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POPULATION DEMOGRAPHICS OF SILVER CARP Hypophthalmichthys molitrix IN KENTUCKY LAKE

A Thesis Presented to the Faculty of the Department of Biological Sciences Murray State University Murray, Kentucky

> In Partial Fulfillment of the Requirements for the Degree of Masters of Science

> > by Allison Lebeda

POPULATION DEMOGRAPHICS OF SILVER CARP Hypophthalmichthys molitrix IN KENTUCKY LAKE

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ABSTRACT

Invasive species continue to threaten aquatic ecosystems in the United States. Silver Carp Hypophthalmichthys molitrix have successfully infiltrated much of the Mississippi River Basin, including Kentucky Lake – a large reservoir located on the Tennessee River in Western Kentucky. Although Silver Carp have been present in Kentucky Lake for at least a decade, until recently, very little was known about the population, how often successful reproduction is occurring, or the environmental conditions that facilitate strong year-classes. Hence, it is difficult for managers to predict the potential impact of Silver Carp on native species. Silver Carp were collected from Kentucky Lake using gill nets, cast nets/anglers, boat electrofishing, and commercial fishing. Population demographics (size, age, growth, condition, and mortality) of Silver Carp within Kentucky Lake were examined by measuring total length and weight for all fish and removing a pectoral fin ray for aging. Additionally, spawning periodicity of mature Silver Carp in Kentucky Lake was examined by calculating gonadosomatic index (GSI) or the weight of the gonads relative to the fish's body weight each month for just over a year. Fecundity (number of eggs per female) was estimated by multiplying the average number of eggs within six 1-g sub-samples by the combined weight of both ovaries. Silver Carp in Kentucky Lake were larger sized, faster growing, relatively heavy, and comparatively unexploited compared to other populations in the United States. Female Silver Carp in Kentucky Lake also exhibited higher fecundity than Silver Carp from other populations in the United States. Silver Carp appear to spawn in mid-spring in conjunction with warming water temperatures and rising water flows similar to other

populations. Additionally, the capture of young-of-the-year Silver Carp suggests that successful natural reproduction is occurring in Kentucky Lake. These data provide a snapshot of a relatively recent invasion of Silver Carp and are among the first to characterize reproduction in a large mesotrophic reservoir. Therefore, the results of this study may serve as a model for other large mesotrophic systems such as the embayments of the Great Lakes.

CHAPTER I: Background Information on Silver Carp *Hypophthalmichthys molitrix* in the United States

Invasive species are considered the second largest threat to species diversity after habitat loss and the third largest threat to fish species diversity in the United States (Wilcove et al. 1998). As of 2005, there were 138 non-native fish species documented in the United States (Pimentel et al. 2005). Invasive species have many negative impacts on native ecosystems. For instance, invasive species can compete with native species, alter habitats, and reduce ecosystem function through population reductions and extinctions of native species (Irons et al. 2007; Eiswerth et al. 2018). Additionally, invasive species also harm economies related to aquatic ecosystems such as commercial and recreational fisheries (Irons et al. 2007). Pimentel and others (2005) conservatively estimated the economic losses caused by non-native fish species at \$5.4 billion each year. Invasive species continue to threaten the biodiversity of aquatic ecosystems and cause substantial economic losses.

Of the many introduced species in the United States, one group that has recently and successfully invaded many waterways across the United States is known as the Asian carp. Asian carp is a term that collectively refers to several non-native members of the Xenocyprididae family and includes Bighead Carp *Hypophthalmichthys nobilis*, Grass Carp *Ctenopharyngodon idella*, Black Carp *Mylopharyngodon piceus*, and Silver Carp *H. molitrix*. Originally from large rivers in eastern Asia, Silver Carp were intentionally introduced into the United States around 1973 to improve water quality in fish-production ponds and sewage lagoons (Freeze and Henderson 1982; Kolar et al. 2005; Schofield et al. 2005; Williamson and Garvey 2005). By 1980, flooding events had allowed Silver Carp to escape from confinement (Freeze and Henderson 1982; Kolar et al. 2005). Since their escape, Silver Carp have established reproducing populations throughout most of the Mississippi River Basin (Kolar et al. 2005; Schofield et al. 2005).

Silver Carp have successfully infiltrated the Mississippi River Basin because of life history traits such as opportunistic feeding behavior, fast growth, early maturity, and high fecundity (United States Fish and Wildlife Service Report 2014). Silver Carp are planktivorous and primarily feed on phytoplankton (Kolar et al. 2005; Schofield et al. 2005). However, Silver Carp are highly opportunistic and also feed on zooplankton and detritus, especially if phytoplankton abundances are low (Kolar et al. 2005). Silver Carp quickly grow to large sizes of up to 1.3 meters and 35 kilograms and are believed to be a fairly long-lived species that may live up to 20 years in their native range (Kolar et al. 2005; Schofield et al. 2005). Silver Carp reach sexual maturity between 2 to 4 years of age (United States Fish and Wildlife Service Report 2014) and males typically mature one year earlier than females (Schofield et al. 2005). Fecundity of Silver Carp is typically high and can range from 265,000 to 2,000,000 eggs per female, but can vary by geographic location, size, and age (Kolar et al. 2005; Schofield et al. 2005). In general, heavier ovaries with more eggs tend to be present in larger sized female Silver Carp (Kolar et al. 2005; Schofield et al. 2005).

Due to their fast growth and high fecundity, Silver Carp introduced into novel habitats within the United States may not be immediately recognized as potential prey by native predators and quickly establish populations in new areas. In fact, native predators may actively avoid the potential dangers of consuming new prey in a behavior known as neophobia (Thomas et al. 2010). Furthermore, such extremely fast growth – Silver Carp can reach sizes of approximately 300 mm by age 1 (Williamson and Garvey 2005) – ensures that this non-native species can outgrow many gape-limited piscivorous fish species within a short amount of time. For instance, Largemouth Bass *Micropterus salmoides* up to 483 mm in length consumed Gizzard Shad *Dorosoma cepedianum* up to maximum lengths of only 221 mm (Lewis et al. 1974). In conclusion, opportunistic feeding behavior, fast growth, early maturation, high fecundity, and lack of effective predators all contribute in the establishment of reproducing Silver Carp populations throughout the Mississippi River Basin.

With the successful establishment of Silver Carp populations, the impact of this invasive species on native aquatic ecosystems and their related economies is becoming realized. Silver Carp are efficient planktivores shown to have high diet overlap with native planktivorous fish species such as Gizzard Shad and Bigmouth Buffalo *Ictiobus cyprinellus* (Sampson et al. 2009; Lebeda 2017). Gizzard Shad are a key forage species for piscivores (Williamson and Garvey 2005; Culver and Chick 2015) while Bigmouth Buffalo are an important commercial fish species. Furthermore, evidence suggests that Silver Carp compete for food with these native planktivorous fish species (Irons et al. 2007). Irons and others (2007) found that body condition of Gizzard Shad and Bigmouth Buffalo declined significantly after Bighead Carp and Silver Carp invaded the Illinois River. Moreover, commercial fish harvests in the Upper Mississippi River Basin declined 13% from historical harvest averages after the establishment of Asian carp (United States Fish and Wildlife Service Report 2014). In addition to environmental impacts, Silver Carp commonly leap

out of the water when disturbed by boat motors and have injured boaters and waterskiers, and they have also damaged personal property (Kolar et al. 2005). With the potential for personal injury and/or property damages becoming more commonplace in waters invaded by Silver Carp, local economies depending upon aquatic recreation may be negatively impacted.

Because of the potential and realized harm Silver Carp populations can have on aquatic ecosystems, it is important to understand the dynamic rates of recruitment, growth, and mortality of these populations. Previous work has been conducted on population dynamics of established populations of Silver Carp throughout the Mississippi River Basin. Williamson and Garvey (2005) first examined the newly established Silver Carp population in the Middle Mississippi River. They found that the Middle Mississippi River Silver Carp population was comprised of multiple year-classes thus indicating that Silver Carp had successfully established a reproducing population there (Williamson and Garvey 2005). Silver Carp in the Middle Mississippi River ranged from 0 to 5 years old, however, age 2 Silver Carp were the most common (Williamson and Garvey 2005). Silver Carp in the Middle Mississippi River appeared to reproduce one year earlier than Silver Carp in their native range, which may have been due to the high proportion of young fish in the population or high growth experienced in early life (Williamson and Garvey 2005). Williamson and Garvey (2005) compared the growth of Silver Carp in the Middle Mississippi River with the growth of two non-North American Silver Carp populations: a native population in the Amur River in Russia and an introduced population in Gobindsagar Reservoir in India. Silver Carp in the Middle Mississippi River grew faster than either of the two non-North American Silver Carp populations

thus indicating that Silver Carp in the Middle Mississippi River are finding sufficient resources (Williamson and Garvey 2005). In conclusion, the newly established population in the Middle Mississippi River was comprised primarily of young, fast growing and reproductively mature Silver Carp (Williamson and Garvey 2005).

Recently, Hayer and others (2014) described the Silver Carp population in three South Dakota tributaries of the Missouri River. Similar to the population in the Middle Mississippi River, Silver Carp in the South Dakota tributaries ranged from ages 0 to 5 (Hayer et al. 2014). However, the Silver Carp population in the South Dakota tributaries was dominated by a single year-class thus indicating that this population was still in the initial invasion/colonization stage and immigration from the Missouri River was likely contributing to the population (Hayer et al. 2014). Similar to Williamson and Garvey (2005), Hayer and others (2014) also reported that Silver Carp in the South Dakota tributaries grew faster than the two non-North American populations mentioned above, but slower than Silver Carp in the Middle Mississippi River. So, Silver Carp in the South Dakota tributaries were young and fast-growing, similar to Silver Carp in the Middle Mississippi River (Williamson and Garvey 2005; Hayer et al. 2014).

Additionally, Stuck and others (2015) compared the Silver Carp population in the impounded Illinois River to the Silver Carp population in the free-flowing Wabash River. They reported that the Silver Carp density in the Illinois River was three times the Silver Carp density in the Wabash River (Stuck et al. 2015). Silver Carp in the Wabash River were significantly larger, in better condition, and grew faster than Silver Carp in the densely populated Illinois River (Stuck et al. 2015). Stuck and others (2015) inferred that interspecific and intraspecific competition in the Illinois River likely explained why

Silver Carp were smaller, in poorer condition and grew slower than Silver Carp in the Wabash River (Stuck et al. 2015). Silver Carp in the Wabash River attained older ages than Silver Carp in the Illinois River; Silver Carp were up to 7 years old in the Wabash River while the oldest Silver Carp in the Illinois River was 6 years old (Stuck et al. 2015). Estimated mortality of Silver Carp in the Wabash River was 20% lower than the estimated mortality of Silver Carp in the Illinois River, possibly because the Illinois River supports commercial fishing of Asian carp but the Wabash River does not yet have commercial harvest (Stuck et al. 2015). In conclusion, Silver Carp in the heavily impounded Illinois River generally were smaller sized, in poorer condition, grew slower and had higher mortality than Silver Carp in the free-flowing Wabash River (Stuck et al. 2015).

Seibert and others (2015) defined baseline population demographics for Silver Carp within specific Midwestern rivers throughout the Mississippi River Basin to quantify the level of exploitation necessary to reduce Silver Carp populations. Specifically, size structure, age structure, condition, recruitment, growth, and mortality of Silver Carp populations from the Mississippi (Upper, Middle, and Lower), Missouri, Ohio, Wabash, and Illinois rivers were examined (Seibert et al. 2015). All populations shared similar population characteristics like stable recruitment, fast growth, longevity, and high mortality (Seibert et al. 2015). The advantage of this study was that it allowed for time-sensitive comparisons across a broad spatial distribution whereas most studies focus on one population at one time.

Finally, Ridgway and Bettoli (2016, 2017) were among the first to examine population demographics of Silver Carp in large reservoirs. Using a standardized

sampling approach with a variety of gear types, they examined the Silver Carp populations in Kentucky Lake and Lake Barkley, which are the lowermost reservoirs of the Tennessee and Cumberland rivers respectively. Ridgway and Bettoli (2016, 2017) determined that Silver Carp in Kentucky Lake and Lake Barkley reached similar large sizes, had similar growth rates, and had similar patterns of strong year-classes, which was unsurprising given these reservoirs are connected by a canal near their dams. They captured young-of-the-year Silver Carp hundreds of miles upriver in each reservoir, which may represent the first confirmation of natural reproduction in these reservoirs and their tributaries.

Related to population demographics, previous work has also been conducted on the reproduction of Silver Carp within riverine systems. Silver Carp typically spawn in large riverine environments when water temperatures are between 17 to 26° Celsius, current velocities are between 0.3 to 3.0 meters/second, and water levels are increasing (Abdusamadov 1987; Kolar et al. 2005; Schofield et al. 2005). The eggs of Silver Carp are semi-buoyant and therefore require some current to prevent from sinking to the bottom and dying (DeGrandchamp et al. 2007). The timing of Silver Carp spawning varied slightly by region but generally occurred between April and the end of July or early August (Kolar et al. 2005). In the Amur River where Silver Carp are native, it is believed that the same female may spawn twice during a single growing season (Kolar et al. 2005). Introduced Silver Carp have been shown to successfully reproduce in artificial canals and in at least one reservoir – the Gobindsagar Reservoir in India (Kolar et al. 2005; Schofield et al. 2005).

It is not well known when or how often Silver Carp spawn in non-native North American populations. Gonadosomatic Index (GSI) is a tool that is often used to determine when fish spawn. GSI is an index of the gonadal weight relative to the total body weight of the fish (Crim and Glebe 1990; Stéquert et al. 2001; Schrank and Guy 2002; Williamson and Garvey 2005). Intuitively, one expects the gonadal weight – especially for females - to steadily increase and peak right before spawning occurs then decline precipitously after spawning takes place. Monthly GSI has successfully shown the spawning period of Skipjack Tuna Katsuwonus pelamis and Yellowfin Tuna Thunnus albacares from the west Indian Ocean (Stéquert et al. 2001). Stéquert and others (2001) examined monthly GSI over a period of one year and could definitively determine when two species of tuna spawned. In the Middle Mississippi River, Williamson and Garvey (2005) examined monthly GSI of Silver Carp between July and November. Female Silver Carp GSI ranged from 0.55% to 13.30% from July through November, but did not differ significantly by month (Williamson and Garvey 2005). In the Missouri River, Schrank and Guy (2002) examined monthly GSI of Bighead Carp between January and May. Female Bighead Carp GSI ranged from 0.2% to 14.7% from January through May but did not differ significantly between winter and spring season (Schrank and Guy 2002). Both Williamson and Garvey (2005) and Schrank and Guy (2002) examined GSI over five months and only one month corresponded with the known spawning season of Asian carp in native and introduced European and Asian populations (Kolar et al. 2005). Alternatively, Camacho and others (2015) followed Silver Carp GSI and gonad development in three Iowa tributaries to the Upper Mississippi River from April to October and reported Silver Carp likely spawned between mid-May and mid-June.

However, they observed females with ripe ovaries and males with streaming milt from June to October (Camacho et al. 2015) suggesting a prolonged spawning season that may contribute to the successful establishment of Silver Carp in the Mississippi River Basin. In conclusion, GSI is a proven and viable tool to determine when fish populations spawn and has been previously used to determine when Silver Carp spawn in North American populations.

