between Silver Carp and Gizzard Shad may be dependent on the ecosystem in which they are located.

Methods

Study Area

In the summer of 2016, sampled the lower Tennessee River downstream of Kentucky Dam, Kentucky Lake, the Clarks River, the Ohio River, and the Illinois River (Figure 1). As an 8th order stream and the largest tributary of the Ohio River, the Tennessee River flows approximately 1,050 km before emptying into the Ohio River (White et al. 2005). Approximately 35 km upstream from the mouth of the Tennessee River is Kentucky Dam (Geological Survey and Speer 1965). The impoundment created a mesotrophic reservoir known as Kentucky Lake, which spans 64,870 ha and is the last impoundment on the Tennessee River (White et al. 2005, Kerns et al. 2009, Yurista et al. 2001). The lower Clarks River is a relatively unchannelized 5th order stream that flows approximately 21 km before emptying into the lower Tennessee River (Brown et al. 2008, Parola et al. 2005). The Ohio River is a dammed, 9th order stream, which flows 1,578 km before emptying into the Mississippi River (White et al. 2005). Lastly, fish were collected from the Illinois River near Havana, IL. The Illinois River drains 75,143 km^2 and flows approximately 434 km before emptying into the Mississippi River (Kofoid 1903).

Sampling Methods

All specimens were handled and euthanized according to the Murray State University Institutional Animal Care and Use Committee (IACUC) protocol number 2014-008. Fish from all five sites were collected via boat electrofishing with a MLES infinity control box, twin booms, and umbrella array droppers. In addition to boat electrofishing, fish from Kentucky Lake were collected with 68.6 m, 10.1 cm bar mesh monofilament gill nets. On June 29th of 2016, Silver Carp, Gizzard Shad, Largemouth Bass *Micropterus salmoides*, and Flathead Catfish *Pylodictis olivaris* were collected from the Ohio River, Clarks River, and downstream of Kentucky Dam on the Tennessee River. These same species were collected from the Illinois River on June 30th of 2016. Lastly, Silver Carp, Gizzard Shad, and Skipjack Herring (*Alosa chrysochloris*) were collected from Kentucky Lake throughout the month of June, 2016. All fish were sacrificed for biological sample collection. I measured total length (mm), weight (g), and extracted a dorsal muscle tissue sample for stable isotope analysis using a 10 mm stainless steel biopsy punch. After extraction, all dorsal muscle plugs were placed into Whirl-Pak bags then immediately placed on ice and frozen for later processing.

Sample and Stable Isotope Preparation

Stable isotope samples were oven dried at 50˚C for a minimum of 48 hours and ground into a fine powder with a mortar and pestle (Mazumder 2013). After grinding, the samples were placed back into the drying oven for an additional 48 hours to ensure the sample was thoroughly dry. Once dry, the powder was evenly mixed and 0.31- 0.34 milligrams of fish tissue was loaded into Costech® pressed 3.5x5 mm tin capsules. Ground samples were analyzed using a Costech Elemental Combustion System 4010 along with a Thermo Delta V Plus Isotope Ratio Mass Spectrometer to obtain isotopic ratios of the samples (Mazumder 2013). The analytical precision of δ^{13}C and δ^{15}N was ±0.06 per mil relative to the standards Vienna Pee Dee Belemnite (VPDB) and air (AIR) for carbon and nitrogen, respectively. Nitrogen-15 ratios were used to determine the trophic position of Silver Carp and shad species. An increase of 3-4‰ in δ^{15}N has been shown to represent an increase in one trophic level (Weber and Brown 2013). Carbon-13 signatures were used to determine the source of carbon flow to consumers. A depleted δ^{13}C signature indicates a pelagic diet whereas more enriched signatures indicate a littoral or benthic diet (Weber and Brown 2013, Nerot et al. 2012).

Analyses

Statistical Analyses – Isotopic ratios from 10 Silver Carp and 10 Gizzard Shad per site, except for the Clarks River, where I captured 7 Gizzard Shad, were used for the following analyses. Following methods developed by Turner et al. 2010, I tested for differences in centroid location (MD), mean distance to centroid (CD), and mean nearest neighbor distance (NND) among species and between sites. Quantifying MDs and NNDs allowed us to compare trophic structure between individual species and sites. Test statistics were contrasted with null distributions produced by a non-parametric residual permutation procedure (RPP; Permutations 9,999: Turner et al. 2010).

