HABITAT SELECTION AND MOVEMENTS OF DIPLOID AND TRIPLOID GRASS CARP IN A LARGE RESERVOIR

A Thesis
presented to
the Faculty of the Graduate School
at the University of Missouri-Columbia

Partial Fulfillment
Of the Requirements for the Degree
Master of Science

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HABITAT SELECTION AND MOVEMENTS OF DIPLOID AND TRIPLOID GRASS CARP IN A LARGE RESERVOIR

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Acknowledgements

Thank you to the members of my advising committee for being there from start to finish in building this project and for a successful product. Thank you, Dr. Craig Paukert, for the fundamentals I learned in classes you taught and the work you put in to ensure this project could be completed as my master's thesis. My knowledge of statistical modeling and use of R would not have been without the guidance and input of Dr. Erin Schliep. Lastly, and certainly not least, thank for to my advisor, Dr. Michael Byrne, for all the silly questions answered and hours spent ensuring this project would be as successful as it possibly could be.

This project would not be possible without the funding provided by the U.S. Geological Survey. Thank you to Mr. Duane Chapman for being receptive of my ambition for a higher level of education and providing the opportunity to use this project as a step in my development as a young professional. Special thanks to all of those at the Columbia Environmental Research Center who tagged and stocked fish, including Curt Byrd, Ben Stahlschmidt, Cayla Carlson, Anne Herndon, and Joel Yeager. Thank you, Sara Tripp and other staff from the Missouri Department of Conservation, who contributed data.

A special thank you must be given to those who spent long, extremely hot and cold days on Truman tracking fish while listening to the static of hydrophones. Thank you, Harper Smith, Ben Bates, and Eric Cox, for the hours you dedicated in acquiring the data needed for study objectives. The time and commitment Joe Deters has put into this project since its origination has been immense. Joe was essential in building equipment, tracking fish, and being receptive of all the crazy ideas and stressful days spent ensuring

this project was as complete as it could be. Finally, thank you to all my friends and family, especially my wife Casey, who supported me through thick and thin in achieving my goals.

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Habitat Selection and Movements of Diploid and Triploid Grass Carp in a Large Reservoir

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Abstract

Grass Carp, an herbivorous fish introduced in North America to control aquatic vegetation, has become an increasing ecological threat to aquatic ecosystems they invade. Grass Carp have the potential to cause declines and alterations in aquatic vegetation communities, which in turn can have negative impacts on native species reliant on aquatic vegetation. In the last ten years, frequent captures and observed spawning of wild fish have increased concerns of Grass Carp establishment in novel waterways. A particular concern is the potential establishment of fish in Lake Erie and its tributaries. Understanding Grass Carp habitat selection might be useful in population control by guiding harvest actions. In addition, understanding movement ecology of Grass Carp might help to predict where Grass Carp go and what cues initiate those movements. Identifying predictable movement behaviors to heavily used sites might also be useful in control efforts. In this study, I tracked Grass Carp to evaluate winter habitat selection and to determine whether using tagged (Judas) fish is effective in removing wild fish during winter. In addition, this study aimed to characterize upstream migrations into lake tributaries and determine if diploid and triploid fish exhibit similar behaviors. From 2017-2019, I tracked 86 Grass Carp tagged with acoustic transmitters in Truman Reservoir, Missouri to answer these questions. I employed Bayesian discrete choice models to determine winter habitat selection of tagged fish. Generalized linear mixed models were used to determine environmental conditions associated with upstream migrations. Tagged Grass Carp showed strong selection for shallow littoral habitats, and 75% of locations were in waters ≤ 3 m deep. Attempts to capture fish with trammel nets using the Judas method proved difficult with only 1.9 fish caught/netting attempt versus 1.2 caught/netting attempt when selecting areas with suitable Grass Carp habitat for harvest. Fish were often observed near inundated vegetation, with food material collected in 29 of the 31 guts I sampled from fish harvested during capture attempts, which is indicative of overwinter feeding. Eleven fish (6 diploid and 5 triploid) exhibited upstream migrations over the 2018 and 2019 spawning seasons on the Osage River above Truman Reservoir, with distances between 13.6 – 108.1 river km observed. Three of the ten fish in 2019 (2 diploid and 1 triploid) made two migrations and one diploid made three migrations. Upstream migrations were observed from late April to early July and were strongly associated with river temperatures between 15 – 26 ℃ when river levels were rising at a rate > 0.9 m/ 12 h. Five lake resident fish made upstream movements into tributaries during rising river events, indicative that fish residing in the lake proper respond to cues to move upstream. Winter habitat selection suggests that efforts to reduce Grass Carp populations via harvest may be difficult in large lake systems when fish are dispersed throughout the available littoral habitat. Upstream migrations were made by both diploid and triploid fish during conditions suitable for spawning, possibly explaining a motive for these large movements. These results may need to be considered with efforts to remove Grass Carp in large lake systems and for the utilization of triploid fish in observing Grass Carp movement behavior in natural systems.

Chapter 1: History and Ecological Impacts of Grass Carp in North America

The rate at which species are being introduced to systems beyond their native range is unparalleled to any other time in human history, with over a third of all introductions reported in the last 50 years (Seebans et al. 2017). In the United States alone, there are over 50,000 non-native species, of which at least 138 are fish (Pimentel et al. 2005). Introduced species that have the potential to cause harm to human health, the environment, or the economy are typically further classified as invasive (Beck et al. 2008). Invasive fish species can be found in aquatic ecosystems throughout the United States, and include but are not limited to, Indo-Pacific Lionfish (*Pterois volitans and P. miles*), Northern Snakehead (*Channa argus*), Round Goby (*Neogobius melanostomus*), and the Asian carps (Kolar et al. 2005; Kornis and Zanden 2010; Albins and Hixon 2013; Love et al. 2015).

Four species of Asian carp have been introduced to the United States and include Silver Carp (*Hypophthalmichthys molitrix*), Bighead Carp (*Hypophthalmichthys nobilis*), Black Carp (*Mylopharyngodon piceus*), and Grass Carp (*Ctenopharyngodon idella*). Silver and Bighead Carp are planktivorous and can outcompete native species such as Bigmouth Buffalo (*Ictiobus cyprinellus*), Gizzard Shad (*Dorosoma cepedianum*), and Paddlefish (*Polyodon spathula*; Irons et al. 2007; Sampson et al. 2009). Black Carp primarily feed on mollusks and insects and are becoming an increasing threat to native mussel beds in waterways throughout the Mississippi River Basin (Kroboth et al. 2019; Poulton et al. 2019). The only Asian carp species still actively stocked in the United States is the Grass Carp (Cudmore et al. 2017), which is herbivorous and used by managers and private owners to control aquatic vegetation in lakes and ponds (Garner et al. 2013; Manuel et al. 2013; Stich et al. 2013). However, Grass Carp that escape into systems they were not intentionally stocked can have serious consequences on aquatic plant communities and organisms that rely on them (Pípalová 2006; Krupska et al. 2012).