In addition to using GSI, egg diameter may be another useful tool to determine spawning periodicity of fish. Kjesbu (1994) reported that the spawning time of female Atlantic Cod *Gadus morhua L*. could be predicted based on the diameter of vitellogenic oocytes measured over the last month before spawning occurred. Schrank and Guy (2002) examined mean egg diameter of Bighead Carp in the Missouri River. They reported that mean egg diameter did not significantly differ by anterior, middle or posterior location in the ovary (Schrank and Guy 2002). Additionally, mean egg diameter of Bighead Carp did not differ significantly by winter or spring seasons, however, this may not be surprising as ovary samples were collected between a relatively short time frame from January through May (Schrank and Guy 2002). Bighead Carp egg diameter exhibited a bimodal distribution, which may support the hypothesis that this species has a protracted or extended spawning season (Schrank and Guy 2002). Therefore, measuring egg diameter is a proven technique to estimate fish spawning periodicity and may be especially valuable used in conjunction with GSI.

Although fecundity has been well-quantified in native and introduced European and Asian populations of Silver Carp (Kolar et al. 2005), there are few studies that quantify fecundity of Silver Carp in the United States. Williamson and Garvey (2005) estimated the fecundity of six two-year-old female Silver Carp captured with mature eggs in the Middle Mississippi River and found that fecundity ranged from 57,283 to 328,538 eggs per female. Schrank and Guy (2002) estimated the fecundity of Bighead Carp in the Missouri River, which ranged from 11,588 to 769,964 eggs per female (Schrank and Guy 2002). Fecundity estimates of Silver Carp and Bighead Carp from North American riverine populations appear very similar to fecundity estimates from European and Asian populations (Schrank and Guy 2002; Kolar et al. 2005; Williamson and Garvey 2005).

In the United States, most of the research focused on Silver Carp population dynamics and reproduction has been conducted on Silver Carp populations within rivers. To my knowledge, however, there is only one other study on Silver Carp population dynamics or reproduction in United States reservoirs. Ridgway and Bettoli (2017) evaluated Silver Carp and Bighead Carp populations in the lower Tennessee and Cumberland rivers, including the reservoirs Kentucky Lake and Lake Barkley. Kentucky Lake is the largest impoundment east of the Mississippi River and is located on the Tennessee River. Kentucky Lake supports a diverse freshwater fish community that provides significant commercial and recreational fisheries. According to the Nonindigenous Aquatic Species List maintained by the United States Geological Survey (USGS), Silver Carp were first reported in Kentucky Lake in 2004 (USGS 2015).

As previous research concerning Silver Carp population dynamics and reproduction in North America has focused on riverine systems and has only recently addressed reservoir systems, my research focused on Silver Carp population characteristics within Kentucky Lake. There are two main objectives I addressed with my thesis research. The first objective was to characterize the population of Silver Carp within Kentucky Lake. Specifically, I characterized size structure, age structure, body condition, growth, and mortality of Silver Carp in Kentucky Lake. The second objective was to characterize the reproduction of Silver Carp within Kentucky Lake. Specifically, I estimated fecundity and examined monthly GSI and egg diameter to determine when and how often Silver Carp spawn in Kentucky Lake. I also examined the importance of environmental factors like water temperature and flow on year-class strength.

Based on the relatively recent arrival of Silver Carp within Kentucky Lake and the large size of the reservoir, the Silver Carp population in Kentucky Lake is likely in the early stages of invasion/colonization and densities are relatively low. Because of low densities, Silver Carp in Kentucky Lake will likely be large sized, have high body condition, will reach older ages and will quickly reach maximum size, similar to Silver Carp in the free-flowing Wabash River (Stuck et al. 2015). The mortality rate of Silver Carp in Kentucky Lake will likely be lower than mortality rates reported by Stuck and others (2015) in the Illinois River due to the relatively recent establishment of commercial fishing within Kentucky Lake. Although both the Illinois River and Kentucky Lake encourage commercial harvest of Asian carp, it is unlikely commercial harvest is as significant a source of mortality in Kentucky Lake as it is in the Illinois River due to the catchability of Asian carp in the reservoir. This research provided a valuable baseline that fisheries managers can use to compare future population data, help determine the impact Silver Carp may have on native species in Kentucky Lake, and is among the first to address Silver Carp population dynamics in a large reservoir.

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CHAPTER II: Size, Age, Growth, and Mortality of Silver Carp *Hypophthalmichthys molitrix* in Kentucky Lake

Abstract

Invasive species continue to threaten aquatic ecosystems in the United States. Silver Carp Hypophthalmichthys molitrix have successfully infiltrated much of the Mississippi River Basin, including Kentucky Lake – a large reservoir located on the Tennessee River in Western Kentucky. Although Silver Carp have been present in Kentucky Lake for at least a decade, until recently, very little was known about the population, making it difficult to predict the potential impact of Silver Carp on native species. Silver Carp were collected from Kentucky Lake using gill nets, cast nets/anglers, boat electrofishing, and commercial fishing. Population demographics (size, age, growth, condition, and mortality) for Silver Carp within Kentucky Lake were examined by measuring total length and weight for all fish. Additionally, a pectoral fin ray was removed for aging. Silver Carp in Kentucky Lake were larger sized, faster growing, relatively heavy, and comparatively unexploited compared to other populations in the United States. Additionally, the capture of young-of-the-year Silver Carp suggests that natural reproduction is occurring in Kentucky Lake. These data provide a snapshot of a relatively recent invasion of Silver Carp in a large mesotrophic reservoir and may serve as a model for other large mesotrophic systems such as the embayments of the Great Lakes.

Introduction

Invasive species continue to threaten the biodiversity of aquatic ecosystems and cause substantial economic losses. Specifically, invasive species can compete with native species, alter habitats, and reduce ecosystem function through population reductions and extinctions of native species (Irons et al. 2007; Eiswerth et al. 2018). Pimentel and others (2005) conservatively estimated the economic losses caused by non-native fish species at \$5.4 billion each year. Of the many introduced species in the United States, one species that has recently and successfully invaded many waterways across the United States is Silver Carp *Hypophthalmichthys molitrix*.

Silver Carp have successfully infiltrated the Mississippi River Basin because of life history traits such as opportunistic feeding behavior, fast growth, early maturity, and high fecundity (United States Fish and Wildlife Service Report 2014). Silver Carp primarily feed on phytoplankton, but are highly opportunistic and also feed on zooplankton and detritus, especially if phytoplankton abundances are low (Kolar et al. 2005; Schofield et al. 2005). Silver Carp grow quickly to large sizes of up to 1.3 meters and 35 kilograms (Kolar et al. 2005; Schofield et al. 2005). In fact, Silver Carp can reach sizes of approximately 300 mm by age 1 (Williamson and Garvey 2005). Their extremely fast growth results in limited predation of young Silver Carp because they grow fast enough to escape most gape-limited predators within their first year. Silver Carp reach sexual maturity between 2 to 4 years of age (United States Fish and Wildlife Service Report 2014) and are believed to be a fairly long-lived species that may live up to 20 years in their native range (Kolar et al. 2005; Schofield et al. 2005). Fecundity of Silver Carp is typically high and can range from 265,000 to 2,000,000 eggs per female, but can vary by geographic location, size, and age (Kolar et al. 2005; Schofield et al. 2005). In general, heavier ovaries with more eggs tend to be present in larger sized female Silver Carp (Kolar et al. 2005; Schofield et al. 2005).

With the successful establishment of Silver Carp populations, the impact of this invasive species on native aquatic ecosystems and their related economies is becoming realized. Silver Carp are efficient planktivores shown to have high diet overlap with native planktivorous fish species such as Gizzard Shad Dorosoma cepedianum and Bigmouth Buffalo Ictiobus cyprinellus (Sampson et al. 2009; Lebeda 2017). Gizzard Shad are a key forage species for piscivores (Williamson and Garvey 2005; Culver and Chick 2015) while Bigmouth Buffalo are an important commercial fish species. Furthermore, evidence suggests that Silver Carp compete for food with these native planktivorous fish species (Irons et al. 2007; Lebeda 2017). Irons and others (2007) found that body condition of Gizzard Shad and Bigmouth Buffalo declined significantly after Bighead Carp and Silver Carp invaded the Illinois River. Moreover, commercial fish harvests in the Upper Mississippi River Basin declined 13% from historical harvest averages after the establishment of Asian carp (United States Fish and Wildlife Service Report 2014). Similarly, Lebeda (2017) found juvenile Silver Carp had a high potential to compete with native planktivores like Gizzard Shad while adult Silver Carp had a lower potential to compete.

In addition to environmental impacts, Silver Carp may negatively impact aquatic recreational economies. Silver Carp commonly leap out of the water when disturbed by boat motors and have injured boaters and water-skiers, and they have also damaged personal property (Kolar et al. 2005). With the potential for personal injury and/or

property damages becoming more commonplace in waters invaded by Silver Carp, local economies dependent upon aquatic recreation may be negatively impacted.

In the United States, the majority of research focused on Silver Carp population dynamics and reproduction has been conducted on Silver Carp populations within rivers. To my knowledge, however, there is only one other study on Silver Carp population dynamics or reproduction in United States reservoirs. Ridgway and Bettoli (2016, 2017) evaluated Silver Carp and Bighead Carp populations in the lower Tennessee and Cumberland rivers, including the reservoirs Kentucky Lake and Lake Barkley. Kentucky Lake is the largest impoundment east of the Mississippi River and is located on the Tennessee River. Kentucky Lake supports a diverse freshwater fish community that provides significant commercial and recreational fisheries. According to the Nonindigenous Aquatic Species List maintained by the United States Geological Survey (USGS), Silver Carp were first reported in Kentucky Lake in 2004 (USGS 2015).

Because of the potential and realized harm Silver Carp populations can have on aquatic ecosystems, it is important to understand the dynamic rates of recruitment, growth, and mortality of these populations. The objectives of this research were to 1) quantify size, condition, age, growth, and mortality of Silver Carp in Kentucky Lake and 2) compare these population characteristics to other populations of nonnative Silver Carp within the United States.

Methods

Study Area

My research focused on the Silver Carp population within the main channel and embayments of Kentucky Lake, a mainstem reservoir of the Tennessee River in western Kentucky (Figure 1). This is not a closed population because fish can move in and out of Kentucky Lake through its lock and through the canal that connects Kentucky Lake to Lake Barkley. Similarly, Silver Carp can move among other reservoirs on the Tennessee River. However, telemetry has indicated that movements into and out of Kentucky Lake are relatively rare (Spier and Morris, unpublished data).

Considered the largest reservoir in the eastern United States since its construction in 1944, Kentucky Lake flows north, beginning in Tennessee at Pickwick Dam and extending 296 kilometers north into Kentucky before ending at Kentucky Dam southeast of Calvert City. At maximum capacity, Kentucky Lake has a surface area of 64,870 hectares (Kerns et al. 2009; Tennessee Valley Authority 2016). Classified as a eutrophic reservoir (Kerns et al. 2009; KDFWR 2016), the lower portion of Kentucky Lake is lacustrine with many embayments and backwater channels (Ridgway and Bettoli 2017). The reservoir provides habitat for a multitude of recreational and commercial fish species including black bass *Micropterus* spp., crappie *Pomoxis* spp., catfish *Ictalurus* spp., and Paddlefish *Polyodon spathula*. In addition to local fisheries, the reservoir is a popular destination for recreational boaters and other outdoor enthusiasts. Lastly, with its connection to the Mississippi River, Kentucky Lake acts as a highway for shipment of goods.

Although a mainstem reservoir of the Tennessee River, the downstream portion of Kentucky Lake shares many characteristics more common with lacustrine systems than riverine systems. For instance, water levels within Kentucky Lake are relatively stable and only fluctuate approximately 1.5 m from winter and summer pools (KDFWR 2016). Similarly, water temperatures are fairly static (KDFWR 2016). However, as a mainstem reservoir of the Tennessee River, Kentucky Lake also shares characteristics more common to riverine systems. For instance, normal rainfall patterns decrease water clarity and limit growth of aquatic vegetation (KDFWR 2016). Additionally, Kentucky Lake is similar to riverine systems because it has flow. Average total discharge from Kentucky Dam ranged from 197 to 8,527 cubic meters per second during the period of this study (Tennessee Valley Authority, personal communication). Hence, Kentucky Lake as a large reservoir is unique from purely lacustrine or riverine systems as it shares characteristics common to both systems. Furthermore, Kentucky Lake is unique from other environments within the United States with established Silver Carp populations because of its larger size, its connection to another large reservoir (Lake Barkley), and its ability to remain resilient to rapid water fluctuations.

Field Sampling

I used a combination of gill nets and boat electrofishing in an effort to achieve a diversified sample of different sized Silver Carp in Kentucky Lake. I set monofilament variable, small mesh, and large mesh gill nets in the embayments of Anderson Bay and Turkey Bay as well as in the main channel (Figure 1). Variable gill nets were 41.15 m long and 3.66 m deep with mesh sizes ranging from 25.4 mm to 76.2 mm bar measure. Small mesh gill nets measured 50.8 mm bar, ranged in length from 36.58 to 68.58 m, and

were 3.66 m deep. Finally, large mesh gill nets measured 101.6 mm bar, ranged in length from 36.58 to 68.58 m, and were 3.66 m deep. All gill nets were deployed at the surface in the late evening and retrieved early the following morning. Additionally, I conducted daytime and nighttime electrofishing on a boat outfitted with twin booms each containing 6 steel umbrella droppers and a Midwest Lake Electrofishing System (MLES) infinity control box driven by a 6,500 watt gas-powered generator. The crew consisted of a boat operator and two netters. A broad range of electrofishing settings were experimented with in an attempt to find an optimum setting to capture Silver Carp. Peak power fluctuated from 5,200 to 9,750 watts, volts ranged from 225 to 675, pulses per second varied from 14 to 115 with 60 being the most common, and duty cycle ranged from 25 to 100 percent with 25 percent being the most common.

Many researchers have found Silver Carp to be evasive and difficult to capture (Williamson and Garvey 2005; Conover et al. 2007; Wanner and Klumb 2009; Hayer et al. 2014). This elusiveness is magnified in a reservoir as large as Kentucky Lake, so I also sampled the catch brought to processing plants by commercial fishermen in order to obtain an adequate sample size. Commercial fishermen captured Silver Carp with large mesh gill nets (typically 108.0 mm bar) then brought their catch to one of two local processing plants: RCB Fish Company in Ledbetter, Kentucky or Two Rivers Fisheries in Wickliffe, Kentucky (Figure 1). No more than 20 Silver Carp per location per day were sampled from processing plants (Figure 1). Although commercial fishermen bring Asian carp from multiple local waterways like Barkley Lake, Tennessee River, Ohio River, Cumberland River, etc., I only collected data from Silver Carp specifically reported by the commercial fisherman as captured in Kentucky Lake.

Biological Data and Statistical Analyses

For all Silver Carp, I measured total length (mm) and removed the first pectoral fin ray for aging. Silver Carp were also weighed to the nearest kg if larger than 600 mm and to the nearest g if smaller than 600 mm. For mature Silver Carp, I identified sex (the pectoral fins of male Silver Carp have a rough feel which females lack; this observation was confirmed via dissection and visual identification of the gonads). The smallest Silver Carp identified to sex was 608 mm. Therefore, any Silver Carp smaller than 600 mm were considered immature. All statistical analyses described below were performed using R software (R version 3.6.1, RStudio Team 2018) and the map was created using ArcGIS software (ESRI 2017).