Stable Isotope Metrics – Before statistical comparison of groups were tested, I first tested for multivariate normality using Henze-Zirkler's normality test. Following assumption testing, I constructed isotopic niches for Silver Carp and Gizzard Shad to determine isotopic niche width and overlap in isotopic space. Quantitative population metrics were calculated using δ^{15}N and δ^{13}C to estimate isotopic niche overlap of Silver

Carp and Gizzard Shad (Jackson et al. 2012). Nitrogen δ^{15} and δ^{13}C used to calculate quantitative population metrics were bootstrapped to 10,000 iterations (Jackson et al. 2012). Standard ellipse area (SEA) was calculated using the variance and covariance from bivariate isotope data. The SEA ellipses contain approximately 40% of the bivariate data that serves as a focus for the isotopic niche of each species (Guzzo et al. 2013, Jackson et al. 2012). SEA has been shown to be less sensitive to sample size than convex hull area (TA; Jackson et al. 2011). Standard ellipse areas controlling for small sample size (SEA_c) were derived from SEA using the following equation, where n = sample size (Jackson et al. 2011):

$$\boldsymbol{SEAc = SEA} \times [(\boldsymbol{n-1}) \div (\boldsymbol{n-2})]$$

SEA_c are influenced even less than SEA by small sample size and were used to calculate isotopic niche overlap, which is a quantitative measure of similarity between the diets of two or more populations (Jackson et al. 2011). The greater the niche width of a species, the more generalized the diet of that species (Guzzo et al. 2013, Mills and Marchant-Forde 2010).

Results

My results showed differences in trophic position, trophic structure, isotopic niche area, and isotopic niche overlap of Silver Carp and Gizzard Shad in five sites in the lower Midwest (Figure 1). Results from the RPP indicated that the mean centroid location was statistically different for most paired comparisons ($\alpha < 0.05$) between fish planktivore groups across systems. However, a few fish planktivore groups' centroid positions were statistically similar (Figure 2). The centroid location of Gizzard Shad in the Ohio River was statistically similar to the centroid position of Gizzard Shad in the Clarks River and in Kentucky Lake ($P = 0.12$; $P = 0.33$, respectively; Figure 2). Similarly, I found that the mean centroid location of Silver Carp in Kentucky Lake and the lower Tennessee River were comparable ($P= 0.90$; Figure 2). Additionally, Silver Carp in the Ohio River had a marginal statistically different trophic position to Silver Carp in the Illinois River ($P= 0.05$; Figure 2). These findings suggest that while centroid locations of Gizzard Shad and Silver Carp are similar across some systems, most Gizzard Shad and Silver Carp trophic positions differ by system.

In addition to making comparisons of centroid locations among Silver Carp and Gizzard Shad across systems, I also checked for statistical differences between the two species within the same system. I found only one system in which the centroid location of Silver Carp and Gizzard Shad was similar. In Kentucky Lake, Silver Carp and Gizzard Shad occupied statistically similar trophic positions ($P= 0.06$; Figure 2). This suggests that Silver Carp and Gizzard Shad in Kentucky Lake are consuming diet resources at a similar trophic level, whereas Silver Carp and Gizzard Shad in other systems are likely consuming diet resources at varying trophic levels.

Although the centroid locations of Silver Carp and Gizzard Shad differed within a system with the lone exception of Kentucky Lake, I did find core isotopic niche overlap in three of the five systems - the Illinois River, the lower Tennessee River, and Kentucky Lake. This suggests shared resource use between Silver Carp and Gizzard Shad in all three of these systems (Figure 3). Point estimates of the SEAc illustrated a 14.51% and 12.78% core isotopic niche overlap between Silver Carp and Gizzard Shad in the Illinois River and lower Tennessee River (Figure 3). Additionally, I found a 4.57% overlap in core isotopic niche area between Silver Carp and Gizzard Shad in Kentucky Lake (Figure 3). Conversely, I found no evidence of core isotopic niche overlap between Silver Carp and Gizzard Shad in the Ohio or Clarks Rivers (Figure 3).