Native Range and Life History

Grass Carp are native to waterways of eastern Asia, from Russia to Vietnam (Nico et al. 2020). They can be found in a variety of water bodies including rivers, lakes, and ponds, but they need swift flowing water to spawn. Grass Carp are generally considered herbivorous, but they have been known to feed on pellet food and invertebrates when vegetation is scarce (Chilton and Muoneke 1992). They can grow > 30 kg (Chilton and Muoneke 1992) and have been observed consuming more than 100% of their body weight in a day in lab conditions (Federenko and Fraser 1978; Osborne and Riddle 1999).

Mature fish initiate migrations for spawning between 15 – 17 °C and spawn when temperatures exceed 18 °C, with an optimal range of 20 – 22 °C (Stanley et al. 1978). Grass Carp typically spawn in fast flowing, turbulent waters as their semi-buoyant eggs require well-oxygenated water where they must remain suspended in the water column before hatching (Stanley et al 1978; Chilton and Muoneke 1992). Fecundity can range from tens of thousands to 2 million eggs (Shireman and Smith 1983). Fish require unimpeded rivers 28 – 100 km in length for eggs to develop before hatching (George and Chapman 2015). Eggs hatch between 26 – 60 hours post fertilization (Hammerson 2004) before larvae enter backwater habitat to feed on rotifers and protozoans (Cudmore and Mandrak 2004). By three weeks post hatch, plant matter begins to be consumed and between 1 – 1.5 months of age nearly exclusive feeding on vegetation begins (Cudmore and Mandrak 2004).

Introduction to North America

Grass Carp were introduced in 1963 to the United States (Sutton 1977). They were brought to aquaculture facilities in Alabama and Arkansas to control aquatic vegetation (Cudmore and Mandrak 2004) and by 1966 had escaped into open waters in Arkansas (Mitchell and Kelly 2006). Grass Carp were first caught in the Missouri and Mississippi Rivers in the early 1970s (Pflieger 1978) and have rapidly spread since by means of intentional stocking for pond management, research projects, and natural dispersal (Cudmore and Mandrak 2004). Currently, Grass Carp are documented in 45 states, with established populations in the Illinois, Missouri, Mississippi, and Ohio River Basins (Nico et al. 2020). Individuals have been captured as far north as the Canadian waters of Lake Erie, Huron, and Ontario, but there is not believed to be an established population in Canadian waters (Nico et al. 2020).

Sterile, triploid fish are commonly used as an alternative to stocking fertile diploid fish. Production of triploid fish began in the late 1970s (Jones et al. 2017a), by shocking eggs with heat, cold or pressure to cause an additional set of chromosomes to be retained (Cudmore and Mandrak 2004). Triploids produce rudimentary gonads in comparison to diploids and only males have been observed releasing gametes when induced (Allen and Wattendorf 1987). However, the induction of triploidy is not 100% effective, and the lack of universal regulations regarding Grass Carp production have allowed diploid fish to continue to be stocked in private and public waterways in the United States (Jones et al. 2017a). The states that still allow the production and stocking of diploid Grass Carp are Alabama, Mississippi, Arkansas, Iowa, and Nebraska (MICRA 2015). Stocking and escapement in open waters of these states draws concern for dispersion into triploid only states where establishment of reproducing populations is a threat.

Ecological Impacts of Invasive Grass Carp

The negative consequences associated with Grass Carp introductions derive from their capability of depleting aquatic macrophyte communities (Pípalová 2006; Jones et al. 2017a), capable of reducing some species by nearly 100% (Jones et al. 2017a). Typically, Grass Carp prefer more palatable aquatic plant species, filamentous algae, and duckweeds, and have been observed to avoid more fibrous plants and those with toxic compounds (Pípalová 2006). Palatable species include those that inherently have chemical and structural traits that are more conducive to ingestion (Elger and Lemoine 2005). Selective feeding has drawn concerns that generalist alien species will replace native species that Grass Carp selectively fed on (Catarino et al. 1997). In a food preference study conducted by Catarino et al. (1997), Grass Carp preferred softer tissue plants like *Azolla filiculoides* and *Lemna* sp., while exotic parrotfeather (*Myriophyllum aquaticum*) and water hyacinth (*Eichhornia crassipes*) were avoided. Krupska et al. (2012) reported abundant charophyte communities disappeared and increased turbidity after Grass Carp were introduced in Lake Czyste Make, Poland. Krupska et al. (2012) further hypothesized this lake would soon be dominated by shade tolerant species due to excess suspended sediments. Parker et al. (2006) reported unpalatable plants like *Micranthemum umbrosum* and *Spirogyra* sp. remained the dominant species in ponds stocked with Grass Carp, but in portions of the ponds where Grass Carp were excluded, a more palatable species *Ludwigia repens* increased over 300-fold. Further, a nearby natural pond that lacked Grass Carp was dominated by *Najas guadalupensis*, a species Grass Carp preferred over *M. umbosum* and *L. repens* (Parker et al. 2006). Parker et al. (2006) concluded this was indicative that selective feeding by Grass Carp eliminated palatable species in favor of less palatable, chemically defended ones.

Reductions in macrophyte abundance caused by Grass Carp have been linked to impacts on several fauna groups including invertebrates, fish, amphibians, and birds (Jones et al. 2017a). Loss of aquatic vegetation beds leads to reductions in invertebrates that rely on vegetation for shelter and a food source (Cudmore and Mandrak 2004). In certain circumstances, relative abundance of present invertebrate taxa has changed when Grass Carp introductions caused changes in littoral vegetation (Hofstra and Clayton 2014). Additionally, Grass Carp could directly impact invertebrate communities through consumption if limited vegetation forces them to switch foraging strategies (Chilton and Muoneke 1992). Aquatic vegetation is a vital food source for many waterfowl species and reductions caused by Grass Carp have been linked to declines in coot (*Fulica atra*) and swan (*Cygnus* sp.; Grabowska et al. 2010). The replacement of palatable vegetation for less palatable species like Eurasian watermilfoil (*Myriophyllum spicatum*) has been presented as a major concern for food availability of waterfowl species (McKnight and Hepp 1995). The removal of aquatic vegetation can lead to decreased habitat for sunfishes and has been shown to change fish assemblages. In Lake Conroe, Texas, Largemouth Bass (*Micropterus salmoides*) that historically fed on sunfish now feed primarily on Gizzard Shad, following the introduction of Grass Carp (*Dorosoma cepedianum*; Ireland 2010). The damage Grass Carp have caused to macrophyte communities has also been linked to increases in Bighead and Silver Carp populations, along with the disappearance of 41 native fish species in Donghu Lake, Wuhan, China (De Silva et al. 2009). In this system, macrophyte loss likely led to excess suspended nutrients and light in the water column allowing planktonic communities to flourish, an important food source for Bighead and Silver Carp. The loss and alteration of aquatic vegetation communities can have detrimental impacts on native fish, including loss of rearing habitat and lower growth rates (Crowder and Cooper 1982; Holland and Huston 1984; Conrow et al. 1990; Dewey and Jennings 1992; Rozas and Odum 1988; Houston and Duivenvoorden 2003). Holland and Huston (1984) investigated habitat use of young of the year Northern Pike (*Esox lucius*) in which 10 times more pike were caught in sites with submerged vegetation compared to those without. Sunfish have been observed to consume larger prey and incidentally have higher growth rates in areas with abundant submerged vegetation (Rozas and Odum 1988). Established Grass Carp populations have the potential to severely decrease aquatic vegetation that many native species are reliant on.