Size Structure and Condition

Size structure of Silver Carp in Kentucky Lake was assessed using length frequency histograms while condition was examined using length-weight regressions and relative weight. The relationship between fish length and weight for Silver Carp was natural log transformed and fit with separate linear regressions specific to fish size. Differences in Silver Carp robustness by size (immature vs mature) were analyzed using dummy variable regression with log₁₀ (weight) as the response variable, log₁₀ (length) as the explanatory variable, and relative size as the quantitative dummy variable (either "0" if immature or "1" if mature) (Ogle 2016). After fitting the linear model for dummy variable regression, an Analysis of Variance (ANOVA, $\alpha = 0.05$) was used to test for significant differences in slopes between juveniles and adults (Ogle 2016). Relative weight was calculated for all Silver Carp larger than 160 mm as $W_r = \frac{actual weight (W_a)}{standard weight (W_s)}$ (Lamer et al. 2019). The standard weight equation provided by Lamer et al. (2019) was based upon the 50th percentile of fish weight at each length rather than the 75th percentile as is typical for relative weights of other species. Mean relative weight for Silver Carp from Kentucky Lake was examined by capture year, Gabelhouse length category, and the interaction between capture year and Gabelhouse length category by using an ANOVA (α = 0.05) followed by Tukey's procedure (Ogle 2016). The Gabelhouse length categories for Silver Carp were previously defined as 160-250 mm, 250-450 mm, 450-560 mm, 560-740 mm, 740-930 mm, and >930 mm (Gabelhouse 1984; Phelps and Willis 2013).

Age, Growth, Mortality, and Year-class Strength

For age analysis, the left pectoral fin ray was removed and dried. Three 700 µm sections were cut from each fin ray using a low-speed diamond blade saw. These sections were immersed in water in an opaque dish, placed beneath a dissecting microscope (15X), and annuli were illuminated using reflected light. It is necessary for the container that holds the pectoral fin ray sections and water to be opaque so that reflected light will illuminate the annuli. Two readers independently aged sections from each fin ray then compared ages. If ages differed, a consensus age was reached. Although Seibert and Phelps (2013) evaluated different aging structures from Silver Carp, as of yet, no clear consensus exists in the Asian carp scientific community regarding the use of specific aging structures. Seibert and Phelps (2013) recommended using lapilli otoliths, but demonstrated high reader agreement with pectoral fin rays, especially within one year. I utilized pectoral fin rays because I found them easy to remove, store, process, and age. Notably, I did not prepare pectoral fin rays the same way described by Seibert and Phelps (2013). In order to investigate the relative precision of this aging technique, the mean

coefficient of variation between the two readers was calculated for each age using $coefficient \ of \ variation = \frac{standard \ deviation}{mean} * 100.$

Growth was modeled using individual lengths at age in 2016 with the von Bertalanffy equation: $L_t = L_{\infty} (1 - e^{-K(t-t_0)})$. In this equation, L_t is the mean length at time t, L_{∞} is the asymptotic length, K is the growth coefficient and t_0 is the time where length would theoretically be 0 (von Bertalanffy 1938; Williamson and Garvey 2005; Hayer et al. 2014; Stuck et al. 2015). I did not model growth in 2015 because of the lack of smaller sized Silver Carp. Differences in growth between fish caught throughout the year were resolved by adding the proportion of year elapsed between a January 1 birth date and the capture date to the estimated age (Stuck et al. 2015). Additionally, growth of juvenile (<600 mm) Silver Carp was examined by tracking monthly mean total length whenever juveniles were captured.

Total annual mortality (A) of Silver Carp within Kentucky Lake was modeled separately for each year and sampling gear (all sampling gears combined vs. commercial fishery only) using weighted catch curves constrained to ages considered fully recruited to the sampling gear (Stuck et al. 2015; Ogle 2016). Catch curves were linear regressions of log-transformed frequency against age (Stuck et al. 2015). The descending limb of the regression line approximates instantaneous total mortality rate (*Z*) and A is determined from: $A = 1 - e^{-Z}$ (Stuck et al. 2015; Ogle 2016). Differences in Silver Carp total annual mortality were tested for a significant interaction between slope (*Z*) and sampling gear (all sampling methods combined, commercial fishery) each year (2015, 2016) using dummy variable regression with natural log (frequency) as the response variable, age as the explanatory variable, and sampling gear as the quantitative dummy variable (either

"0" if all sampling gears combined or "1" if limited to commercial catch only) (Ogle 2016). After fitting the linear model for dummy variable regression, an ANOVA ($\alpha = 0.05$) was used to test for significant differences in slopes between all sampling gears and commercial catch only within each year (Ogle 2016).

Finally, year-class strength was evaluated using Studentized residuals from capture year-specific catch curves. Catch curves for 2015 and 2016 were fit separately using Silver Carp captured with all sampling gears in Kentucky Lake. For each year, Silver Carp ages 4-10 were considered fully recruited to the sampling gears. Critical Studentized residual values corresponding to the 20th and 80th percentiles of the t distribution were calculated to identify "weak" vs "strong" year-classes respectively (Ogle 2016).

Results

Data were collected from 464 Silver Carp captured from Kentucky Lake in 2015 and 2016 (Table 1). Large mesh gill nets accounted for 98% of the 253 collected Silver Carp in 2015 and 65% of the 211 collected Silver Carp in 2016 (Table 1). No Silver Carp were captured using variable or small mesh gill nets (Table 1). Boat electrofishing yielded 27% of the captured Silver Carp in 2016, however, no Silver Carp were caught via boat electrofishing in 2015 (Table 1). Interestingly, 55 of the 76 or 72% of the total immature (<600 mm) Silver Carp were captured by boat electrofishing. Furthermore, immature Silver Carp were only captured via boat electrofishing in 2016 despite 7 hours of effort in 2015 (Table 1), suggesting that immature Silver Carp do not recruit to boat electrofishing until approximately 200 mm and therefore, the 2014 year-class was not present in the reservoir (Figure 2). Catch-per-unit-effort (CPUE) in Kentucky Lake for large mesh 101.6 mm bar gill nets was 0.06 and 0.01 Silver Carp per hour for 2015 and 2016 respectively (Table 1). Comparatively, CPUE for boat electrofishing in Kentucky Lake was 0 and 1.39 Silver Carp per hour in 2015 and 2016 respectively (Table 1). It is important to note that a substantial number of Silver Carp used in this study were collected from the commercial fishery; since commercial fishermen only target and keep the largest fish, the results of my study do not necessarily reflect the entire Kentucky Lake Silver Carp population.

Size Structure and Condition

Silver Carp in Kentucky Lake ranged in length from 72 to 1,100 mm in 2015 (mean = 853 mm) and from 197 to 1000 mm in 2016 (mean = 678 mm; Table 2; Figure 2). Female Silver Carp were larger than males both years (Mann-Whitney U: 2015: W = 7,715.5, p-value < 0.05; 2016: W = 3,756.5, p-value < 0.05; Table 2). More than 83% of Silver Carp collected from Kentucky Lake measured 700 mm or larger (Figure 2). A handful of representatives of the successful 2015 year-class were captured as young-of-the-year during summer 2015; that same year-class recruited to boat electrofishing in spring and late summer 2016 (Table 2; Figure 2). Very few individuals measuring between 450 and 700 mm were captured in either 2015 or 2016 (Figure 2).

Silver Carp in Kentucky Lake ranged in weight from 3.6 g to 13.88 kg in 2015 (mean = 7.67 kg) and from 67 g to 12.53 kg (mean = 5.55 kg) in 2016 (Table 2). On average, females were heavier than males in both years (Mann-Whitney U: 2015: W = 7,694, p-value < 0.05; 2016: W = 3,609.5, p-value < 0.05; Table 2). The total lengthweight relationships for Silver Carp in Kentucky Lake were as follows (Figure 3):

Immature:

 Log_{10} (weight) = -5.02 (95% CI: -5.16, -4.89) + 3.00 (95% CI: 2.94, 3.05) Log_{10} (length)

 $R^2 = 0.99$

Mature:

 Log_{10} (weight) = -6.47 (95% CI: -7.05, -5.89) + 3.52 (95% CI: 3.32, 3.72) Log_{10} (length) $R^2 = 0.76$

The total length-weight regression for immature Silver Carp in Kentucky Lake had a significantly different slope than the regression from mature Silver Carp ($F_{1, 459} = 25.28$, p-value < 0.05). The slope for mature Silver Carp was 0.52 higher (95% CI: 0.32, 0.73) higher than the slope for immature Silver Carp in Kentucky Lake meaning that mature Silver Carp put weight on faster than immature Silver Carp.

Similarly, mean relative weight of Silver Carp also differed by fish size with smaller Silver Carp in relatively poor condition and adult Silver Carp in relatively good condition (Figure 4). Additionally, mean relative weight of Silver Carp did not differ significantly by the interaction of capture year and Gabelhouse length category ($F_{1, 451} = 0.0622$, p-value = 0.80). Therefore, I refit the model without the interaction between capture year and Gabelhouse length category. Mean relative weight was significantly higher in 2015 ($F_{1, 452} = 3.7863$, p-value = 0.05).

Mean relative weight also differed significantly by Gabelhouse length category $(F_{4, 452} = 13.6491, p-value < 0.00001)$. Specifically, smaller Silver Carp had significantly lower mean relative weights than larger Silver Carp (Figure 5). Smaller Silver Carp sized 160-250 and 250-450 mm had statistically similar mean relative weights at 91 and 94

respectively, yet these were statistically different than mean relative weights for larger Silver Carp sized 740-930 and >930 mm at 104 and 109 (Figure 5). To clarify, the two length categories on either side of the scale had statistically similar mean relative weights to the next size length category but Silver Carp belonging to the two smallest sized length categories had significantly lower mean relative weight than Silver Carp belonging to the two largest sized length categories (Figure 5). Medium sized Silver Carp in the 560-740 mm length category had statistically similar mean relative weight to all other length categories (Figure 5).

Age, Growth, Mortality, and Year-class Strength

Two readers independently aged 351 Silver Carp collected from Kentucky Lake between 2015 and 2016 using pectoral fin ray sections. Silver Carp ages ranged from 1 to 10 years old with ages 3, 4, and 5 the most common in 2015 and ages 1, 4, 5, and 6 most prevalent in 2016 (Figure 6). Two-year-olds were noticeably absent in both capture years (Figure 6). Strong year classes occurred in 2006, 2010, and 2011 with representatives from the 2005-2012 and 2015 year classes present (Figures 6 and 11). Although representatives from 9 different year-classes were found, 90% of aged Silver Carp belonged to either the 2010, 2011, 2012, or 2015 year-classes (Figure 6). No representatives from either the 2013 or 2014 year classes were observed (Figure 6). Complete reader agreement was 87% and where readers differed, 93% were within one year. Across all aged Silver Carp, 99% of readings differed by one year or less. The mean coefficient of variation by age increased with age, especially for Silver Carp ages 6-9 (Figure 7). Furthermore, reader agreement was 100% for the 61 representatives from the 2015 year-class, which are essentially known-age fish. Although we did not age any age-0 fish from the 2015 year-class, we aged 61 age-1 fish in 2016. Fifty-one of these fish were captured in April/May and had not yet laid down their annuli while the remaining ten were captured in September/October and had laid down their first annulus.

Finer divisions of aged Silver Carp based on time elapsed between capture date and a January 1 birth date were calculated to account for differences in growth due to different capture rates throughout the year and ranged from 3.4 to 10.4 years (mean = 5.1 years, standard deviation = 1.2 years) in 2015 and 1.2 to 10.7 years (mean = 4.2 years, standard deviation = 2.4 years) in 2016 (Figure 6). The paucity of young Silver Carp captured in 2015 (n = 5) ensured that growth could only be completely modeled in 2016 (Figure 8). Growth of 175 Silver Carp in 2016 was modeled using the equation: L_t = 917 (1 - $e^{-0.82(t-0.93)}$). Theoretical maximum length (L_{∞}) was 917 (95% CI: 906, 930) for Silver Carp in 2016 and the growth coefficient was 0.82 (95% CI: 0.73, 0.93). Silver Carp in Kentucky Lake are growing extremely fast and are reaching their asymptotic length by age 4 (Figure 8).

As mentioned previously, juvenile Silver Carp (<600 mm) were only captured sporadically: once by cast net anglers in 2015 and primarily by boat electrofishing in 2016. Despite this, juvenile Silver Carp were caught frequently enough to allow me to follow their growth during their first year. For instance, young-of-the-year (YOY) Silver Carp captured in July 2015 were approximately 100 mm and had doubled in size to 200 mm by the next spring (Figure 9). Only a few months later in the fall of 2016, one-year-old Silver Carp had again doubled in size from 200 to 400 mm (Figure 9). Hence, within

the course of a year-and-a-half, Silver Carp had quadrupled their size from 100 to 400 mm and had outgrown the maximum length Gizzard Shad (221 mm) found in the stomachs of 483 mm Largemouth Bass by Lewis and others in 1974 (Figure 9).

In 2015, total annual mortality (A) for Silver Carp in Kentucky Lake was estimated at 55.8% (95% CI: 33.1%, 70.8%) using Silver Carp fully recruited to all sampling gears and 47.7% (95% CI: -12.5%, 75.7%) using only Silver Carp fully recruited to the commercial fishery (Figure 10). Comparatively, total annual mortality for Silver Carp in Kentucky Lake during 2016 was estimated at 32.2% (95% CI: 16.0%, 45.3%) using Silver Carp fully recruited to all sampling gears and 49.2% (95% CI: 14.0%, 70.0%) using only Silver Carp fully recruited to the commercial fishery (Figure 10). No statistically significant differences in total instantaneous mortality (*Z*) were detected between catch curve regressions created using all sampling gears vs. regressions created using only commercial catch in 2015 (Dummy Variable Regression: $F_{1,9} = 0.459$, p-value = 0.515) or in 2016 (Dummy Variable Regression: $F_{1,10} = 0.329$, p-value = 0.579).

Tables and Figures

Table 2-1. Total Silver Carp collected (n=464) by sampling year (2015, 2016) and gear type or collection method (gill nets, boat electrofishing, or cast nets/anglers). The small, variable and large mesh gill nets were set by me while Silver Carp sampled at processing plants were brought in by commercial fishermen using large mesh gill nets (typically 108.0 mm bar mesh). The number of Silver Carp collected and effort in hours is shown for each category. Effort for commercially caught Silver Carp sampled at processing plants is shown as the number of trips to the plant within that year. Effort for Silver Carp collected by anglers or cast nets are also reported as number of trips.