Paired comparisons of trophic structure (CD and NND) aided with the interpretation of core isotopic niche area estimates to establish similarities or differences in trophic structure across systems and between species (Table 1). Results from the RPP suggest that the mean distance to centroid of Gizzard Shad in the Illinois River was significantly different than those of Gizzard Shad in the Ohio River, lower Tennessee River (marginally), and Kentucky Lake ($P < 0.01$, $P = 0.05$, $P < 0.01$, respectively). Further, the mean distance to centroid of Gizzard Shad in the Illinois River was also significantly different than Silver Carp ($P = 0.01$). In addition to examining trophic structure using CD, I also showed significant differences in NND. I found that the NND of Gizzard Shad in the Clarks River was significantly different than Gizzard Shad in the Ohio River ($P = 0.03$). Furthermore, the NND was marginally significant when comparing Gizzard Shad and Silver Carp from the Clarks River ($P = 0.05$). All paired comparisons of NND and CD between systems for Silver Carp were statistically similar. My results indicate that the trophic structure of Gizzard Shad is more variable between systems than the trophic structure of Silver Carp.

Lastly, as another measure of trophic structure, the isotopic niche area of Silver Carp and Gizzard Shad were compared among and between systems (Figure 3; Table 1). I found that the isotopic niche area was greater for both Silver Carp and Gizzard Shad in the Clarks and Illinois Rivers than in the Ohio River, lower Tennessee River, and Kentucky Lake (Table 1; Figure 3). Interestingly, Silver Carp and Gizzard Shad in the

Ohio River had a relatively small isotopic niche area with little variability (Figure 3; Table 1). The more variable and larger core isotopic niche areas of Silver Carp and Gizzard Shad in the Clarks and Illinois Rivers suggests a generalized diet while the less variable and relatively small core isotopic niche area of Silver Carp and Gizzard Shad in the Ohio River suggest a more specialized diet.

Discussion

My study demonstrates similarities and differences in trophic structure and trophic position of Silver Carp and Gizzard Shad at five sites in the lower Midwest. I found that Silver Carp and Gizzard Shad are likely sharing resources in the Illinois River, lower Tennessee River, and in Kentucky Lake, while niche partitioning may be occurring in the Clarks and Ohio Rivers (Figure 3). Although Silver Carp and Gizzard Shad are sharing statistically similar trophic positions in Kentucky Lake, I did find core isotopic niche overlap between the two species in three out of the five systems, which suggests shared resource use between these species (Figure 3). When two species share a limited resource, competition may occur. For example, Mittelbach 1988 found that Bluegill *Lepomis macrochirus* and Pumpkinseed Sunfish *L. gibbosus* growth was directly correlated to Bluegill densities. Moreover, juvenile Bluegill and Pumpkinseed Sunfish growth was correlated to prey abundance (Mittelbach 1988). The previous example illustrates the importance of understanding how interspecific competition may affect Gizzard Shad populations. If a similar scenario occurs between Silver Carp and Gizzard Shad in large Midwestern Rivers, then it could be hypothesized that Silver Carp and Gizzard Shad growth rates may decrease. Therefore, not only would Silver Carp and Gizzard Shad have a limited food supply, but due to slowed growth, they would also be more susceptible to gape-limited predators for a longer period of time. Consequently, the combination of limiting resources and increased predation may cause a decrease in abundance.

In addition to finding core isotopic niche overlap of Silver Carp and Gizzard Shad, I also found differences in trophic structure (CD and NND) of Gizzard Shad across the five systems. In contrast, I found no statistical differences in trophic structure of Silver Carp across the five study sites. The differences in trophic structure of Gizzard Shad and the similarities in trophic structures of Silver Carp across systems suggests that the trophic structure of Silver Carp is more predictable and less varied than that of Gizzard Shad. Additionally, I found that the core isotopic niche area of Silver Carp and Gizzard Shad varied greatly between systems suggesting that the diversity of Silver Carp and Gizzard Shad diets is system dependent and that the resources available to the fish also differ. This conclusion is further supported by findings by Minder and Pyron 2017, who found that the gut contents of Silver Carp are reflective of what is available in the system.