Further, reduced water quality can be linked to the introduced Grass Carp, both through the release of nutrient rich excrement and removal of vegetation (Pípalová 2006; Jones et al. 2017b). Excess nutrients present in carp waste can lead to excessive growth of phytoplankton, leading to rapid eutrophication (Pípalová 2006). Increases in turbidity have been documented as Grass Carp decrease vegetation abundance (Pípalová 2006), likely due to the role aquatic vegetation has in preventing excessive sediment from resuspending in the water column (Coops et al. 1996; Madsen et al. 2001; Rooney et al.

2003). Decreased oxygen concentrations is also a concern as macrophyte abundance is reduced and photosynthesis rates decline (Pípalová 2006).

The risk Grass Carp pose to aquatic ecosystems is drawing much attention to the Great Lakes where environmental conditions of all five lakes are likely to support establishment of viable Grass Carp populations (Wittmann et al. 2014). Increased capture rates and evidence of spawning (Embke et al. 2016) suggests establishment is eminent, especially in Lake Erie (Jones et al. 2017b). Jones et al. (2017b) stated it is highly likely a Grass Carp population will establish itself in Lake Erie by 2022 and very likely one will establish in Lake Huron, Michigan, and Ontario by 2027. Established populations would likely lead to elimination and alterations of vegetation communities in Great Lakes wetlands (Jones et al. 2017a), impacting native fauna that rely on aquatic vegetation. More than 50% of Great Lakes fish use aquatic vegetation for important needs including spawning, refuge, and foraging habitat (Gertzan et al. 2017) and it is estimated half the fish biomass use wetlands (Trebitz et al. 2009). Of 47 bird species evaluated, Gertzan et al. (2017) predicted high and moderate impacts on 18 and 29 species, respectively, from a Grass Carp invasion through impacts on feeding, nesting, and migratory stopovers. Predicted ecological impacts will also have ramifications for the Great Lakes economy, where the fisheries alone are valued > $7 billion annually (Embke et al. 2016).

Monitoring and Control

Efforts to control and reduce the spread of Grass Carp have increased in the last decade, especially in waterways associated with Lake Erie and Lake Michigan. The Asian Carp Regional Coordinating Committee (ACRCC) was established in 2010 to oversee and coordinate prevention activities, particularly in the Great Lakes basin

(ACRCC 2020). The ACRCC has implemented monitoring efforts through a range of methods including eDNA sampling, contracting commercial fishermen, and telemetry to monitor movements (ACRCC 2020). The ACRCC has implemented eDNA sampling to collect genetic material of Asian carp in waterways as an early detection method (ACRCC 2014). However, genetic material can degrade quickly, and it is possible to receive false negatives when determining a species presence (Jones et al. 2017a). Although eDNA sampling for Grass Carp specifically is limited in the Great Lakes proper, efforts to detect Bighead and Silver Carp have led to many detections in waters around Lake Michigan (Jones et al. 2017a). The ACRCC contracts with commercial fishermen who conduct fish removal projects, and in 2019 removed > 1.5 million pounds of Asian carp from the upper Illinois Waterway (ACRCC 2020). The majority of these fish were Bighead and Silver Carp, but Grass Carp were harvested as well. Several agencies have partnered in tracking tagged Grass Carp, both for removal and to study movements to find where adult fish prefer to aggregate (ACRCC 2020). The use of tagged fish for exploitation purposes is still in the early stages and will be further studied as a method in controlling populations, particularly in Great Lakes tributaries.

Resource agencies in the United States and Canada have identified Lake Erie as a high priority in preventing the spread of Grass Carp and have implemented response teams for targeted removal of adult Grass Carp in the basin (ACRCC 2020). Additional crews have been assembled to sample for eggs and assess the risk of reproduction in other Lake Erie tributaries in Ohio (ACRCC 2020). The Ohio Department of Natural Resources (ODNR) Division of Wildlife’s response strategy through the year 2023 lists multiple objectives to prevent the introduction of diploid fish beyond Lake Erie and the

Maumee and Sandusky Rivers (ODNR Division of Wildlife 2019). These objectives include ensuring all aquaculture fish in the state are verified sterile triploids, identifying effective approaches to reducing populations, working with partners in removing present populations, and evaluating the potential of barriers to limit reproduction and recruitment in the Maumee and Sandusky Rivers (ODNR Division of Wildlife 2019). In addition, a major goal is to prevent current populations in Ohio waterways from reaching levels that compromise aquatic communities (ODNR Division of Wildlife 2019).

Control of Grass Carp could be aided by increased understanding of movement ecology and habitat selection. Harris et al. (2020) found extensive use of Lake Erie tributaries by tagged Grass Carp and identified hot spots where fish would aggregate at different times of the year. Other efforts are currently underway to track and better predict areas fish will use (John Buszkiewicz, Michigan Department of Natural Resources, personal communication). Such telemetry-based projects are essential to understanding Grass Carp movement ecology and habitat selection. There has been some success in capturing Grass Carp that aggregate in a warmwater discharge to Lake Erie, where fish appear to be aggregating over the winter (John Buszkiewicz, personal communication). Crews utilize tagged (Judas) fish to find and exploit aggregations that tagged fish associate with. The Judas fish method has been used in lake systems to conduct mass harvest efforts for other invasive carp species including Common Carp (*Cyprinus carpio*) and Silver and Bighead Carp (Bajer et al. 2011; Taylor et al. 2012; Duane Chapman, U.S. Geological Survey, personal communication). Targeting Grass Carp in a similar manner could be a viable method in controlling lake populations.

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Chapter 2: Winter Habitat Selection of Grass Carp in a Large Reservoir

Introduction

Grass Carp were first brought to the United States from Asia in 1963 to manage nuisance aquatic vegetation (Osborne and Sassic 1981; Shireman and Maceina 1981; Martyn et al. 1986). Managers commonly stocked these phytophagous fish to control vegetation as it was a cheaper and a less environmentally harmful alternative to chemical herbicides (Chilton and Muoneke 1992). Adult Grass Carp grow to 30 - 50 kg (Cudmore and Mandrak 2004) and consume large quantities of aquatic vegetation (Fedorenko and Fraser 1978; Osborne and Riddle 1999). Thus, overgrazing by invasive populations can have significant detrimental effects on native aquatic communities (Edwards 1973, Bain 1993, Dibble and Kovalenko 2009). Documented impacts of Grass Carp include reduced water quality (Lembi et al. 1978; Fedorenko and Fraser 1978), declines in native fish populations (Mitchell 1986; Bettoli et al. 1993), and severe reduction or elimination of native plant species (Van Dyke 1994). Introductions may lead to unexpected and undesirable changes in plant communities, as McKnight and Hepp (1995) reported in some areas Grass Carp reduced native vegetation while a targeted introduced species, Eurasian watermilfoil (*Myriophyllum* spicatum), remained unaffected. Grass Carp overgrazing raises concerns of the ecological impact a severe alteration in aquatic vegetation could have on waterways these fish inhabit, and those they have the potential to invade.