	2015		2016		_	
	Total Silver Carp (n)	Effort	Total Silver Carp (n)	Effort	Total Silver Carp (n)	Total CPUE
Small Mesh 50.8 mm bar gill nets	0	208 hrs	0	0 hrs	0	0.000 carp/hr
Variable Mesh 25.4-76.2 mm bar gill nets	0	116 hrs	0	0 hrs	0	0.000 carp/hr
Large Mesh 101.6 mm bar gill nets	74	1,188 hrs	3	213 hrs	77	0.055 carp/hr
Processing Plant ~108.0 mm bar gill nets	174	10 trips	135	8 trips	309	17.167 carp/trip
Boat Electrofishing	0	7 hrs	57	41 hrs	57	1.188 carp/hr
Cast Nets/Anglers	5	1 trip	16	1 trip	21	10.500 carp/trip
Total Silver Carp (n)	253	-	211	-	464	-

Table 2-2. Sample size (n), mean length (mm), and mean weight (g) of Silver Carp captured from Kentucky Lake by year (2015, 2016) and by sex (male, female). Standard deviation is shown in parentheses. The smallest sized Silver Carp identified to sex was 608 mm. Therefore, Silver Carp larger than 600 mm were considered mature while those Silver Carp smaller than 600 mm were considered immature. Mature (>600 mm) Silver Carp combines mature male and female Silver Carp, but note that not all mature Silver Carp were identified to sex due to time limitations at commercial processing plants.

	2015			2016			
	Total Silver Carp (n)	Mean Length (mm)	Mean Weight (g)	Total Silver Carp (n)	Mean Length (mm)	Mean Weight (g)	
Immature (<600 mm)	5	81 (±11)	6 (±3)	71	255 (±55)	182 (±161)	
Mature (>600 mm)	248	869 (±59)	7,822 (±1943)	140	893 (±45)	8,278 (±1,878)	
All Silver Carp	253	853 (±124)	7,667 (±2,212)	211	678 (±306)	5,554 (±4,128)	
Mature Females	89	892 (±52)	8,602 (±1,996)	86	912 (±39)	8,959 (±1,792)	
Mature Males	112	836 (±50)	6,675 (±1,360)	54	863 (±37)	7,192 (±1,462)	

Table 2-3. Number of Silver Carp from Kentucky Lake in each Gabelhouse length category by year.

Year	160-250	250-450	450-560	560-740	e 740-930	>930
	mm	mm	mm	mm	mm	mm
2015	0	0	0	4	206	38
2016	46	25	0	0	108	32

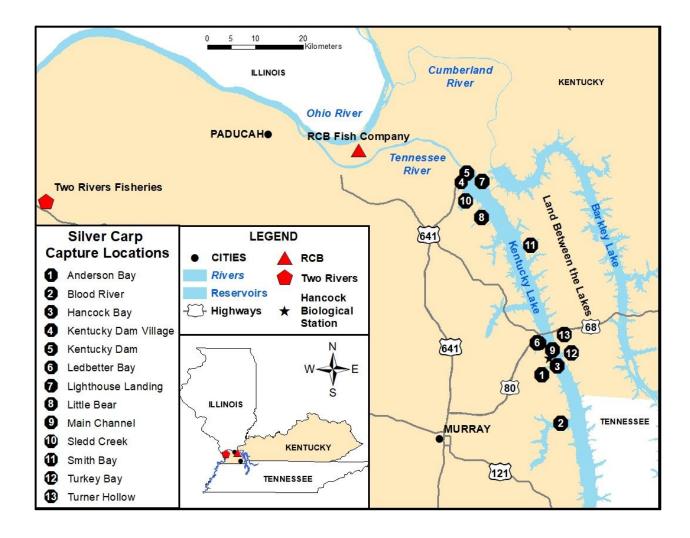


Figure 2-1. Capture locations of Silver Carp from Kentucky Lake during 2015 and 2016 are labeled with black octagons. Commercial processing plants (Two Rivers Fisheries and RCB Fish Company) are shown in red and the field station (Hancock Biological Station) is depicted with a black star. In general, sites in close proximity to Hancock Biological Station are where I used electrofishing and gill nets to collect fish. Locations located closer to the tailwaters of the reservoir are generally where commercial fishermen collected Silver Carp in gill nets then brought their catch to either of the two local processing plants for distribution. Map created in ArcGIS (ESRI 2017).

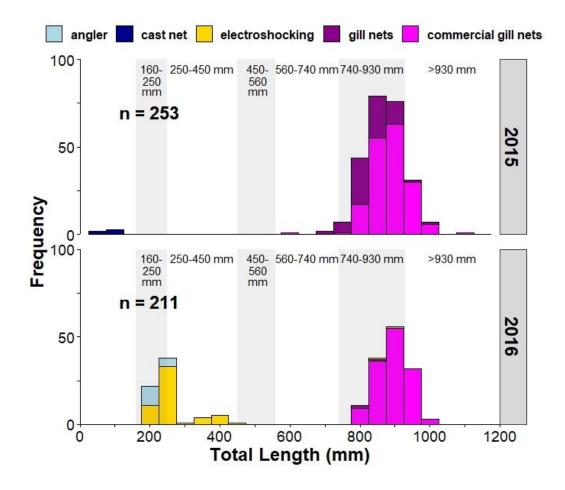
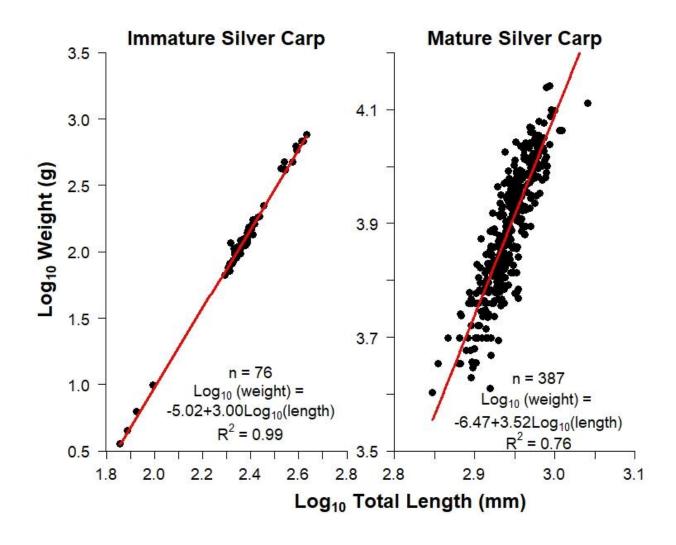
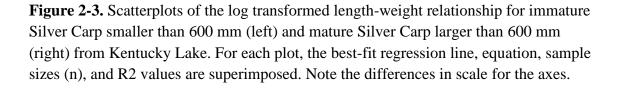


Figure 2-2. Length frequency histograms by gear type (cast nets, anglers, boat electrofishing, gill nets I set, or commercial gill nets) of Silver Carp captured in Kentucky Lake in 2015 (top) and 2016 (bottom). The two modes for Silver Carp <600 in 2016 represent fish collected during spring vs. fall sampling. Alternating light gray and white shaded rectangles represent the five Gabelhouse length categories for Silver Carp (160-250 mm, 250-450 mm, 450-560 mm, 560-740 mm, 740-930 mm, >930 mm).





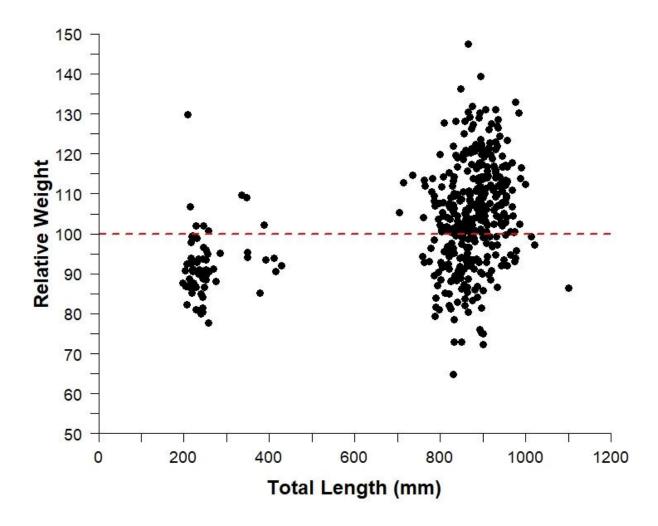


Figure 2-4. Scatterplot of relative weight and total length (mm) for Silver Carp in Kentucky Lake. The dashed red line represents a relative weight of 100 or a Silver Carp in median condition. Relative weight values greater than 100 represent Silver Carp in above median condition while relative weight values less than 100 represent Silver Carp in below median condition (Lamer et al. 2019).

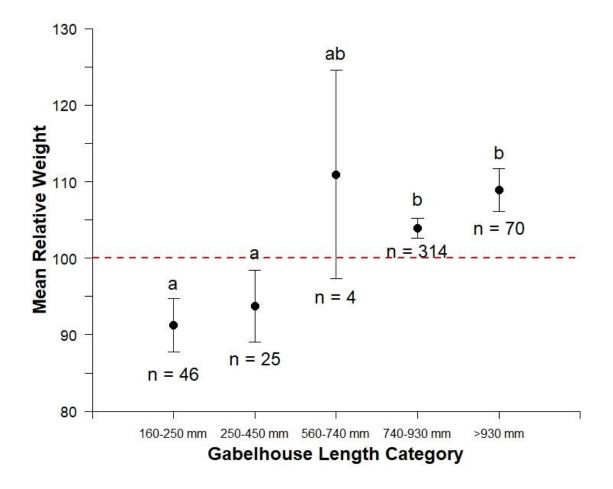


Figure 2-5. Mean relative weight of Silver Carp in Kentucky Lake in 2015 and 2016 by Gabelhouse length category. Error bars are ± 1 standard error. Identical letters represent statistically similar mean relative weight between length categories while differing letters signify statistically different mean relative weights using α of 0.05. No Silver Carp were captured in the 450-560 mm category. The dashed red line represents a relative weight of 100 or a Silver Carp in median condition. Relative weight values greater than 100 represent Silver Carp in above median condition while relative weight values less than 100 represent Silver Carp in below median condition (Lamer et al. 2019).

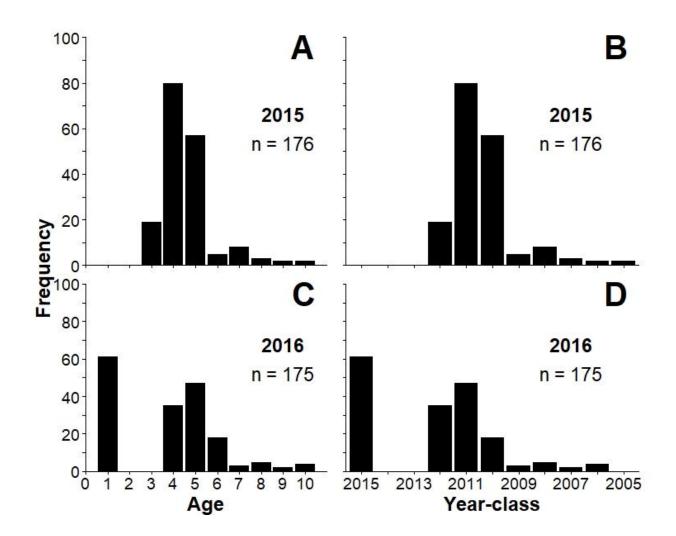


Figure 2-6. On the left, frequency histograms depicting ages of Silver Carp from Kentucky Lake captured in 2015 (A) versus 2016 (C). On the right, frequency histograms showing Silver Carp year-classes from Kentucky Lake represented in 2015 (B) versus 2016 (D). Sample sizes (n) are also shown on each plot.

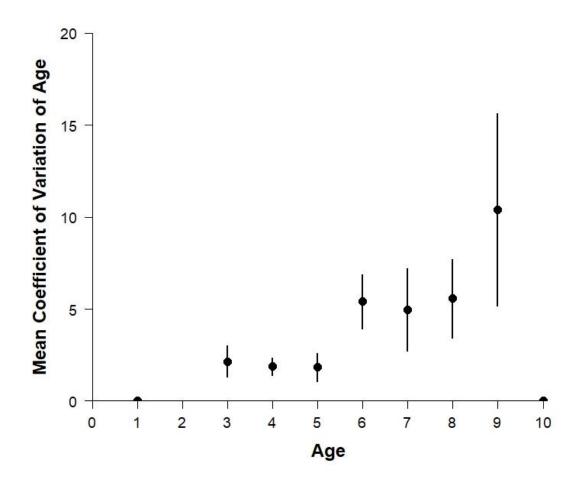


Figure 2-7. Mean coefficient of variation of age between two readers by agreed-upon age across 351 aged Silver Carp from Kentucky Lake. Error bars represent standard error of the mean.

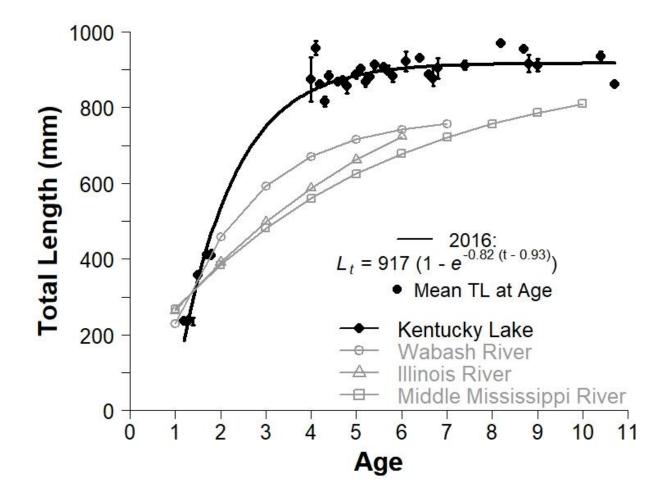


Figure 2-8. The solid black line represents the von Bertalanffy growth models developed using individual lengths at age for Silver Carp captured in 2016 in Kentucky Lake. Black circles depict mean total length (mm) at each age proportional to time elapsed from a January 1 birth date and capture date according to the methods of Stuck et al. 2015. Error bars are ± 1 standard error. Gray solid lines and symbols represent the von Bertanlanffy growth models and mean total lengths at integer ages for Silver Carp in the Wabash River (open circles, Stuck et al. 2015), Illinois River (open triangles, Stuck et al. 2015), and Middle Mississippi River (open squares, Seibert et al. 2015).

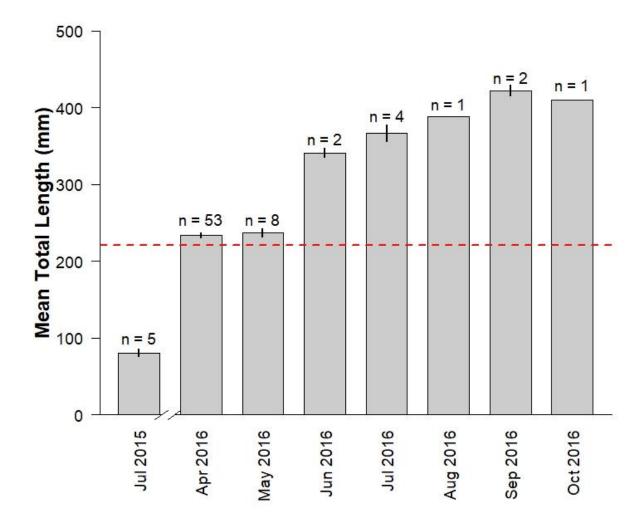


Figure 2-9. Gray bars represent monthly mean total length (mm) of juvenile Silver Carp in Kentucky Lake in July 2015 and April-October 2016. Error bars signify ±1 standard error and sample sizes (n) are shown above each bar. The dashed red line signifies the maximum length of Gizzard Shad (221 mm) consumed by 483 mm Largemouth Bass (Lewis et al. 1974).