Although I found evidence of shared resource use among Silver Carp and Gizzard Shad, it is important to remember that temporal shifts in resource use and availability could occur (Minder and Pyron 2017). Therefore, the potential for competition between Silver Carp and Gizzard Shad may also vary across a temporal scale. Furthermore, the phenology of the river systems may have influenced my results. For example, if the phenology of resources in the Ohio River trails Kentucky Lake, then Silver Carp and Gizzard Shad may be sharing resources in the Ohio River, just not during the same temporal frame as in Kentucky Lake. In addition to temporal shifts in resource use and potential differences in the phenology of the river systems, a potential drawback to the study was that I only used adult fish. Lebeda and others (*unpublished data*) found that juvenile Silver Carp and juvenile Gizzard Shad in Kentucky Lake had a higher potential for competition than adults of the same species, which may be influenced by site and size dependent gill raker morphology (Walleser et al. 2014). Differences in gill raker morphology of Gizzard Shad among sites may explain my findings of differences in trophic structure across multiple systems and niche partitioning in the Ohio and Clarks Rivers.

In conclusion, my findings suggest that competition between Silver Carp and Gizzard Shad is system dependent. I found that Silver Carp have the potential to directly compete with and negatively influence Gizzard Shad populations in the Illinois River, lower Tennessee River, and in Kentucky Lake. However, it's possible that if the intensity of competition increases in the future (higher population density, limiting resources), the diets of Silver Carp and Gizzard Shad may diverge. Gizzard Shad and Silver Carp have the ability to feed on the same food items, although Gizzard Shad feed extensively on detritus in some systems (Mundahl, and Wissing 1987). Therefore, it is possible that as competition for resources increase, Gizzard Shad diets may shift primarily to detritus. Few systems may have the necessary components to support populations of Gizzard Shad and Silver Carp, although Kentucky Lake is a large reservoir where space will likely not be a limiting factor. I do acknowledge that food resources could become limiting, although more research is needed to determine the carrying capacity of planktivorous fish species in Kentucky Lake.

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Tables

Table 3-1: Dispersion metrics and niche area estimates for Silver Carp (51) and Gizzard Shad (47) collected from Kentucky Lake (KYL), lower Tennessee River (KYD), Ohio River (OH), Clarks River (CR), and the Illinois River (IL) during June of 2016.

	n	**CD**	**NND**	**SEAc**	**SEA**	**TA**
Silver Carp (KYL)	11	0.96	0.51	1.85	1.67	3.06
Silver Carp (KYD)	10	0.87	0.61	1.58	1.40	3.14
Silver Carp (OH)	10	0.47	0.30	0.49	0.44	0.80
Silver Carp (CR)	10	1.41	0.44	2.82	2.51	4.06
Silver Carp (IL)	10	0.93	0.60	1.99	1.77	3.05
Gizzard Shad (KYL)	9	0.83	0.59	1.28	1.12	2.00
Gizzard Shad (KYD)	10	1.06	0.55	1.64	1.46	2.85
Gizzard Shad (OH)	10	0.80	0.42	1.04	0.92	1.91
Gizzard Shad (CR)	7	1.22	0.98	3.75	3.12	4.75
Gizzard Shad (IL)	10	1.63	0.76	4.10	3.65	5.65