In 1970 commercial fishermen on the White River in Arkansas were the first to detect Grass Carp in an open system in North America (Guillory and Gasaway 1978). Since then, they have been reported in 45 states, with established populations in many states along the Mississippi River Basin (Arkansas, Illinois, Louisiana, Minnesota, Missouri, Mississippi, and Tennessee) as well as Kentucky and Texas (Cudmore and Mandrak 2004) and have pushed north into the Great Lakes (excluding Lake Superior), where concerns of establishment now exist (Nico et al. 2020). Predictions from species distribution models parameterized based on environmental conditions within the Grass Carp's native and established ranges suggest all Great Lakes provide suitable conditions for Grass Carp establishment (Wittmann et al. 2014). Bioenergetic models predict Grass Carp growth and survival is possible in the Great Lakes, that adults could consume up to 90 kg of macrophytes annually, and that young-of-year would reach critical minimum lengths required for overwinter survival (Jones et al. 2017). Van der Lee et al. (2017) predicted Grass Carp could remove > 50% of aquatic vegetation from Great Lakes wetlands within one year of establishment, and there is potential for moderate to high ecological impact in the Great Lakes (Wittmann et al. 2014; Cudmore et al. 2017; Gertzan et al. 2017). In 2012 juveniles confirmed to have been the result of wild reproduction were discovered in the Sandusky River, a tributary to Lake Erie (Chapman et al. 2013). Following this discovery, Embke et al. (2016) collected Grass Carp eggs in the Sandusky River, providing further evidence of wild reproduction. With sufficient food availability, mild temperature regime and evidence to suggest successful spawning in tributaries, Lake Erie is a prime candidate for a Grass Carp invasion, which may affect its > $1 billion annual sport fishing economy (Lake Erie Foundation 2019). Commercial fishing and numerous recreational activities also contribute to the lake area economy, many of which could face negative consequences from the ecological impacts of a Grass Carp invasion.

The potential serious impact of Grass Carp on Great Lake ecosystems and economies warrants research into effective methods to control and remove carp from these large systems. Strategies to control invasive carp primarily focus on methods that attempt to remove fish in large quantities. Efforts have included commercial harvest (Tsehaye et al. 2013; Varble and Secchi 2013; MacNamara et al. 2016) and the use of the modified unified method, a relatively new approach using a combination of fishing techniques to harvest large numbers of carp from targeted water bodies, specifically Bighead (*Hypophthalmichthys nobilis*) and Silver (*Hypophthalmichthys molitrix*) Carp (Chapman 2020). Bajer et al. (2011) successfully harvested large numbers of Common Carp (*Cyprinus carpio*) in three Minnesota lakes using large seines pulled under ice around aggregations of carp. These wintertime aggregations were located using fish implanted with radio transmitters (Judas fish) that were consistently found within dense aggregations of Common Carp which were susceptible to mass harvest, with upwards of 4,000 fish caught in a single netting attempt (Bajer et al. 2011). This technique was also implemented in controlling Common Carp in two Australian lakes, one of which saw the complete eradication of carp while the other showed a significant reduction in the population (Taylor et al. 2012). However, these techniques have been primarily used in smaller, natural lakes and their use in more complex systems like reservoirs has not been explored thoroughly. Additionally, they have not been used to specifically target Grass Carp and their effectiveness is unknown.

The Judas fish method, in which a tagged animal leads researchers to the location of wild fish in a system, has been employed for several uses including control of invasive carp species (Bajer et al. 2011; Taylor et al. 2012) and locating cryptic fishes such as the

Robust Redhorse (*Moxostoma robustum,* Grabowski and Jennings 2009). The theory behind the Judas fish method is that a tagged fish will eventually find and associate with conspecifics, effectively leading researchers and managers to the locations of other members of the population. One of the benefits of the Judas fish method is that Judas fish can be reared in hatcheries and stocked into water bodies where the species resides but is difficult to locate or capture.

The use of Judas fish could be an effective tool to determine if wintering Grass Carp are susceptible to harvest and determine lake habitats used over winter months. Studies in lakes and their connected tributaries found Grass Carp movement to generally decline in winter months compared to the spring and summer seasons, but never do they completely stop (Bain et al. 1990; Clapp et al. 1993; Harris et al. 2020). It is generally agreed upon that they reside in deep holes in the rivers during the winter (Fischer and Lyakhnovich 1973; Shireman and Smith 1983), but there is no evidence to suggest they will reside in deep areas of lakes as well. However, if Grass Carp form open water winter aggregations similar to Common Carp (Bajer et al. 2011; Taylor et al. 2012) then they could be susceptible to mass harvest in a similar fashion.

The objectives of this study were to model winter habitat selection of Grass Carp, determine if Grass Carp form exploitable winter aggregations, and to test if the Judas fish method is an effective tool to locate and harvest Grass Carp aggregations. In this study I used stocked fish implanted with acoustic telemetry tags to answer these questions. A better understanding of Grass Carp habitat selection during winter months will help to determine where to focus control efforts, and whether the habitat they use is conducive to mass harvest efforts if found to be forming aggregations. I hypothesized Grass Carp would migrate from near shore habitat used during warm months to deeper waters associated with the main channel of the reservoir during winter months where they would find more stable conditions to those near the surface. In moving to open water, they would gather with other Grass Carp and be susceptible to harvest.

Methods

Study Site

This study was conducted on Truman Reservoir and its tributaries in west-central Missouri. Created when the U.S. Army Corps of Engineers dammed the Osage River near Warsaw, Missouri in 1979 (Payton and Payton 2012), Truman Reservoir is the largest flood control reservoir in the state, covering 22,500 ha at normal pool with a drainage of 29,785 km^2 covering west-central Missouri and east-central Kansas (DiStefano and Hiebert 2000). Truman Reservoir is comprised of four major tributaries which include the Osage, Pomme de Terre, and South Grand Rivers and Tebo Creek (Fig. 2.1). Several other minor tributaries feed the lake, including Barker, Deepwater, Hogles, and Little Tebo Creek. Truman Reservoir lies in the transition area from the plains in the north and west to the Ozark Highlands in the south and east. The South Grand River and Tebo Creek Arms on the northwest portion of the lake that follow the plains are characterized by expansive mud flats with channels that become significantly deeper downstream towards Truman Dam. The Osage River arm flows both through plains and Ozark Highlands, and on the main stem of the lake is characterized by deep water with rocky coves and bluff banks. Upstream portions of the Osage River arm are characterized by expansive mud flats bordering a deep (>4.5 m) main channel. The Pomme de Terre River is regulated upstream by Pomme de Terre Dam, and runs downstream into Truman Reservoir through Ozark Highlands, with rocky shores throughout.