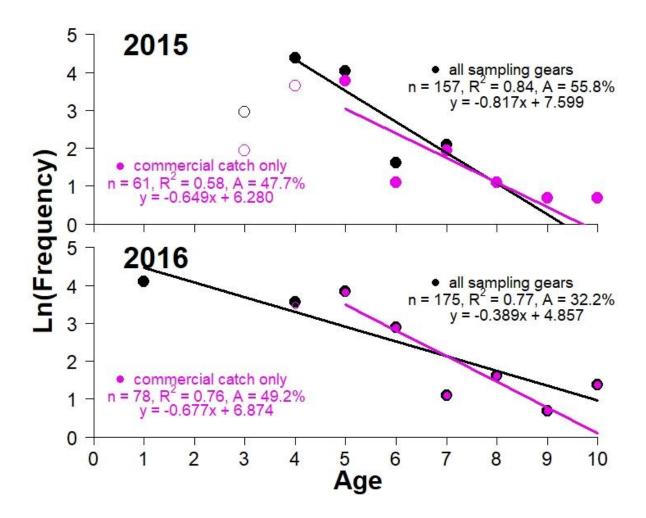


Figure 2-10. Weighted catch-curve regressions for Silver Carp in Kentucky Lake in 2015 (top) and 2016 (bottom). For each year, best estimates for instantaneous total mortality rate (Z), total annual mortality rate (A), the number of fish considered fully recruited to the gear used to create catch-curve regressions (n and closed circles), and the best fit equations are shown using all sampling gears (black) and only commercial catch (magenta). Silver Carp ages 4+ and 1+ were considered fully recruited using all sampling gears in 2015 and 2016 respectively. Comparatively, Silver Carp ages 5+ were considered fully recruited using only commercial catch in both 2015 and 2016.

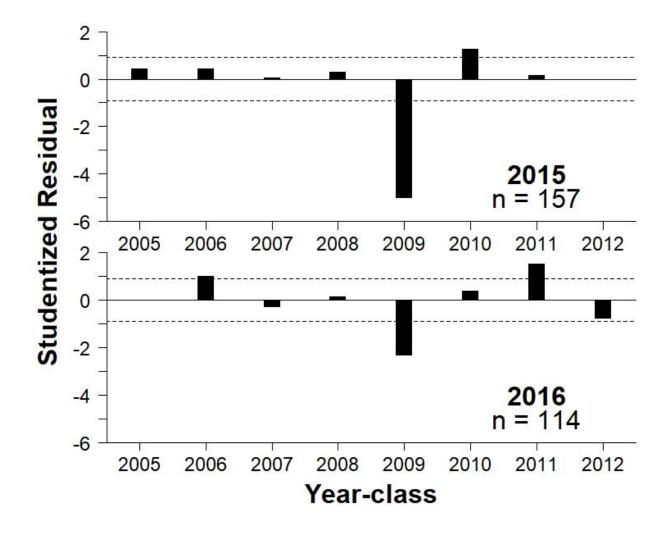


Figure 2-11. Studentized residuals from the year-specific weighted catch curves for age-4 to age-10 Silver Carp captured using all sampling gears in Kentucky Lake in 2015 (top) and 2016 (bottom). Horizontal dashed lines represent the upper and lower 20% of residuals. Year-classes above the upper dashed lines are considered "strong" while yearclasses below the lower dashed lines are considered "weak" (Ogle 2016). For each year, sample sizes (n) are shown.

Discussion

Since the escape and continuing successful establishment of nonnative Silver Carp throughout the Mississippi River Basin, much research has been performed to study the demographic information of this species in riverine systems including the Wabash River (Seibert et al. 2015; Stuck et al. 2015), Illinois River (Seibert et al. 2015; Stuck et al. 2015), Ohio River (Seibert et al. 2015), Mississippi River (Williamson and Garvey 2005; Seibert et al. 2015) and its Iowa tributaries (Camacho 2016), and lastly, the Missouri River (Seibert et al. 2015) and its North Dakota tributaries (Hayer et al. 2014). To date, however, there has been a paucity of research describing the population characteristics of nonnative Silver Carp within United States reservoirs. My research adds to this knowledge by 1) describing baseline population demographic information (size, condition, age, growth, and mortality) of Silver Carp within Kentucky Lake and 2) comparing these population characteristics to other nonnative Silver Carp populations in the Mississippi River Basin.

Many researchers have found Silver Carp difficult to capture with traditional sampling methods even in areas with high densities (Stancill 2003; Williamson and Garvey 2005; Conover et al. 2007; Wanner and Klumb 2009; Hayer et al. 2014; Ridgway and Bettoli 2017). The low catch-per-unit-effort (CPUE) values for gill netting and boat electrofishing methods observed during my research continued this trend (Table 1). The restricted number of Silver Carp caught can make it challenging to evaluate population characteristics (Wanner and Klumb 2009). I anticipated that the evasiveness of Silver Carp would be magnified in a reservoir the size of Kentucky Lake, so I employed a variety of methods including gill netting, boat electrofishing, and sampling commercial fishermen's catch.

While other researchers have found boat electrofishing the most effective method to provide a diversified sample representative of the different size and age classes of Silver Carp (Butler et al. 2013), I found boat electrofishing more effective at capturing juveniles (<600 mm; Table 1; Figure 2). Only 2 large sized fish (>600 mm) were captured by boat electrofishing (Figure 2). Small (50.8 mm bar) and variable (25.4-76.2 mm bar) mesh gill nets never caught Silver Carp (Table 1) and instead filled with bycatch, so this method was abandoned in 2016. Larger sized Silver Carp were better sampled using large mesh gill nets fished by either me or commercial fishermen (Table 1; Figure 2). Ridgway and Bettoli (2017) utilized a combination of standardized gill nets, boat electrofishing, hoop nets, and cast nets to capture a variety of different sized Silver Carp within Kentucky Lake and its sister reservoir, Lake Barkley; however, the former two methods accounted for 97% of their Silver Carp catch. My opportunistic strategy also worked well and I obtained a diversified sample of the Silver Carp population within Kentucky Lake, which allowed me to further explore population characteristics like size structure, condition, growth, and mortality. I recognize that my results are heavily influenced by commercial catch and are not necessarily representative of the true Silver Carp population within Kentucky Lake.

Size structure of Silver Carp within Kentucky Lake was similar in both 2015 and 2016 and consisted primarily of large-sized fish (>800 mm) with the exception of the emerging 2015 year-class (Table 2; Figure 2). In 2015, only a handful of these young-of-the-year (YOY) carp were captured accidentally while a Kentucky Department of Fish

and Wildlife Resources biologist was cast netting for live bait (Ridgway and Bettoli 2016; Michael Flinn, Hancock Biological Station, personal communication). This same year-class was more easily captured by boat electrofishing methods the following year in 2016 (Figure 2). Ridgway and Bettoli (2016, 2017) found the same bimodal size structure in Kentucky Lake and its sister reservoir, Lake Barkley. Despite using a variety of sampling gears throughout the length of the reservoir, neither Ridgway and Bettoli (2016, 2017) nor I could capture medium sized (500-700 mm) Silver Carp within Kentucky Lake, suggesting the absence of these size classes (Figure 2). The unimpounded lower Wabash River, which is the longest (810 km) free-flowing river east of the Mississippi River, had the most similar size structure to Kentucky Lake with an abundance of large sized (~700-800 mm) Silver Carp and at least one younger strong year-class (~200-400 mm) (Seibert et al. 2015; Stuck et al. 2015). In contrast, the Illinois River and Mississippi River lack larger sized Silver Carp as they are targeted by commercial fisheries (Stuck et al. 2015). When compared to riverine populations, Silver Carp are considerably larger and grow faster in Kentucky Lake (Hayer et al. 2014; Seibert et al. 2015; Stuck et al. 2015; Camacho 2016; Ridgway and Bettoli 2016, 2017).

Age structure of Silver Carp within Kentucky Lake was comprised primarily of younger fish with some representatives of older fish present (Figure 6). This is similar to what other researchers have reported for United States Silver Carp populations. Although other researchers have found fairly constant recruitment in Silver Carp (Seibert et al. 2015), I found a boom-and-bust recruitment pattern common to many fish species with most Silver Carp belonging to either the 2010, 2011, 2012, or 2015 year-classes. Using a different aging structure – lapilli otoliths – Ridgway and Bettoli (2016, 2017) found similar ages and year-classes in Kentucky Lake. Seibert and Phelps (2013) compared various aging structures for Silver Carp and recommended using lapilli otoliths, but agreed that pectoral fin rays displayed 78% agreement. I found pectoral fin rays to have high reader agreement (87%), easy to age, and gave me similar ages reported in other studies (Seibert et al. 2015; Stuck et al. 2015; Ridgway and Bettoli 2016, 2017). Seibert and Phelps (2013) cautioned that pectoral fin rays could underestimate the true age of the fish, especially older fish; however, note that I prepared the pectoral fin rays in a different manner than Seibert and Phelps. The oldest age I found was 10 years (Figure 6) whereas Ridgway and Bettoli (2016, 2017) reported 13 years old as the maximum age for Silver Carp in Kentucky Lake. In summary, the Silver Carp population in Kentucky Lake was comprised primarily of young fish, but older age-classes were present, which is similar to other riverine populations.

Growth of Silver Carp within Kentucky Lake is among the fastest recorded in the United States. Silver Carp in Kentucky Lake grew quickly to large sizes (>800 mm) as early as age-4 and growth slowed as they aged (Figure 8). Ridgway and Bettoli (2016, 2017) observed similar growth patterns in Kentucky Lake and Lake Barkley. Additionally, I was able to document the fast growth of juvenile Silver Carp in Kentucky Lake once these fish recruited to boat electrofishing (Figure 9). In July 2015, young-ofthe-year Silver Carp were approximately 100 mm and had quadrupled in size by the following summer (Figure 9). If Silver Carp outcompete native planktivorous prey species like Gizzard Shad, such fast growth of Silver Carp ensures they are not a suitable replacement prey for native gape-limited piscivores. Although my study design was more opportunistic and did not allow for point estimates of relative abundance, such fast growth documented in Kentucky Lake anecdotally suggests that the population of Silver Carp within Kentucky Lake is newly established and not yet limited by densities.

Condition of Silver Carp within Kentucky Lake was constant between years and differed by fish size (Figures 4 and 5). Specifically, smaller sized Silver Carp had poorer condition than larger sized Silver Carp (Figures 4 and 5). This supports Lebeda's (2017) findings that Silver Carp consume different foods at different sizes and therefore possess different niches. Lebeda (2017) suggested that Silver Carp would have a higher potential to compete with Gizzard Shad at smaller size classes while adult Silver Carp had different niches and would have a lower potential to compete with Gizzard Shad. Interestingly, the 2015 year-class experienced a large fish kill due to Pseudomonas infection in spring 2017. My data suggest this year-class was already stressed and in relatively poor condition perhaps because of inter- and intraspecific competition, which made them more susceptible to the bacterial infection.

Although I estimated annual mortality based on catch curves developed using all sampling gears vs. only commercial catch, the abundance of one-year-olds in 2016 appeared to greatly underestimate annual mortality of Silver Carp in Kentucky Lake (32% compared to 49%; Figure 10). Annual mortality rates of Silver Carp within Kentucky Lake based on the commercial fishery, however, were relatively high and similar both years (47% and 49% respectively; Figure 10). Boom and bust recruitment patterns commonly seen in many fish species, including Silver Carp, can drastically impact mortality estimates. Therefore, collecting data over a longer time period would allow me to better understand mortality estimates for the Silver Carp population in Kentucky Lake. Other researchers have reported high mortality rates within this species in Midwestern rivers throughout the Mississippi River Basin (Seibert et al. 2015). The Illinois River and Lower Mississippi River have the highest annual mortality rates (77% and 62% respectively) and also support significant commercial fisheries for larger sized Silver Carp. Interestingly, although Kentucky Lake has advocated commercial fisheries for several years, annual mortality rates were considerably lower than those reported in the Illinois and Mississippi rivers (Seibert et al. 2015), probably because the commercial fishery is not as established in Kentucky Lake. Also, the higher growth rates in Kentucky Lake compared to the Illinois and Mississippi rivers suggest the density of Silver Carp in Kentucky Lake is much lower than in those rivers. Thus, Kentucky Lake Silver Carp likely experience less density-dependent competition, which might also influence mortality rates.

In summary, Silver Carp in Kentucky Lake are larger sized, faster growing, in good condition, and relatively unexploited when compared to other populations within the Mississippi River Basin. Such large sizes reached at young ages suggests that this population is newly established and not yet limited by density dependence. Future directions would be to compare 2015 and 2016 population characteristics (i.e. size, age, growth, and mortality) with recent years to examine the trajectory of the population. Such information can be valuable to managers as they look for ways to control and eradicate this nonnative species. Additionally, the size of Kentucky Lake, while considerable, is a similar size to embayments on the Great Lakes. Despite this discrepancy and the obvious differences in habitat types and environmental conditions, large reservoirs like Kentucky Lake may serve as the only models available for how populations of Silver Carp may respond when they reach the Great Lakes.

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CHAPTER III: Characterization of Silver Carp Hypophthalmichthys molitrix Reproduction in Kentucky Lake

Abstract

Invasive species continue to threaten aquatic ecosystems in the United States. Silver Carp Hypophthalmichthys molitrix have successfully infiltrated much of the Mississippi River Basin, including Kentucky Lake – a large reservoir located on the Tennessee River in western Kentucky. Although Silver Carp have been present in Kentucky Lake for at least a decade, until recently, very little was known about the population or the environmental conditions that facilitate strong year-classes, making it difficult to predict the potential impact of Silver Carp on native species. Silver Carp were collected from Kentucky Lake using gill nets, boat electrofishing, and commercial fishing. Fecundity (number of eggs per female) was estimated by multiplying the average number of eggs within six 1-g sub-samples by the combined weight of both ovaries. Additionally, spawning periodicity of Silver Carp in Kentucky Lake was examined by calculating gonadosomatic index (GSI) or the weight of the gonads relative to the fish's body weight each month for just over a year. Silver Carp in Kentucky Lake were larger sized and as a result exhibited higher fecundity than Silver Carp from other populations in the United States. Silver Carp appear to spawn in mid-spring in conjunction with warming water temperatures and rising water flows similar to other populations. Additionally, the capture of young-of-the-year Silver Carp suggests that successful natural reproduction is occurring in Kentucky Lake. These data likely represent the first

characterization of reproduction of Silver Carp within a large reservoir in the United States.

Introduction

Silver Carp *Hypophthalmichthys molitrix* are a large planktivorous fish species endemic to eastern Asia (Kolar et al. 2005). They were originally introduced into the United States to improve water quality in sewage lagoons and aquaculture ponds, but flooding events allowed them to escape into the wild (Freeze and Henderson 1982; Kolar et al. 2005). After their initial escape, Silver Carp expanded throughout the Mississippi River Basin and established reproducing populations (Kolar et al. 2005; Schofield et al. 2005). With the successful infiltration of Silver Carp throughout the Midwestern United States, the impact this species has on native ecosystems and aquatic recreation is becoming realized. Silver Carp are efficient planktivores shown to compete with native planktivorous fish species like Gizzard Shad Dorosoma cepedianum and Bigmouth Buffalo Ictiobus cyprinellus (Irons et al. 2007; Lebeda 2017). Gizzard Shad are a key forage species for piscivores (Williamson and Garvey 2005; Culver and Chick 2015) while Bigmouth Buffalo are an important commercial fish species. In addition to environmental impacts, Silver Carp may negatively impact aquatic recreational economies. Silver Carp commonly leap out of the water when disturbed by boat motors and have injured boaters and water-skiers, and they have also damaged personal property (Kolar et al. 2005). With the potential for personal injury and/or property damages becoming more commonplace in waters invaded by Silver Carp, local economies dependent upon aquatic recreation may be negatively impacted.