Figures

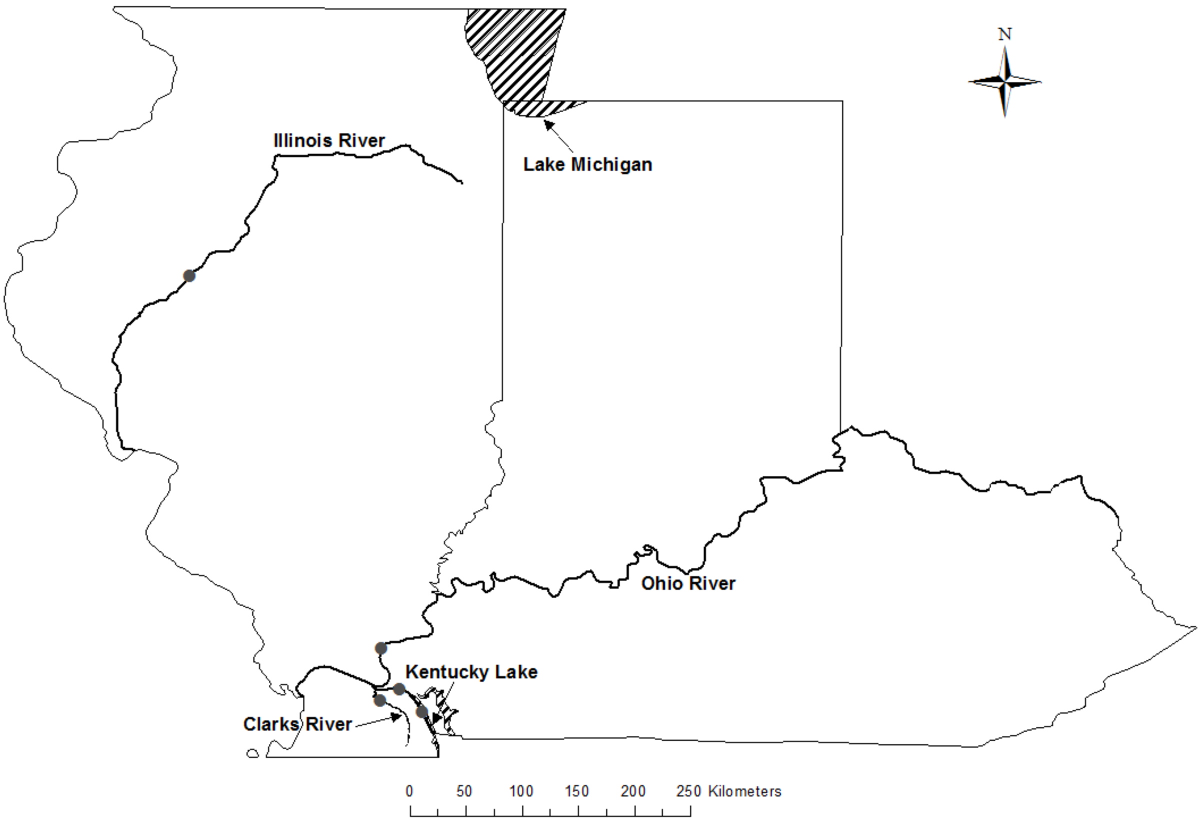

Figure 3-1: Map of sampling locations in June of 2016. The gray circles represent sampling sites. Black lines represent rivers, and the hashed areas represent large water bodies.

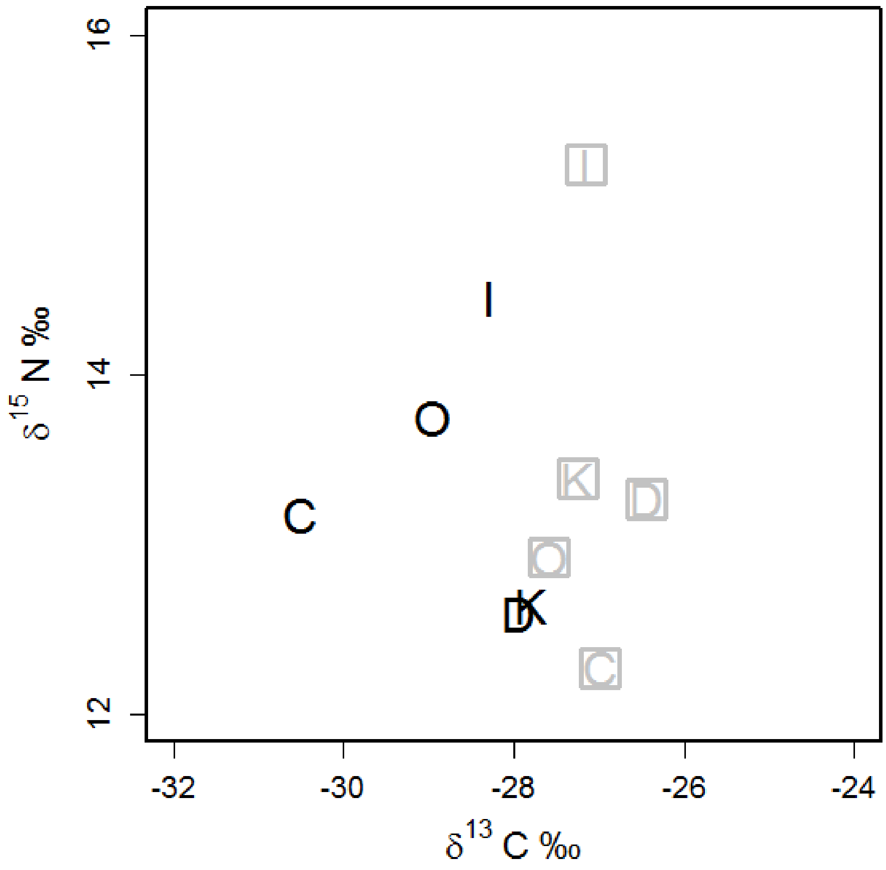

Figure 3-2: Centroid locations of Silver Carp (black) and Gizzard Shad (gray & squares) for Kentucky Lake (K), Kentucky Dam (D), Illinois River (I), Ohio River (O), and Clark’s River (C) in June of 2016.