Truman Reservoir is up to 23 m deep in the main channel and has depths > 15 m on large flats outside the main channel at normal pool. Truman Reservoir varies greatly in shoreline habitat from steep, rocky bluffs to shallow flats (< 1 m) that at times extend over 1 km from the shoreline. Shoreline variation and extensive areas of deep and shallow water provide habitat for a variety of warm water fish species including Channel and Blue Catfish (*Ictalurus punctatus* and fucatus), White Bass (*Morone chrysops*), and White and Black Crappie (*Poxomis annularis* and *nigromaculatus*). Pelagic species make use of large, deep areas of the lake while coves and backwater areas provide habitat for species that reside in shallower waters. The upstream portions of the main reservoir arms provide riverine-like conditions for common river species in the area.

Truman Reservoir is used by the U.S. Army Corps of Engineers to minimize fluctuations in Lake of the Ozarks downstream where there is extensive residential property along the shoreline. As such water levels on Truman Reservoir can fluctuate considerably, as much as 6 m in two weeks (USGS gage 06922440). Large fluctuations in water levels make it difficult for submerged macrophyte communities to persist, but fluctuating shorelines do promote plant growth along the bank as waters rise and recede. Most vegetation available for Grass Carp in the main lake area consists of shoreline vegetation that becomes inundated or areas near the back of shallow coves that are less influenced by water level changes allowing for macrophytes to persist. The reservoir is far enough north for ice coverage in areas that are shielded from the wind to persist for up to a month in winter. Open areas of the main lake exposed to wind may freeze for brief periods during harsh winters but normally do not completely freeze.

There is an established Grass Carp population on Truman Reservoir that has likely existed since the reservoir was formed. Missouri has allowed the production of diploid Grass Carp since they were first introduced and were common in many farm ponds and a hatchery along the Osage River before it was dammed in Warsaw. Subsequent flooding has allowed fish to enter the reservoir, and now are frequently caught and sought after by bow fishermen. Egg production and fertilization has been documented in the Osage River (Hayer et al., U.S. Fish and Wildlife Service, unpublished data) indicating the population is self-sustaining. An established Grass Carp population and extensive shallow and deep-water habitat make Truman Reservoir a suitable site to study Grass Carp habitat use and harvest potential in a large lake system.

Tagging and Telemetry

Fifty Grass Carp (25 diploid and 25 triploid) were stocked into Truman Reservoir 20 January 2017, and 36 (18 diploid and 18 triploid) stocked on 29 October 2018. Diploid fish were reared at the USGS Columbia Environmental Research Center, and triploid fish were purchased from a commercial fish hatchery (Hopper-Stephens Hatchery, Inc., Arkansas). Total length of diploid fish ranged from 570-905 mm and weight from 2.16-10.45 kg. Total length of triploid fish ranged from 550-840 mm and weight from 1.78-6.66 kg. All fish were implanted with 34 g acoustic transmitters (VEMCO, Bedford, Nova Scotia, Canada) in the peritoneal cavity. Fish were anesthetized with tricaine methanesulfonate (MS-222) before a 25 mm incision was cut halfway between the pectoral and pelvic fins. The incision was made slightly to one side of the midline to prevent agitation of the site from rubbing against the bottom of holding tanks and reservoir substrate. Transmitters were inserted through the incision and allowed to move freely inside the body cavity before the incision was closed with 2 to 4 surgeon's knots. Fish were then injected with 0.1 ml/kg body weight of oxytetracycline to prevent infections. Tag weight did not exceed 3% of the fish's body weight. All fish were tagged following VEMCO (2010) procedures and given ≥ 1 month to heal before being released.

Telemetry was conducted during winters (December – March) of 2017-2018 and 2018-2019 when water temperatures were typically < 10°C throughout the lake. This tracking period allowed fish time to transition from summer/fall to wintering habitat and lasted until fish began to make upstream movements geared towards spawning. While tracking I systematically searched shorelines in a boat with a VR100 acoustic receiver (VEMCO, Bedford, Nova Scotia, Canada) and omnidirectional hydrophone mounted on each side, listening for tags in all accessible aquatic habitats. Tracking primarily occurred near shorelines because main reservoir arms were often too wide to confidently hear tags across the arm's entire width. When a fish was detected I used a directional hydrophone to hone in on the fish's location until a strong, unidirectional signal was heard. Early trials with dummy tags indicated location accuracy within 3 m.

I recorded GPS coordinates and water depth of a carp's location using the boat's onboard depth finder (Helix 10 Mega, Humminbird, Wisconsin, USA) and measured distance to the nearest bank using a handheld rangefinder (TruPulse 360R, Laser Technology, Inc., Colorado, USA). Water temperature was measured using a water quality sonde (YSI 6600 V2, Xylem, New York, USA) at the water's surface and at 5 m intervals through the water column. Temperatures near the bottom were never more than

0.75 °C greater than surface temperature at the same location, and as such I only considered surface temperature when quantifying habitat. Identical habitat measurements were taken at three random locations within a 1 km radius of a fish’s location. Random locations represented a sample of available habitat for resource selection analysis and were based on the maximum movement rate I detected over a 1-hour period. Random locations were generated in the field using ArcMap (ESRI, California, USA) and sampled within 1-hour of locating a Grass Carp to minimize temporal variation in water conditions among used and available locations. I used three random sites as it was the maximum number of locations that could confidently be measured in a 1-hour time frame.

Habitat Selection Models

Resource selection functions, which compare habitat at used locations to habitat at randomly sampled locations available to an individual are frequently used to quantify habitat selection (Boyce and McDonald 1999; Anderson et al. 2005; Morato et al. 2018). Discrete choice models are an alternative to traditional logistic regression models to assess resource selection in temporally dynamic systems because that can easily account for temporal changes in resource quality and availability (Morato et al. 2018). Discrete choice models calculate the probability of an individual selecting a location as a function of the habitat characteristics at that location and all other available locations (Cooper and Millspaugh 1999; Manly et al. 2002, Edge et al. 2020). They are built on the assumption that an individual gains utility (e.g., protection from predators, improved foraging quality, reduced energy expenditure) from selecting particular locations with resource characteristics (e.g., vegetation coverage, substrate type, and density of cover) that maximize utility relative to other available locations (Cooper and Millspaugh 1999, Manly et al. 2002). The combination of used and available samples represents a choice set, which in this study, was defined by each carp location and three random sites sampled within a 1 km radius.

I developed eleven *a priori* hypotheses to describe winter habitat selection by Grass Carp. These hypotheses were developed as Bayesian discrete choice models to evaluate the effect of depth (D), distance to bank (DTB), water temperature (T), and Julian day (J) on Grass Carp habitat selection. Julian day was included in some models as an interaction with other terms to determine if the selection of variables changed over time. The models represented different hypotheses regarding the effect of habitat variables on Grass Carp habitat selection. Models took the form:

Equation 1

$$U_{ijk} = \beta_1 D_{ijk} + \beta_2 D_{ijk}^2 + \beta_3 DTB_{ijk} + \beta_4 DTB_{ijk}^2 + \beta_5 T_{ijk} + \beta_6 J_{ijk}$$

where the utility *U* of each location *i* in a choice set *j* for individual *k* is a function of the parameters at that location. The probability of an individual choosing resource *A* rather than any of the other *n* resources available is written as follows (Cooper and Millspaugh 1999).