Silver Carp are quite prolific and have found suitable spawning conditions throughout the Midwest U.S. Silver Carp typically spawn in large riverine environments when water temperatures are between 17 to 26° Celsius, current velocities are between 0.3 to 3.0 meters/second, and water levels are increasing (Abdusamadov 1987; Kolar et al. 2005; Schofield et al. 2005). The eggs of Silver Carp are semi-buoyant and therefore require some current to prevent them from sinking to the bottom and dying (DeGrandchamp et al. 2007). The timing of Silver Carp spawning varied slightly by region but generally occurred between April and the end of July or early August (Kolar et al. 2005). In the Amur River where Silver Carp are native, it is believed that the same female may spawn twice during a single growing season (Kolar et al. 2005). Introduced Silver Carp have been shown to successfully reproduce in artificial canals and in at least one reservoir – the Gobindsagar Reservoir in India (Kolar et al. 2005; Schofield et al. 2005).

Once Silver Carp find suitable spawning conditions, they have the ability to produce large numbers of offspring. Fecundity of Silver Carp is typically high and can range from 265,000 to 2,000,000 eggs per female, but can vary by geographic location, size, and age (Kolar et al. 2005; Schofield et al. 2005). In general, heavier ovaries with more eggs tend to be present in larger sized female Silver Carp (Kolar et al. 2005; Schofield et al. 2005). Gonadal weight as a percentage of body weight (the gonadosomatic index or GSI) can vary throughout the year and can be used to infer Silver Carp spawning (DeGrandchamp et al. 2007).

Previous research estimating the fecundity and spawning periodicity of nonnative Silver Carp in the United States has focused on riverine systems. To date, there has been a paucity of information regarding reproduction of non-native Silver Carp in United States reservoirs. Kentucky Lake is the largest impoundment east of the Mississippi River and is located on the Tennessee River. Kentucky Lake supports a diverse freshwater fish community that provides significant commercial and recreational fisheries. According to the Nonindigenous Aquatic Species List maintained by the United States Geological Survey (USGS), Silver Carp were first reported in Kentucky Lake in 2004 (USGS 2015), however, the capture of young-of-the-year Silver Carp in 2015 is the first documented evidence suggesting natural reproduction in any U.S. reservoir (Ridgway and Bettoli 2017).

Because of the potential and realized harm Silver Carp populations can have on aquatic ecosystems, it is important to understand their recruitment and the environmental conditions that facilitate strong year-classes. Kentucky Lake is unique compared to other systems containing Silver Carp in the United States because managers may have some control over reservoir conditions and may therefore be able to influence recruitment in order to limit population growth of Silver Carp. The objectives of this study were to 1) estimate fecundity of Silver Carp within Kentucky Lake; 2) determine when and how often Silver Carp reproduce in Kentucky Lake; and 3) compare fecundity and spawning periodicity of Silver Carp in Kentucky Lake to other non-native Silver Carp populations in Midwestern rivers across the United States.

Methods

Study Area

My research focused on the Silver Carp population within the main channel and embayments of Kentucky Lake, a mainstem reservoir of the Tennessee River in western Kentucky (Figure 1). This is not a closed population because fish can move in and out of Kentucky Lake through its lock and through the canal that connects Kentucky Lake to Lake Barkley. Similarly, Silver Carp can move among other reservoirs on the Tennessee River. However, telemetry has indicated that movements into and out of Kentucky Lake are relatively rare (Spier and Morris, unpublished data).

Considered the largest reservoir in the eastern United States since its construction in 1944, Kentucky Lake flows north, beginning in Tennessee at Pickwick Dam and extending 296 kilometers north into Kentucky before ending at Kentucky Dam southeast of Calvert City. At maximum capacity, Kentucky Lake has a surface area of 64,870 hectares (Kerns et al. 2009; Tennessee Valley Authority 2016). Classified as a eutrophic reservoir (Kerns et al. 2009; KDFWR 2016), the lower portion of Kentucky Lake is lacustrine with many embayments and backwater channels (Ridgway and Bettoli 2017). The reservoir provides habitat for a multitude of recreational and commercial fish species including black bass *Micropterus* spp., crappie *Pomoxis* spp., catfish *Ictalurus* spp., and Paddlefish *Polyodon spathula*. In addition to local fisheries, the reservoir is a popular destination for recreational boaters and other outdoor enthusiasts. Lastly, with its connection to the Mississippi River, Kentucky Lake acts as a highway for shipment of goods.

Although a mainstem reservoir of the Tennessee River, the downstream portion of Kentucky Lake shares many characteristics more common with lacustrine systems than riverine systems. For instance, water levels within Kentucky Lake are relatively stable and only fluctuate approximately 1.5 m from winter and summer pools (KDFWR 2016). Similarly, water temperatures are fairly static (KDFWR 2016). However, as a mainstem reservoir of the Tennessee River, Kentucky Lake also shares characteristics more common to riverine systems. For instance, normal rainfall patterns decrease water clarity and limit growth of aquatic vegetation (KDFWR 2016). Additionally, Kentucky Lake is similar to riverine systems because it has flow. Average total daily discharge from Kentucky Dam ranged from 197 to 8,527 cubic meters per second during the period of this study (Tennessee Valley Authority, personal communication). Hence, Kentucky Lake as a large reservoir is unique from purely lacustrine or riverine systems as it shares characteristics common to both systems. Furthermore, Kentucky Lake is unique from other environments within the United States with established Silver Carp populations because of its larger size, its connection to another large reservoir (Lake Barkley), and its ability to remain resilient to rapid water fluctuations.

Field Sampling

I used a combination of gill nets and boat electrofishing in an effort to achieve a diversified sample of different sized Silver Carp in Kentucky Lake. I set monofilament variable, small mesh, and large mesh gill nets in the embayments of Anderson Bay and Turkey Bay as well as in the main channel (Figure 1). Variable gill nets were 41.15 m long and 3.66 m deep with mesh sizes ranging from 25.4 mm to 76.2 mm bar measure. Small mesh gill nets measured 50.8 mm bar, ranged in length from 36.58 to 68.58 m, and

were 3.66 m deep. Finally, large mesh gill nets measured 101.6 mm bar, ranged in length from 36.58 to 68.58 m, and were 3.66 m deep. All gill nets were deployed at the surface in the late evening and retrieved early the following morning. Additionally, I conducted daytime and nighttime electrofishing on a boat outfitted with twin booms each containing 6 steel umbrella droppers and a Midwest Lake Electrofishing System (MLES) infinity control box driven by a 6,500 watt gas-powered generator. The crew consisted of a boat operator and two netters. A broad range of electrofishing settings were experimented with in an attempt to find an optimum setting to capture Silver Carp. Peak power fluctuated from 5,200 to 9,750 watts, volts ranged from 225 to 675, pulses per second varied from 14 to 115 with 60 being the most common, and duty cycle ranged from 25 to 100 percent with 25 percent being the most common.

Many researchers have found Silver Carp to be evasive and difficult to capture (Williamson and Garvey 2005; Conover et al. 2007; Wanner and Klumb 2009; Hayer et al. 2014). This elusiveness is magnified in a reservoir as large as Kentucky Lake, therefore, I also sampled the catch brought to processing plants by commercial fishermen in order to obtain an adequate sample size. Commercial fishermen captured Silver Carp with large mesh gill nets (typically 108.0 mm bar) then brought their catch to one of two local processing plants: RCB Fish Company in Ledbetter, Kentucky or Two Rivers Fisheries in Wickliffe, Kentucky (Figure 1). No more than 20 Silver Carp per location per day were sampled from processing plants (Figure 1). Although commercial fishermen bring Asian carp from multiple local waterways like Barkley Lake, Tennessee River, Ohio River, Cumberland River, etc., I only collected data from Silver Carp specifically reported by the commercial fisherman as captured in Kentucky Lake.

Biological Data

I measured total length (mm) and weight (kg if larger than 600 mm and g if smaller than 600 mm) and removed an aging structure for all Silver Carp. I also identified sex and characterized the gonads according to a classification system based on field observations (Figure 2). The smallest carp I was able to identify to sex was 608 mm. Therefore, all Silver Carp larger than 600 mm were considered adults and those below this length were considered juveniles. Next, I extracted and weighed the gonads (g). Gonadosomatic index (GSI) was later calculated using the following equation: GSI = $100 * \frac{\text{wet gonad weight (g)}}{\text{wet body weight (g)}}$. Field observations suggested that fish with a GSI greater than 1% were sexually mature. Additionally, female gonads were visually assigned to one of five development stages based on the classification system used by Hintz et al. 2017 (Figure 2).

Fecundity and Egg Diameter

Samples from each ovary of 23 mature female Silver Carp from Kentucky Lake were stored separately in 10% buffered formalin. Three 1-g sub-samples were weighed from each ovary and placed into a glass dish. Excess formalin solution was blotted from each sub-sample using a KimwipeTM to ensure consistency in weight among sub-samples. After weighing, sub-samples were rehydrated with distilled water. Eggs in each subsample were then distributed evenly across the glass dish and placed beneath a dissecting microscope (6.7x scope zoom) with an attached camera (Figure 3). Using the microscope camera, six images were captured and saved for each sub-sample: 1 image showing each of the center, top-left, top-right, bottom-left, and bottom-right portions of the glass dish, and the sixth image was of a ruler for size reference (Figures 3 and 4). Each undamaged and fully visible egg in each image was manually traced using a digital pen and tablet. After all eggs within an image had been traced, the cell counter plugin in ImageJ was used to count all large eggs (Figure 3). I did not count small eggs because the number of them within a sample was highly variable and they were likely still developing (Figure 3). It became apparent that several of the images (center, bottom-left, bottom-right, topleft, top-right) per sub-sample overlapped. Rather than stitching the images together, I only used the center image from each sub-sample to ensure that I did not double count any eggs or overestimate the number of eggs per female.

Each center microscope camera image was ~13% of the total area of the glass dish (Figure 4). Therefore, the number of large eggs counted in the center image was multiplied by 7.69 (100/13) to estimate the total number of eggs per 1-g sub-sample. It is important to note that eggs were likely not perfectly distributed (for example, eggs were likely more in the center of the glass dish rather than in the edges), therefore, fecundity (number of eggs per female) is likely slightly overestimated. Fecundity was estimated by multiplying the average number of large eggs across six 1-g sub-samples (three 1-g subsamples per ovary) by total gonad weight (g) per female.

Finally, egg diameter was measured using the wand auto measure and mark macro in ImageJ. First, the ruler image was used to calibrate the image scale, then the traced egg image was loaded and its threshold adjusted so the black traced egg outlines were easily detected. Next, the wand/mark tool was activated and area (mm²) was measured for each traced egg. I assumed each egg was a perfect circle so I could calculate the diameter of each egg from the measured area. Egg diameter was only

measured for female Silver Carp with F2 and F3/F4 stage ovaries because these stages had measurable eggs.

Water Temperature

Daily water temperature data (°C) for Kentucky Lake were supplied by Hancock Biological Station's long-term water quality monitoring efforts. Since 1988, water quality data were collected by Hancock Biological Station staff using YSI sondes deployed at 12 sites located on the lower 30 km of Kentucky Lake. At each site, water temperatures were recorded 1 m from the surface and 1 m off the bottom unless the water depth was over 10 m deep (Michael Flinn, Hancock Biological Station, personal communication; Watershed Studies Institute 2016).

In 2015, daily water temperature was not available for July 14 so I used the water temperature collected when lifting gill nets that day. Similarly, daily water temperature was not available for July 15. Because water temperature had not been collected when lifting gill nets that day, I applied the water temperature used on July 14. In 2016, water temperature data were not available for January, February, or March from Hancock Biological Station, but I used the water temperatures recorded during electrofishing efforts. Daily water temperature was not available for May 6, therefore, I applied the water temperature was not available for July 13, therefore, I used the water temperature for August, September, or October of 2016.

Water Flow

Daily average total water flow data (cms) for Kentucky Lake were supplied by Tennessee Valley Authority's long-term monitoring of reservoir daily water records using turbine flow, generation flow, and spill flow. Turbine flow was measured continuously in real-time using flow meters in each generating unit. Generation flow was then averaged in hourly time steps. Spill flow was calculated from the headwater elevation and spill gate arrangement in hourly time steps. Finally, generation and spill flows were combined to calculate the total flow each hour (RSO Engineer, Tennessee Valley Authority, personal communication). I used the daily average total flow (cms) for each collection day. If no water flow data were available, I applied the water flow data closest in time. In 2016, no water flow data were available for November or December.

Statistical Analyses

Multiple linear regression was used to characterize the relationship between female GSI, water temperature, and discharge by capture year. Additionally, an interaction was tested between water temperature and discharge in 2015 and 2016. Simple linear regression was used to determine the relationship between fecundity (number of eggs per female) and female total length. I also used simple linear regressions to describe the relationship between time (month) and mean egg diameter, water temperature, discharge, and female total length. All statistical analyses described below were performed using R software (R version 3.6.1, RStudio Team 2018) and the map was created using ArcGIS software (ESRI 2017).

Results

I used gill nets, boat electrofishing, and commercial catch to capture 388 adult Silver Carp (>600 mm) from Kentucky Lake, but was able to obtain reproductive data from only 339 of them (identified to sex, gonads weighed, and GSI calculated; Table 1). Of these 339 Silver Carp, 200 were captured in 2015 and 139 were captured in 2016 (Table 1). Females comprised 45% of the catch in 2015 and 61% in 2016 (Table 1). Interestingly, sex ratios were approximately 1:1 for fish sampled at commercial processing plants while the large mesh gill nets I used captured predominately male Silver Carp (Table 1). In 2015, total length ranged from 608 to 1,021 mm (n = 200, mean = 860 mm, st. dev = 58 mm; Figure 5). In comparison, total length ranged from 789 to 1,000 mm in 2016 (n = 139, mean = 893 mm, st. dev = 45 mm; Figure 5). On average, females were longer than males both years (Mann-Whitney U: 2015: W_{1, 199} = 7715.5, pvalue <0.05; 2016: W_{1, 138} = 3756.5, p-value < 0.05; Figure 5).

Female Ovary Development and Fecundity

The field classification system was used to assess ovary development stages for 70 female Silver Carp in Kentucky Lake between May-October in 2015 and in January, March, May, September, and October in 2016 (Figure 2). The majority (57%) of females had enlarged or ripe ovaries with yellow oocytes (Figure 2: F3/F4). An additional 29% of females had gelatinous red ovaries without oocytes visible (Figure 2: F1). The remaining 6% and 9% of females were classified as F2 and F5 respectively (Figure 2).