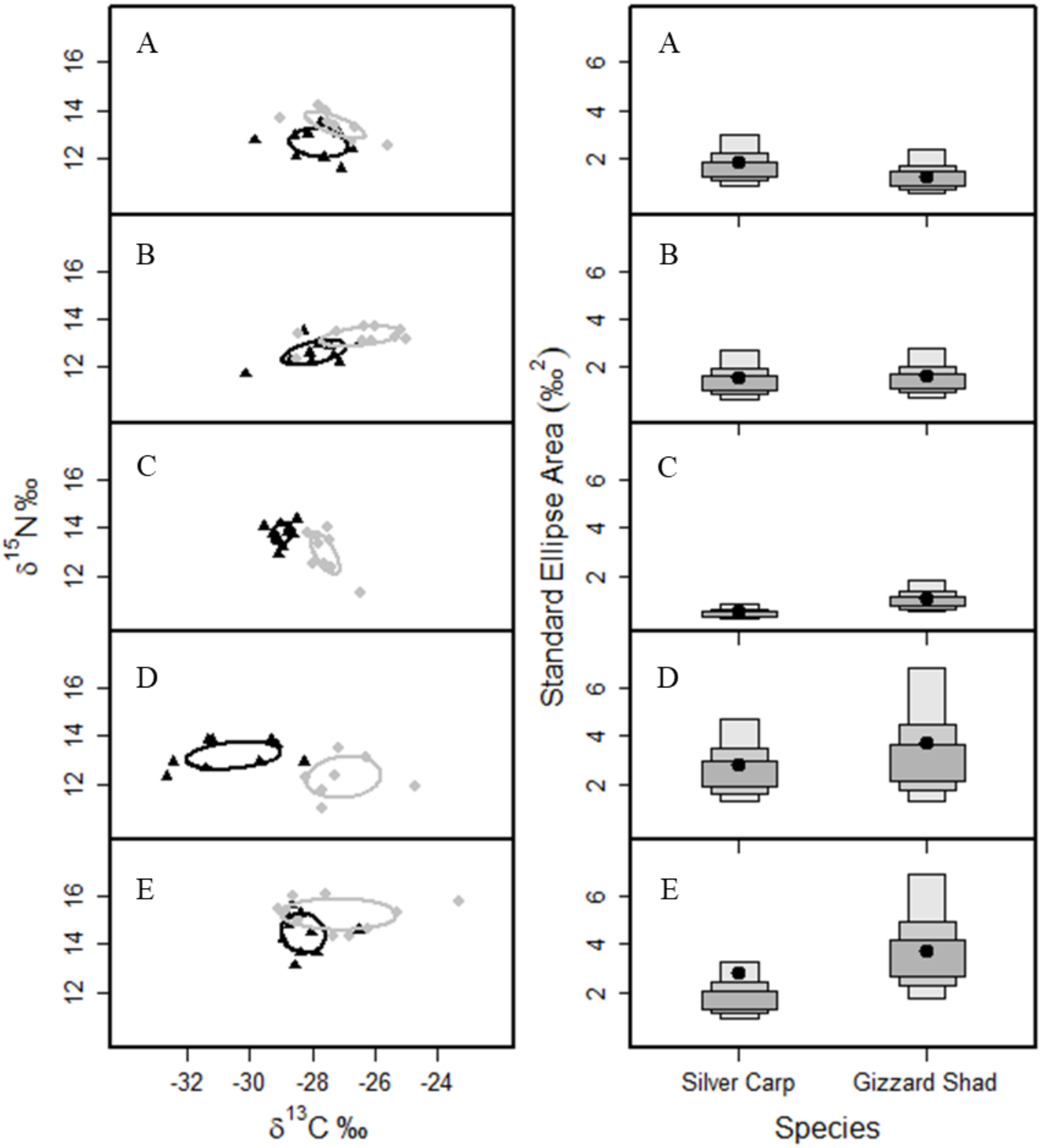

Figure 3-3: Core isotopic niche areas (left) and highest density areas box plots of the standard ellipse areas (right) for Silver Carp (black) and Gizzard Shad (gray) at Kentucky Lake, lower Tennessee River, Ohio River, Clarks River, and Illinois River in June of 2016. From darkest to lightest, the shading on the boxes reflect the 50th, 75th, and 95th percentiles. The black points on the highest density area box plots represent the maximum likelihood estimates for SEAc. The sampling sites are as follows; Kentucky

Lake (A), the lower Tennessee River (B), Ohio River (C), Clarks River (D), and Illinois River (E).

Conclusions

To my knowledge, my research is the first to use stable isotopes to measure core isotopic niche overlap between Silver Carp and native planktivores. This is important because stable isotopes reveal what is metabolically important for fish, not simply what a fish has been eating (gut contents). Diet information gained from stable isotopes is useful when determining if Silver Carp are actually competing for metabolically important food resources with native planktivores. Findings from my research show that in Kentucky Lake, lower Tennessee River, and Illinois River, Silver Carp are sharing metabolically important resources with Gizzard Shad and therefore, have a potential to compete.

Silver Carp have already been shown to reduce the body condition of native planktivores in the Illinois River (Irons et al. 2007). This brings to question, at what point will the effects of Silver Carp be seen in Kentucky Lake and the lower Tennessee River? Sass and others 2010 estimated that there are 2,544 Silver Carp per river kilometer in the La Grange reach of the Illinois River. Notably, the La Grange reach of the Illinois River is the same area where Irons and others 2007 found reduced body condition of native planktivores (Gizzard Shad and Bigmouth Buffalo). Therefore, densities of Silver Carp in other river systems with similar productivity would likely have to reach a similar level before decreases in condition of native planktivores could be expected. Although the densities of Silver Carp in Kentucky Lake and the lower Tennessee River are unknown, based off personal observations while conducting research, it is unlikely that Silver Carp densities in Kentucky Lake and the lower Tennessee River are anywhere near the levels in the Illinois River. However, it’s possible that with differences in productivity levels among the