Equation 2

$$P_{ijk}(A) = \frac{\exp(U_{ijk})}{\sum_{\forall i} \exp(U_{ijk})}$$

I included quadratic terms for both water depth and distance to bank because I hypothesized fish might select for intermediate depths or distances from the bank relative to what was available. All continuous covariates were standardized to a mean of zero and a standard deviation of one except for Julian day.

I fit models via Markov chain Monte Carlo (MCMC) using the JAGS package (package version 4.9, Plummer 2019) in R (R core team 2019). I ran three MCMC chains of 40,000 iterations with the first 10,000 used as burn in and retained every 10th iteration to generate estimates of model parameters. I assumed vague priors for all parameters, with normal distribution of μ (mean=0; variance=100) and uniform prior distribution of σ (min=0; max=10), where $\beta j \sim N(\mu_\beta, \sigma_\beta^2)$. To test for convergence in MCMC chains, I used the Gelman-Rubin convergence statistic, $\hat{R}$, with values less than 1.1 indicating convergence (Gelman and Shirley 2011).

After fitting the 11 candidate models, I used an information-theoretic approach to identify the most supported models from the full set of candidate models (Burnham and Anderson 2002). Model selection was determined using the deviance information criterion (DIC), a Bayesian alternative to Akaike Information Criterion (AIC: Burnham and Anderson 2002; Thomas et al. 2006). Similar to AIC, DIC ranks a set of competing models based on how well they explain the data with an increasing penalty term as the number of model parameters increases. Thus, DIC is useful in finding the best performing and most parsimonious models in a set of competing candidate models. I considered all models with ΔDIC values ≤ 2 as being well supported, which I evaluated further in my analysis. This threshold is considered acceptable for AIC and as such was used in selecting my models using DIC (Burnham and Anderson 2002). To further evaluate well supported models based on predictive ability, a k-fold, cross validation was used where the choice sets were randomly divided between an 80% training set and 20%

test set before the models were rerun for validation. Cross validation was repeated 10 times, and each time the choice sets were randomly divided between the training and test set. Within each cross validation run, a rank was given to each site in the test choice sets based on the probability that the individual would choose that site over the other three sites available (Boyce et al. 2002). The ranks were compiled over the 10 cross validation runs and accuracy was determined by the percentage of times the used location was classified as most likely to be selected (Bonnot et al. 2011). Given that there are four sites available in each choice set, I would expect a 25% predictive success in this manner by chance alone.

Effectiveness of Judas Fish in Winter Harvest

To test the applicability of using Judas fish to efficiently locate and harvest large aggregations of Grass Carp, I made attempts to harvest Grass Carp during February and March 2019 with multiple boats in cooperation with U.S. Geological Survey biologists at sites where tagged Grass Carp (Judas fish) were located, and sites believed to be good Grass Carp habitat to serve as controls. Comparing the number of Grass Carp caught at locations where Judas fish were located to those caught at control sites allows me to test the effectiveness of using Judas fish relative to targeting locations based on habitat conditions and expert opinion. Consistently catching larger numbers of carp using Judas fish compared to control sites would support the effectiveness of this method. A combination of methods was used to harvest fish. Trammel nets (6.4-8.9 cm mesh, 91 m long and 3 m deep) were deployed at all harvest locations where I surrounded Judas fish at a distance (typically > 50 m from fish’s location) in which not to spook any other fish that may be in the area. Nets were stretched from shoreline to shoreline to close off a cove or to encircle fish along the bank. At control sites, I deployed nets in a similar fashion assuming fish were associated with the shoreline or any inundated vegetation present. Once targeted areas were surrounded by nets, boats moved into the confined area and using a combination of sound produced by the boat prop and electrofishing, I pushed Grass Carp into the direction of the nets. This was done by starting near the shoreline and making parallel movements against the shore until the boat got to the nets. At sites with Judas fish, carp were driven until either I had confidence tagged fish were in the net or it was evident they had escaped, and at control sites I drove the area being fished from the shoreline to the nets at least twice or a total of 15 minutes. The nets were immediately pulled after driving fish and all Grass Carp were collected while native fish were released. I excised guts of Grass Carp captured to determine gut fullness and assess the potential of winter foraging activity as an explanation for observed habitat selection. Gut contents were given a score of 0 (no material), 1 (1-33% full), 2 (34-66% full), 3 (67-99% full) or 4 (no visible empty space in the gut).

Results

I recorded 116 locations of 53 unique fish, with a mean of 2.2 relocations per individual (range: 1 – 6 relocations) and mean duration of 17.2 days between relocations (range: 5-58 days) within a winter tracking season. Fish were observed moving distances > 1 km within a day and as such 5 days was considered enough time to assume independence between locations. Tag loss from fish expelling tags or mortality was high in fish released in 2017, with 6 (12%) confirmed lost tags, and 11 (22%) tags suspected lost based on no detected movement during the study. No tag loss or mortality was observed in the cohort of fish stocked in 2018. As a result, 74% of telemetry data were collected during winter of 2018-2019. Grass Carp were often located in water <5 m deep (median = 1.42 m, range 0.5 - 17.7 m), within 100 m of shore (median = 21 m, range 5 - 347 m; Fig. 2.2) and in temperatures ranging from -0.1 °C - 11.4 °C (median = 2.99 °C).

Habitat Selection Models

Discrete choice models incorporated 94 complete choice sets from 38 Grass Carp. All models converged based on the $\hat{R}$ statistic. Three models were well supported, with ΔDIC values < 2, and the top two models were nearly identical with a ΔDIC of 0.07 (Table 2.1). These two models included the quadratic form of depth and the quadratic forms of depth and distance to bank, respectively (Table 2.1). Parameter estimates for the quadratic form of depth were informative for both models based on 95% credible intervals, however, parameter estimates indicated distance to bank was not informative (Table 2.2). K-fold cross validation was performed to further assess model strength for the top three models. The top two models both accurately predicted the used site 70% of the time and the model of the quadratic form of depth and distance to bank correctly predicted 67% of used sites. The quadratic form of depth model had informative parameter estimates and the highest predictive power of candidate models, suggesting depth was the most important variable impacting habitat selection. Model predictions suggest relative probability of use decreased rapidly as depth increased, with fish 7 times more likely to select locations in 1 m compared to 5 m (Fig. 2.3).

Fish Harvest

I made harvest attempts over a two-week period between 18 February 2019 – 22 February 2019 and 11 March 2019 – 12 March 2019. I targeted 10 locations associated with Judas fish and 6 control sites. I captured 43 Grass Carp in total from the 16 harvests attempts. I targeted 12 unique tagged fish (1-3 tagged fish at a site) and was able to successfully capture 2 of them which were then returned to the reservoir for further tracking. 36 fish in total were caught when targeting tagged fish with an average of 3.6 (range: 0-19) fish per harvest attempt (Table 2.3). At control sites I caught 7 fish with an average of 1.17 (range: 0-5) fish per harvest attempt. I was able to score gut fullness on 31 of the fish captured, with scores greater than 0 for 29 of the fish (Fig. 2.4). Material present in the stomachs of harvested Grass Carp is indicative of feeding during the period fish were captured.