Twenty-three female Silver Carp had egg samples collected for later fecundity and egg diameter analyses. Across all female Silver Carp in Kentucky Lake, fecundity was highly variable and ranged from 17,280 to 1,169,837 eggs per female (n = 23, mean = 490,464, st. dev = 315,116; Figure 6). Mean number of eggs per g was 836 (st. dev = 576). For female Silver Carp with F3/F4 stage ovaries, fecundity was slightly higher and ranged from 46,640 to 1,169,837 eggs per female (n =17, mean = 534,665, st. dev = 302,765). Mean number of eggs per g was 711 (st. dev = 513). Fecundity was not correlated with female total length (Figure 6).

Gonadosomatic Index (GSI)

Individual GSI values for female Silver Carp were highly variable within a given month and a considerable number of female Silver Carp had elevated (>10%) GSI values throughout the year in both 2015 and 2016 (Figures 7 and 8). During April to November of 2015, female Silver Carp GSI ranged from 0.74 to 23.03 (n = 93, mean = 7.25, st. dev = 5.07; Figure 9). Comparatively, during January to October of 2016, female Silver Carp GSI ranged from 0.28 to 27.80 (n = 85, mean = 9.44, st. dev = 6.63; Figure 9). In contrast, male Silver Carp GSI in 2015 ranged from 0.07 to 3.78 (n = 111, mean = 0.84, st. dev = 0.99; Figure 9) and in 2016 ranged from 0.09 to 1.23 (n = 54, mean = 0.46, st. dev = 0.31; Figure 9). In 2015, female Silver Carp GSI appeared to peak then decrease during the months of April-June (Figure 9). Male Silver Carp GSI peaked then fell precipitously during the months of April and May (Figure 9). Alternatively, in 2016, mean male and female Silver Carp GSI remained high during June, suggesting that either spawning occurred later or not at all and females reabsorbed their eggs (Figure 9). Silver Carp GSI data were considerably influenced by commercial catch, particularly in 2016 (Figures 10 and 11).

Water Temperature and Water Flow

Monthly water temperatures in Kentucky Lake followed similar trends in 2015 and 2016 where water temperatures began warming to ~20°C in April, reached maximum temperatures of ~30°C in July then slowly cooled below 10°C during the winter months (Figure 7). The highest GSI values for female Silver Carp in 2015 occurred during April and May when reservoir water temperatures warmed to ~20°C (Figure 7). However, the highest GSI values for female Silver Carp in 2016 occurred in June when reservoir water temperatures approached ~30°C, suggesting water temperature is not the only influential environmental variable to trigger Silver Carp reproduction in Kentucky Lake (Figure 7).

Comparatively, monthly discharge levels in Kentucky Lake followed different trends in 2015 and 2016 (Figure 8). In 2015, monthly discharge in Kentucky Lake remained high at ~3,000 cms between March and April before dropping precipitously in May to below 1,000 cms (Figure 8). Interestingly, the highest GSI values for female Silver Carp in 2015 occurred in April and May, coinciding with water temperatures warming to ~20°C and high water flows (Figures 7 and 8). Comparatively, in 2016, monthly discharge in Kentucky Lake peaked at ~5,000 cms during the winter months of December through February, then gradually declined below 1,000 cms by April (Figure 8). The highest GSI values for female Silver Carp in 2016 were observed in June, after a two-month period of warming water temperatures ~20°C but relatively low flows below 1,000 cms, suggesting flow may be more important than water temperature in triggering Silver Carp spawning (Figures 7 and 8).

In 2015, neither water temperature (p = 0.312), discharge (p = 0.493), nor the interaction between these two variables (p = 0.346) were significant predictors of female

GSI ($R^2 = 0.03$). Comparatively, in 2016, both water temperature (p = 0.0001) and discharge (p = 0.044) were positively related to female GSI, but their interaction had no effect (p = 0.790, $R^2 = 0.12$). For 2016, the linear regression equation for female GSI is:

Female GSI = -9.205 + 0.706(water temperature) + 0.003(discharge)

Egg Diameter

Egg diameter frequency histograms of 23 female Silver Carp in Kentucky Lake during June through August 2015 were bimodal with the first mode at 0.5 mm and the second mode at 1.2 mm (Figure 12). Larger sized eggs were more common than smaller sized eggs for females collected in June through August 2015 (Figure 12) and as a result, the average number of eggs per female was greater during these months with the exception of July (Table 2). By October 2015, egg diameter distribution still appeared bimodal, however, larger sized eggs were equally as common as smaller sized eggs (Figure 12). This suggests females had finished spawning and/or were reabsorbing eggs. In January 2016, egg diameter distribution was still bimodal, however, hardly any larger sized eggs were present and the first mode was 0.6 mm (Figure 12). Therefore, average fecundity in January was low (Table 2). Finally, by March 2016, egg diameter appeared normally distributed with the mode increasing to 0.8 mm (Figure 12).

Mean egg diameter differed significantly by month (ANOVA: p-value < 0.001). Mean egg diameter was positively correlated with mean water temperature (p = 0.063; $R^2 = 0.74$) and negatively correlated with discharge (p = 0.038; $R^2 = 0.70$). Average female total length had no effect on mean egg diameter (p = 0.876, $R^2 = 0.01$).

Tables and Figures

Table 3-1. Number of Silver Carp with reproductive data (identified to sex, gonads weighed, gonadosomatic index [GSI] calculated) sampled in 2015 and 2016 by sampling method (boat electrofishing, large mesh 102 mm bar gill nets, commercial processing plant). For each year and sampling method, effort in hours or number of trips is shown.

	2015				2016			
	Female	Male	Total		Female	Male	Total	
	Silver	Silver	Silver	Effort	Silver	Silver	Silver	Effort
	Carp	Carp	Carp	LIIOIt	Carp	Carp	Carp	
	(n)	(n)	(n)		(n)	(n)	(n)	
Boat Electrofishing	0	0	0	7 hours	2	0	2	41 hours
Large Mesh Gill Nets	19	54	74	1,188 hours	0	3	3	213 hours
Commercial Processing Plant	70	57	174	10 trips	83	51	135	8 trips
Total	89	111	200	-	85	54	139	-

Table 3-2. Average fecundity (number of eggs per female) by month for Silver Carp collected in June 2015 through March 2016. For each month, sample size (n) and standard error of the mean (\pm SE) is shown. Fecundity was not estimated for months that are not shown.

Month	n	Mean (±SE)
June	5	512,091 (±59,487)
July	1	181,566 (±NA)
August	5	587,399 (±174,389)
October	3	536,662 (±162,991)
January	5	252,693 (±56,370)
March	4	682,051 (±241,863)
Total	23	490,464 (±65,706)

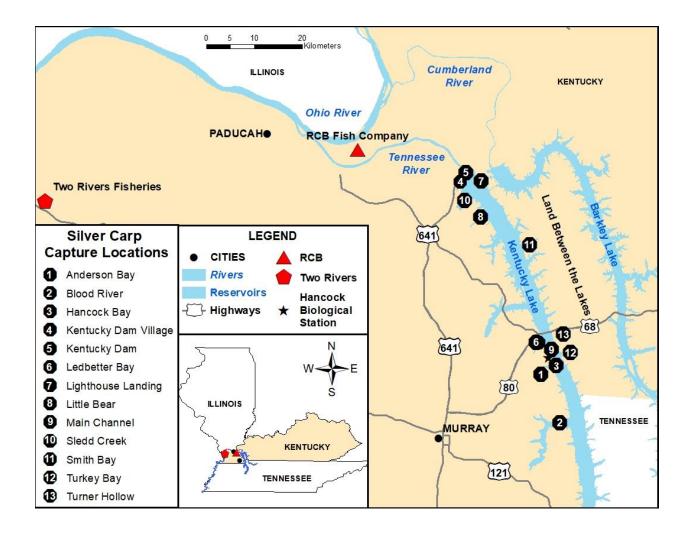


Figure 3-1. Capture locations of Silver Carp from Kentucky Lake during 2015 and 2016 are labeled with black octagons. Commercial processing plants (Two Rivers Fisheries and RCB Fish Company) are shown in red and the field station (Hancock Biological Station) is depicted with a black star. In general, sites in close proximity to Hancock Biological Station are where fish were collected by myself using electrofishing and gillnetting methods. Locations located closer to the tailwaters of the reservoir are generally where commercial fishermen collected Silver Carp in gillnets then brought their catch to either of the two local processing plants for distribution.

GONAD DEVELOPMENT STAGES IN KENTUCKY LAKE

IMMATURE – gonads are not visible or appear thread-like and transparent; GSI = <1% MATURE – gonads are easily distinguishable as either ovaries or testes; GSI = >1%

MALE

- M1: Testes are opaque and distinct but do not milt when pressure is exerted on abdomen NO PICTURE AVAILABLE
 - FEMALE
- · F1: Small gelatinous red ovaries without oocytes visible
- · F2: Medium black to dark gray ovaries containing small underdeveloped oocytes
- · F4: Ripe ovaries enlarged with yellow oocytes that expel when pressure is applied to

M2: Ripe engorged testes; milt expelled when pressure is exerted on abdomen NO PICTURE AVAILABLE

abdomen · F5: Spent ovaries with residual oocytes present

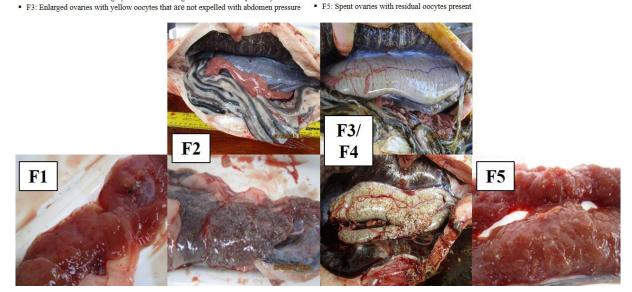
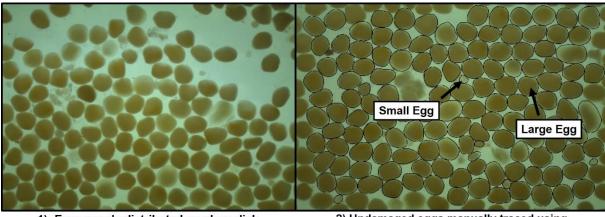


Figure 3-2. Gonad development classification system based on Hintz et al. 2017 used to characterize observed gonad stages of Silver Carp in Kentucky Lake.



1) Eggs evenly distributed on glass dish.

2) Undamaged eggs manually traced using pen and tablet.

Figure 3-3. Image of 1-g sub-sample from a female Silver Carp ovary (left) and manually traced eggs ready for egg diameter measurement process using ImageJ (right). Small eggs were counted separately from large eggs for each image (right).

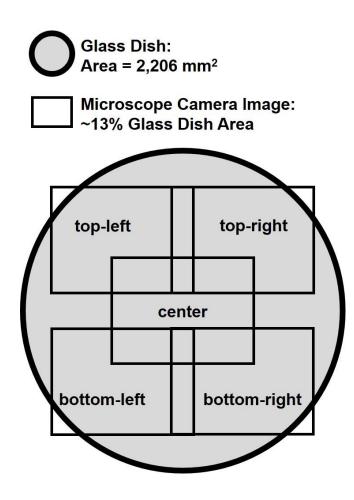


Figure 3-4. Diagram showing the glass dish (gray shaded circle) eggs were distributed in and the relative location of the five images (rectangles: top-left, top-right, center, bottom-left, bottom-right) captured from each 1-g sub-sample. To avoid counting and measuring the same eggs twice, I only used the center image from each 1-g sub-sample to estimate the number of eggs per female and to measure the egg diameter. The total area of the glass dish was 2,206 mm2 and center images taken by the microscope camera covered ~13% of the glass dish's area.

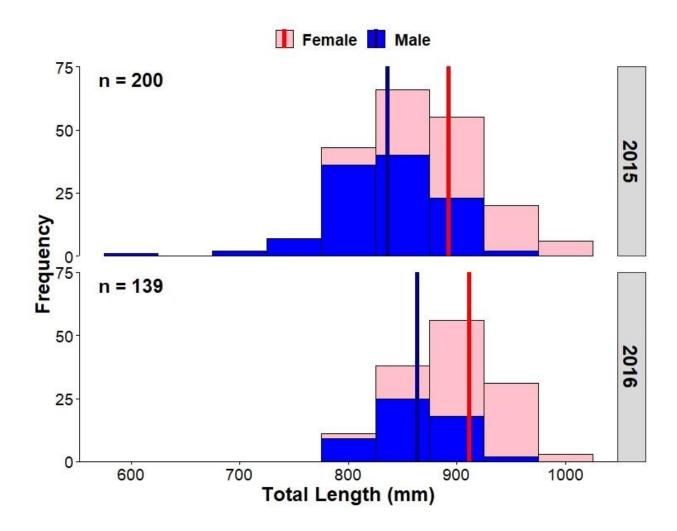


Figure 3-5. Length frequency histograms for male and female Silver Carp in Kentucky Lake in 2015 (top) and 2016 (bottom). Mean total length (mm) for males (blue vertical line) and females (red vertical line) is shown for each year.

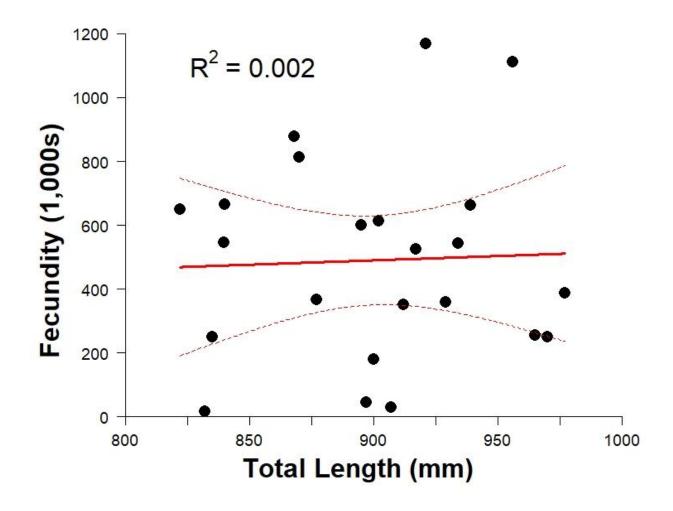


Figure 3-6. Fecundity (1,000s of eggs per female) by total length (mm) of female Silver Carp within Kentucky Lake in 2015 and 2016. Dashed red lines represent 95% confidence intervals around the line of best fit (solid red line) with the R2 value shown.

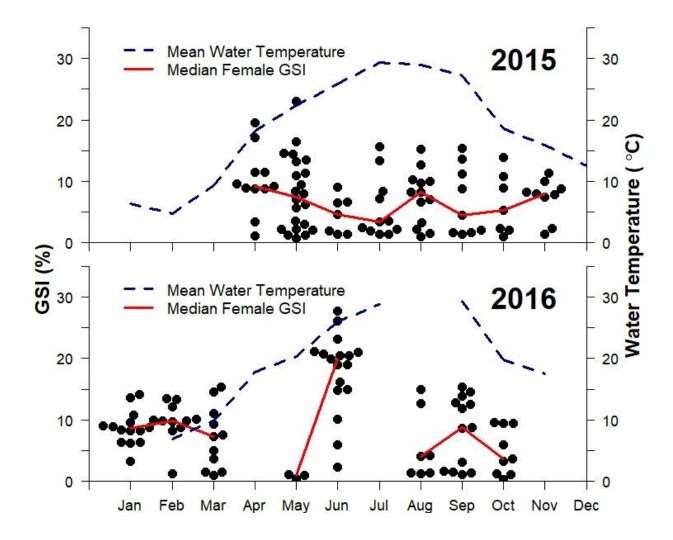


Figure 3-7. Gonadosomatic index (GSI) distribution of individual female Silver Carp (black circles) in Kentucky Lake in 2015 (top) and 2016 (bottom). Median monthly GSI (red solid line), and water temperature (°C, blue dashed line) of Kentucky Lake are shown for reference.