three systems that densities in Kentucky Lake and the lower Tennessee River may not need to reach similar levels to the Illinois River before competition ensues. Therefore, I suggest that baseline data is collected on planktivores (e.g. Gizzard Shad, Bigmouth Buffalo) in Kentucky Lake and the lower Tennessee River. By collecting data on planktivores in these systems now, it will allow researchers to establish body condition of these native planktivores before Silver Carp reach densities high enough to start negatively influencing planktivore populations.

Not only does my research show that there is a potential for competition in three lower river systems, to my knowledge, it is the first study to provide evidence of ontogenetic shifts in Silver Carp diets. I found that juvenile Silver Carp have greater core isotopic niche overlap with Gizzard Shad than their adult counterparts. Therefore, my data suggests that juvenile Silver may have a greater influence on native planktivores than adult Silver Carp. More research is needed to determine the specific differences in juvenile and adult Silver Carp diets. In systems where food resources are limiting, I suggest that managers focus on strategies to reduce juvenile Silver Carp populations to alleviate competition or the potential thereof, and to allocate more prey resources for native planktivores.

In conclusion, Silver Carp are a much larger planktivore than Gizzard Shad and are capable of consuming a larger volume of resources (e.g. plankton) at a higher rate. Because of this, it is likely that if competition occurs, it will be asymmetric. Due to asymmetric competition, in areas of shared resource use and growing populations, or high densities of Silver Carp (e.g. Kentucky Lake, lower Tennessee River, Illinois River), Gizzard Shad may eventually express a reduced body condition. If competition between Silver Carp and shad occurs, then reduced populations and body conditions of shad's native predators may also be observed. Therefore, I recommend additional research to (i) better understand the differences in juvenile and adult Silver Carp diets, (ii) establish body conditions or other measures of fish planktivore health in systems that have not yet reached high Silver Carp densities such as Kentucky Lake and the lower Tennessee River, (iii) research management strategies to reduce juvenile populations of Silver Carp (e.g. reduce spawning habitat and mass removal methods).

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