Discussion

Contrary to my hypothesis that fish would move to deeper water where temperature fluctuation is less severe, fish in this study exhibited strong selection for shallow littoral habitats during winter months. Resource selection modeling suggested depth was the primary driver of Grass Carp habitat selection, predicting carp were most likely to use habitats ≤ 3 m deep. I located tagged Grass Carp in water ≤ 3 m deep 75% of the time, often dispersed along the bank using much of the shallow littoral habitat available. When I did find fish in deeper water, they were either actively crossing from one side of the reservoir to the other or were moving along the bank through deeper water associated with bluffs. It was very rare to find a fish in deep water with no movement detected. This is one of two studies that exist investigating Grass Carp winter habitat selection in a large lake system in true cold weather climates where ice coverage forms at least a portion of the year (Harris et al. 2020). However, in the Harris et al. (2020) study fish primarily used tributaries overwinter and microhabitat selection on the lake proper wasn’t measured. In warmer climates, Grass Carp are routinely found near vegetation during winter months (Bainet al. 1990; Clapp et al. 1993). This is consistent with the results of this study where fish were often located near shoreline and inundated vegetation. Shallow winter habitat selection observed in this study was contrary to how Grass Carp are believed to behave in riverine habitats where they move to deeper parts of the channel (Fischer and Lyakhnovich 1973; Shireman and Smith 1983). This is also contrary to winter behavior by other carp species in lakes, where evidence suggests Common Carp move offshore to deeper water during winter months (Penne and Pierce 2008; Bajer and Sorensen 2010; Taylor et al. 2012). Bighead and Silver Carp have also been observed offshore during winter harvest efforts (D. Chapman, U.S. Geological Survey, personal communication). The results of this study and others (Bain et al. 1990; Clapp et al. 1993; Harris et al. 2020) are indicative that Grass Carp may be more mobile than other carp species over winter months in both lake and river systems.

Of 31 fish captured during harvest attempts that had gut contents examined, 94% had significant material in their gut, indicating feeding occurred through the winter months. This offers a plausible explanation to the strong selection for shallow water, as the littoral habitats and large shallow flats used by Grass Carp represent areas where inundated or emerging vegetation was most likely to be encountered. In contrast, overwintering Grass Carp caught on large rivers are commonly found with empty guts (D. Chapman, personal communication), possibly from lack of food available in those habitats during winter months. However, little information is available on Grass Carp in riverine systems where food is available overwinter, and more research is needed to evaluate overwinter feeding in rivers. Further research on the ubiquity of winter foraging is also needed on cold water lakes that have established macrophyte beds.

Lake Erie is the shallowest of the Great Lakes and as such has ample wetlands and expansive macrophyte stands (Herdendorf 1992), especially along the west side of the lake which boasts the warmest mean annual temperature of all the Great Lakes (Schwab et al. 1992; Dobiesz and Lester 2009). Previous risk assessments of Grass Carp in Lake Erie have indicated a large impact to vegetation, with some estimates of <50% vegetation remaining in invaded wetlands after one year (van der Lee et al. 2017). However, these models assumed that Grass Carp would move to deeper waters in the winter and feeding would slow significantly or cease. If Grass Carp in Lake Erie are foraging throughout the winter similar to this study, then studies may be underestimating the potential impact of Grass Carp in Great Lakes ecosystems.

Tagged Grass Carp were dispersed widely in abundant near-shore habitat throughout Truman Reservoir, making it difficult to catch large numbers of Grass Carp per netting attempt (3.6 fish/attempt with Judas fish). Fish in shallow waters would often spook during trammel net deployment. An abundance of submerged obstacles also made capturing fish difficult, as I often had to spend time removing snags from nets which allowed fish to get around exposed areas of the net or free themselves after initially being caught. By-catch was also an issue, with upwards of 65 Smallmouth Buffalo (*Ictiobus bubalus*) being caught during some netting attempts. The many obstacles present when targeting tagged Grass Carp in shallow waters made this method of capture inefficient in capturing large numbers of carp. I only captured 2 Judas fish in 10 attempts (12 unique fish in total), which indicates I likely missed untagged fish as well. It is worth noting that the one site where I captured 19 Grass Carp was on the upper reaches of the reservoir in a creek where I was able to block off upstream and downstream movement completely.

This is not representative of other locations targeted in the actual reservoir and omitting this attempt yields 1.9 fish/harvest attempt. Attempting to harvest Grass Carp in systems where they select shallow water winter habitats is an inefficient and costly method for population control.

If the harvest attempt in the creek is omitted from the results, there is only a 0.73 fish difference in capture success between sites where I targeted tagged Judas fish and control sites targeted based on favorable habitat characteristics. From the low number of fish harvested, it can be concluded that targeting Judas fish did not appreciably increase harvest success. It should be noted that gear used and total effort could have resulted in low capture rates, larger efforts with commercial boats and nets may have had more success capturing large numbers of fish. Additionally, fish were observed moving ≥ 115 river km (rkm) from release sites, making it difficult to employ the Judas method in a large reservoir with a lot of area to search. However, in areas with less water to search like tributaries and smaller lakes, targeting Judas fish may be useful as was seen with Common Carp (Bajer et al. 2011, Taylor et al. 2012). This possibility is currently being explored for Grass Carp with the discovery of tributary use during winter months in the Lake Erie basin (Harris et al. 2020). With only a small difference in number of fish harvested when targeting Judas fish compared to targeting suitable habitat, and considering the significant time-cost of finding Judas fish in a large body of water, I conclude that overall the Judas method is likely not an efficient method of removal in large lake systems.

Truman Reservoir is primarily used in flood control and is a highly dynamic system with large fluctuations in water levels that don’t promote the growth of large beds of aquatic vegetation. As a result, available food resources are spread out and ephemeral in nature. This may be the reason fish moved so often during the winter and were not commonly found in large aggregations as they were looking for food. Conversely, systems with more stable conditions allow the establishment of large and persistent vegetation beds (Wilcox and Meeker 1991; Paillisson and Marion 2011). Lake Erie water fluctuations have rarely exceeded 1 m in the last 20 years (USGS gage 04215900), allowing for establishment of large vegetation beds (Ghioca-Robrecht et al. 2008; Miller et al. 2018). No study has observed winter habitat selection in the Great Lakes proper, however, evidence suggests that Grass Carp show considerable movement even during the winter in Lake Erie tributaries where many tagged fish reside (Harris et al. 2020). Permanent vegetation beds with abundant food resources available in the main body of the lake may allow Grass Carp to remain in profitable areas for longer periods of time before moving on in search of more food. The potential for less movement and an easier task of locating tagged Grass Carp makes it worth exploring similar research in a natural lake system.

Management Implications

Harvest strategies that have been useful for removal of Common Carp and other species of Asian Carp may not be transferable to Grass Carp in large lakes and reservoirs. The results from my study indicate that Grass Carp will use shallow water habitat during winter months and do not assemble in large shoals that have made the capture of other invasive species easier (Bajer et al. 2011; Taylor et al. 2012). Success may be had with harvesting Grass Carp using a similar Judas method in tributaries to Lake Erie where fish have been observed to reside over winter months (Harris et al. 2020). The more confined nature of tributaries and selection of particular habitats is more conducive to aggregating carp into exploitable concentrations (DeGrandchamp et al. 2008; MacNamara et al. 2016) where movements upstream and downstream can be inhibited with nets. In large lake systems, it may be more efficient to focus reduction efforts in connected tributaries rather than the main lake.