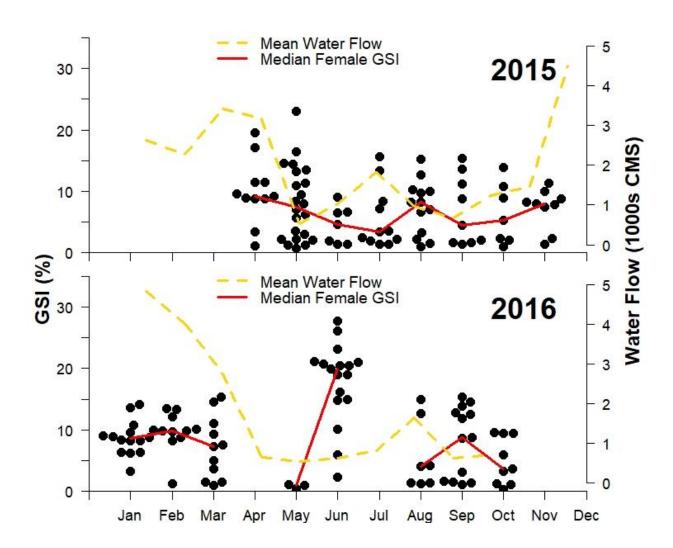


Figure 3-8. Gonadosomatic index (GSI) distribution of individual female Silver Carp (black circles) in Kentucky Lake in 2015 (top) and 2016 (bottom). Median monthly GSI (red solid line) and water flow (cubic meters per second [CMS], gold dashed line) in Kentucky Lake are shown for reference.

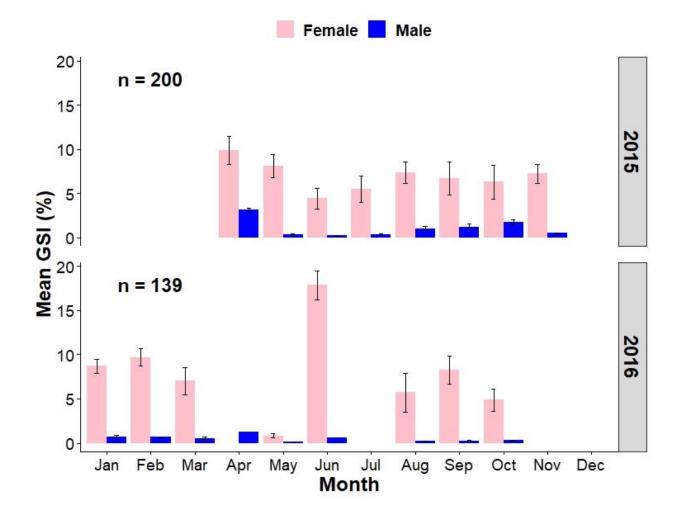


Figure 3-9. Mean monthly gonadosomatic index (GSI) of male (blue) and female (pink) Silver Carp in Kentucky Lake in 2015 (top) and 2016 (bottom). Error bars represent standard error of the mean. Sample sizes (n) are shown for each capture year.

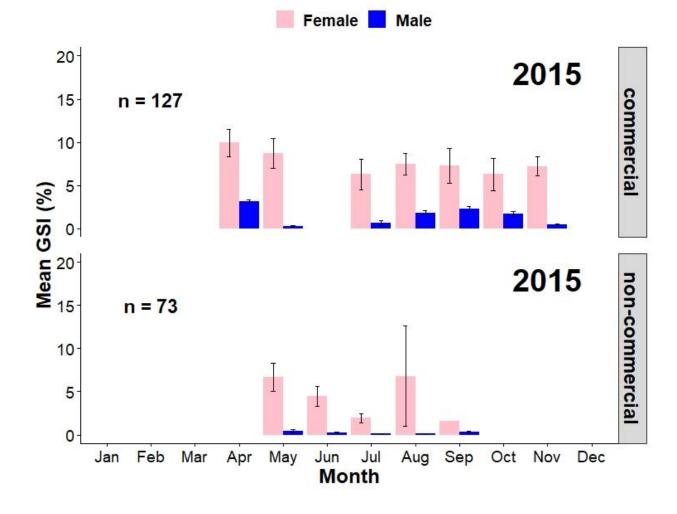


Figure 3-10. Mean monthly gonadosomatic index (GSI) of male (blue) and female (pink) Silver Carp in Kentucky Lake by capture source in 2015. Silver Carp captured from the commercial fishery are shown on top while Silver Carp captured using gill nets and boat electrofishing by myself (non-commercial) are shown on the bottom. Error bars represent standard error of the mean and sample sizes (n) are shown for each capture source.

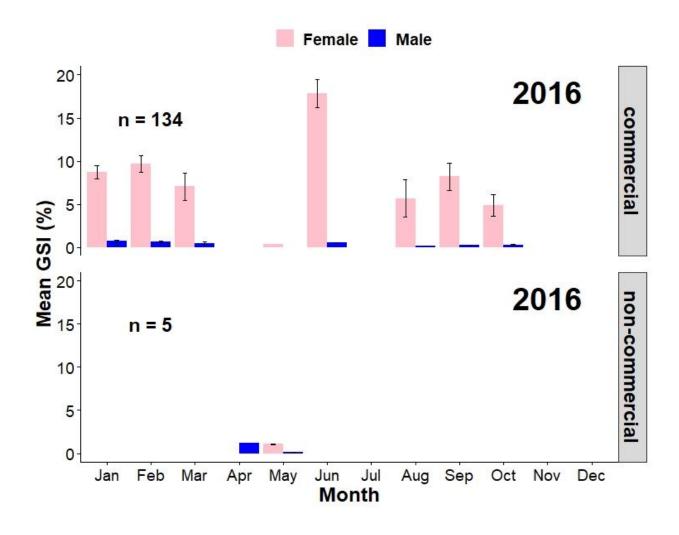


Figure 3-11. Mean monthly gonadosomatic index (GSI) of male (blue) and female (pink) Silver Carp in Kentucky Lake by capture source in 2016. Silver Carp captured from the commercial fishery are shown on top while Silver Carp captured using gill nets and boat electrofishing by myself (non-commercial) are shown on the bottom. Error bars represent standard error of the mean and sample sizes (n) are shown for each capture source.

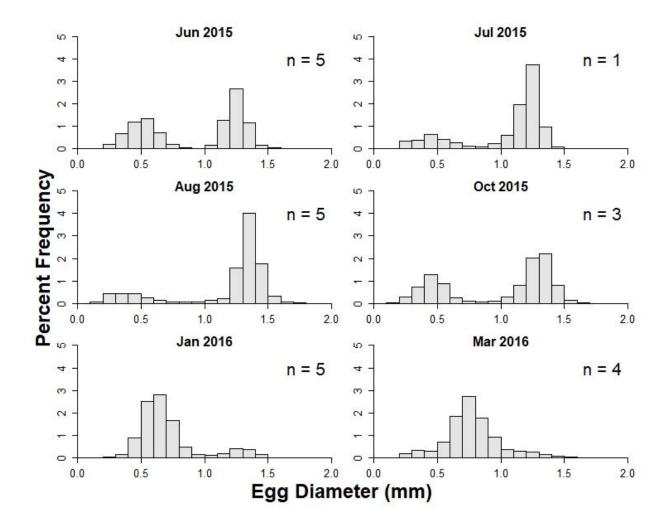


Figure 3-12. Monthly egg diameter percent frequency distributions for female Silver Carp collected in June-August and October of 2015 and in January and March of 2016. Sample size for each month (n) is shown on the right of each plot. Egg diameter was only measured for female Silver Carp with F2 and F3/F4 stage ovaries because these stages had measurable eggs.

Discussion

Nonnative Silver Carp continue to expand and establish populations throughout the Mississippi River Basin, suggesting favorable conditions for reproduction. It is critical to understand Silver Carp recruitment within a waterbody and the environmental conditions that facilitate strong year-classes to better understand both the trajectory of the population and its impact on native species. In the United States, a handful of studies have examined the reproduction of this species in riverine systems including the Illinois River (DeGrandchamp et al. 2007), Mississippi River (Williamson and Garvey 2005; Lohmeyer and Garvey 2009) and its Iowa tributaries (Camacho 2016). To date, however, there has been a paucity of research exploring the reproduction of Silver Carp in United States reservoirs. My research adds to this knowledge by 1) estimating fecundity of Silver Carp within Kentucky Lake; 2) determining when and how often Silver Carp reproduce in Kentucky Lake; and 3) comparing fecundity and spawning periodicity of Silver Carp in Kentucky Lake to other non-native Silver Carp populations in Midwestern rivers across the United States.

Fecundity of Silver Carp in Kentucky Lake was highly variable and ranged from 17,280 to 1,169,837 with an average of 490,464 eggs per female. This variability makes sense as I collected data throughout the year from a broad array of ovary stages ranging from developing, ripe, and spent females. For female Silver Carp with ripe ovaries, fecundity was slightly higher and ranged from 46,640 to 1,169,837 with an average of 534,665 eggs per female. Fecundity of Silver Carp has been well-studied outside of the United States and has been found to be high and vary both by female size and geographic location (Kolar et al. 2005). Fecundity has ranged from 315,000 to 1,340,500 eggs per

female for fish 4.2 kg to 9.3 kg (Abdusamadov 1987). To my knowledge, only one other study in the United States has estimated the fecundity of female Silver Carp. Williamson and Garvey (2005) estimated the fecundity of six two-year-old female Silver Carp with mature eggs from the Middle Mississippi River. They reported that fecundity ranged from 57,283 to 328,538 and averaged 156,312 eggs per female (Williamson and Garvey 2005). However, these females were only two years old and likely had just reached sexual maturity. As in many other fish species, fecundity has been shown to be higher in larger sized female Silver Carp (Kamilov and Salikhov 1996), but I found no relationship between fecundity and fish length (Figure 6). This may be because all the female carp I sampled were very similarly sized and for the most part, similarly aged.

Other research has shown that Silver Carp typically spawn in large riverine environments between April and early August when water temperatures are between 17 and 26° Celsius, current velocities range from 0.3 to 3.0 meters/second, and water levels are increasing (Abdusamadov 1987; Kolar et al. 2005; Schofield et al. 2005). However, some researchers suggest that impounded river segments associated with dams, like areas of the Upper Mississippi River, display reservoir-like characteristics and lack sufficient water velocity to either initiate spawning or facilitate the survival of Silver Carp semibuoyant eggs (Lohmeyer and Garvey 2009; Camacho 2016). It was thought that the reservoir of Kentucky Lake lacked sufficient flow to produce favorable conditions for successful recruitment. However, the appearance of young-of-the-year (YOY) in 2015 was a clear indicator that Silver Carp successfully spawned in Kentucky Lake between April and May. Alternatively, in 2016, no YOY Silver Carp were captured in the reservoir. Silver Carp spawned in 2015, but no clear signal was detected in the GSI data. Typically, GSI climbs to a peak just before spawning and then drops precipitously as gonads are emptied during spawning. However, no such pattern was detected in Silver Carp during 2015 (Figures 7 - 11). Conversely, a very large spike in GSI was measured in June of 2016 followed by a large drop off, even though no YOY Silver Carp were captured in the reservoir in 2016. In general, female GSI was highly variable among individuals throughout both years except for June 2016 (Figures 7 and 8). Perhaps conditions in Kentucky Lake are such that Silver Carp remain in a protracted "pre spawn" state throughout the year, and only in rare conditions do the females progress from this pre spawn condition to actually attempt to spawn. If the carp actually did spawn in April or May of 2015, I may have just missed an opportunity to measure a spike in GSI. Note that three females in my sample had very high GSI values during these months (Figures 7 and 8), and it is possible that the spike in GSI occurred in March or early April and I just missed it.

Why, then, did I observe such a spike in female GSI in June 2016, but no YOY Silver Carp were captured that year? Perhaps the carp did spawn in this year, too, but the conditions were not quite right for their fertilized eggs to survive and thus, Silver Carp did not recruit that year. Water temperatures were similar between the two years, but discharge was quite different. Specifically, discharge was much higher in March and April 2015 and remained high through the summer (Figure 8). Perhaps this high water in early spring was the trigger to induce spawning in combination with rising water temperatures, and the high discharge through late spring kept the fertilized eggs from sinking and they were able to develop properly. High flows might also improve the survival of larval Silver Carp by increasing productivity, keeping food suspended, creating more suitable larval habitat, etc. However, the lower flows during this time in 2016 may have caused the fish to delay spawning, and once they did spawn the eggs were not able to survive due to the lower flows. The water temperatures may have been too warm in 2016, too.

My research has several considerable limitations. First, early on in my research, it was unclear whether the fat should be included with the gonad weight. Fat is included when estimating the fecundity and gonad weight of female Paddlefish (Neal Jackson, personal communication). Although I observed fat more often in males rather than females, particularly going into winter, this tendency to include the fat in the gonad weight may account for some of the variation observed in fecundity and GSI values, particularly in males in the fall of 2015.

Second, the evasive behavior of Silver Carp makes them difficult to capture with traditional sampling methods (Stancill 2003; Williamson and Garvey 2005; Conover et al. 2007; Wanner and Klumb 2009; Hayer et al. 2014; Ridgway and Bettoli 2017). The restricted number of Silver Carp caught can make it challenging to evaluate population characteristics (Wanner and Klumb 2009). To augment my sample size, I also collected data from commercially caught Silver Carp. Therefore, the results of my research are heavily influenced by the commercial catch. Commercial fishermen are paid by the pound and as such, are highly motivated to catch large sized Silver Carp, which tended to be female. Also, at the time of my research, the commercial fishery within Kentucky Lake was in its early stages of establishment. As such, it was difficult to obtain GSI

samples every month and several noteworthy gaps in GSI data made it challenging to determine definitively when Silver Carp were spawning in Kentucky Lake.

In conclusion, Silver Carp in Kentucky Lake exhibit similar high fecundity and appear to spawn during the same time frame as they do in other locations in the United States and in eastern Asia. Similar to other systems, Silver Carp in Kentucky Lake appear to be triggered by rising water flows and warming water temperatures and appear to retain or reabsorb their eggs if environmental flows are unsuitable for spawning. It is unclear whether Silver Carp are successfully spawning in Kentucky Lake, in its tributaries, or in its sister reservoir Lake Barkley. It is unlikely that YOY Silver Carp were hatched below Kentucky Dam, navigated the lock system, and swam ~30 or more rkm to capture locations midway in the reservoir. Future research, however, should utilize otolith microchemistry and telemetry movements to determine when and where successful spawning is occurring. Because Kentucky Lake is an impoundment of the Tennessee River, managers may have some control in limiting further successful reproduction and population growth of Silver Carp.

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