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Tables and Figures

Table 2.1. Deviance information criterion (DIC) model selection results for Bayesian discrete choice models of Grass Carp winter habitat selection in Truman Reservoir, Missouri, 2017 – 2019, including change in DIC compared to the lowest value (ΔDIC) and number of parameters (K). Predictive power for models 1 – 3 represents results of 10-fold cross validation.

Model[a]	K	DIC	ΔDIC	Predictive Power
$D + D^2$	2	153.75	0	70%
$D + D^2 + DTB + DTB^2$	4	153.82	0.07	70%
$D + D^2 + DTB$	3	155.39	1.64	67%
$D + D^2 + DTB + DTB^2 + T$	5	155.79	2.04	-
D + DTB + D*DTB	3	156	2.25	-
$D + D^2 + DTB + DTB^2 + T + J +$ T*J	7	156.62	2.87	-
D	1	159.10	5.35	-
D + DTB	2	159.82	6.07	-
$DTB + DTB^2$	2	188.42	34.67	-
DTB	1	200.88	47.13	-
T + J + T*J	3	261.66	107.91	-

[a] D = Depth, DTB = Distance to Bank, T = Temperature, J = Julian Day

Table 2.2. Beta coefficients for the top two supported Bayesian discrete choice models of Grass Carp winter habitat selection in Truman Reservoir, Missouri. Models were selected using the deviance information criterion (DIC) and predictive power via 10-fold cross validation. Included are the upper and lower 95% credible intervals of beta coefficients.

Model	Covariate[a]	β	95% CI
Model 1	D	-2.185	-2.797 - -1.642
	D^2	0.562	0.132 - 0.936
Model 2	D	-1.920	-2.695 - -1.236
	D^2	0.471	0.020 - 0.867
	DTB	-0.448	-1.002 - 0.102
	DTB^2	0.335	-0.033 - 0.657

[a] D = Depth, DTB = Distance to Bank

Table 2.3. Harvest attempts made between 18 February 2019 – 22 February 2019 and 11 March 2019 – 12 March 2019 on Truman Reservoir, Missouri. Ten sites used the Judas fish method to capture Grass Carp and six additional sites were fished, selected for quality habitat (no Judas fish). Water temperature was taken at the surface before harvesting began, and number of fish caught only includes those that successfully made it into the boat.

Date	Judas fish	Water Temperature (°C)	Grass Carp Caught
20 Feb	Yes	2.7	0
20 Feb	Yes	2.6	2
21 Feb	Yes	4.0	0
21 Feb	Yes	3.8	19
22 Feb	Yes	1.9	0
22 Feb	Yes	3.9	0
11 Mar	Yes	6.6	4
11 Mar	Yes	6.7	8
12 Mar	Yes	4.2	2
12 Mar	Yes	4.2	1
21 Feb	No	3.8	1
22 Feb	No	3.9	0
11 Mar	No	5.8	0
11 Mar	No	5.8	1
12 Mar	No	5.2	0
12 Mar	No	4.9	5

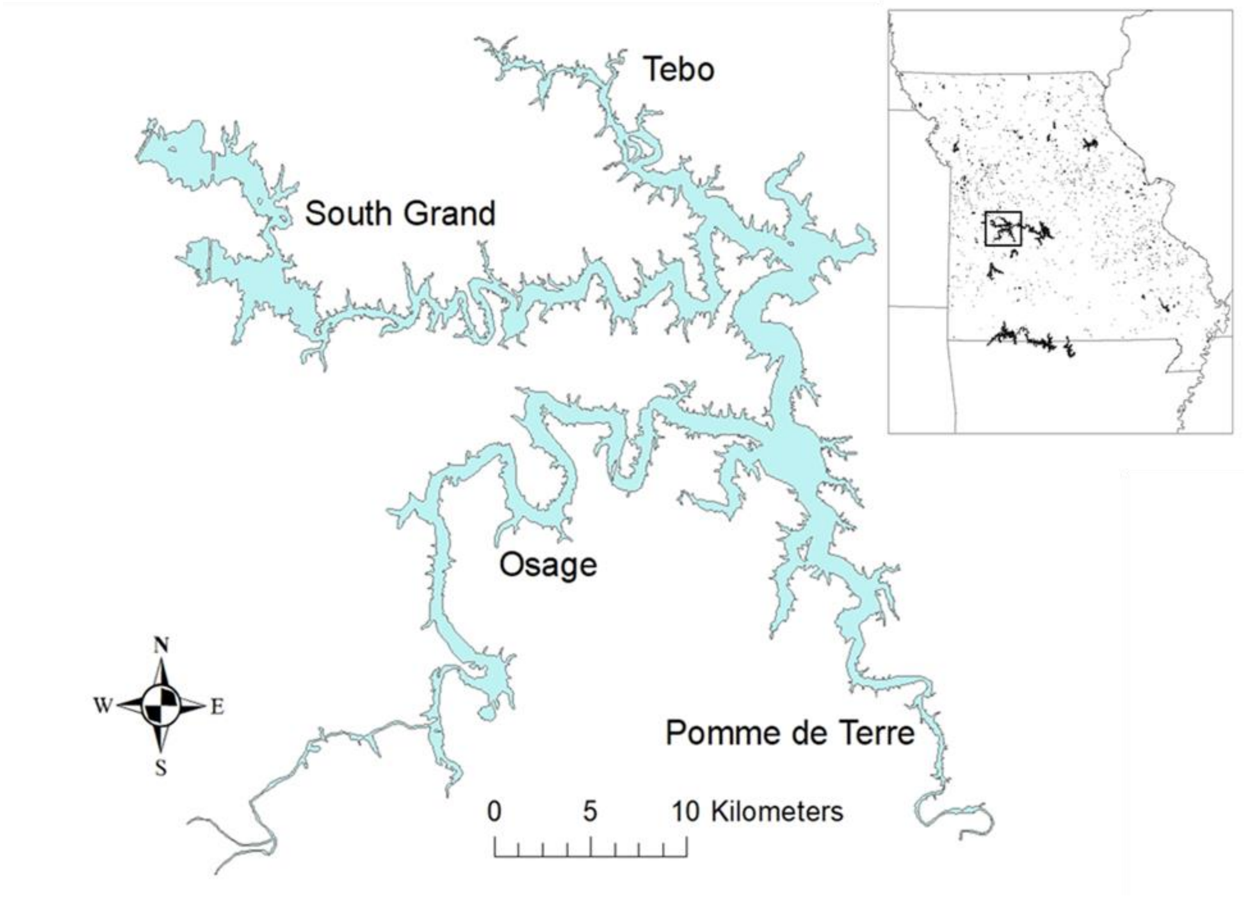

Figure 2.1. Truman Reservoir located in west central Missouri. My focus reach was the Osage River arm where all but three detected fish were located.

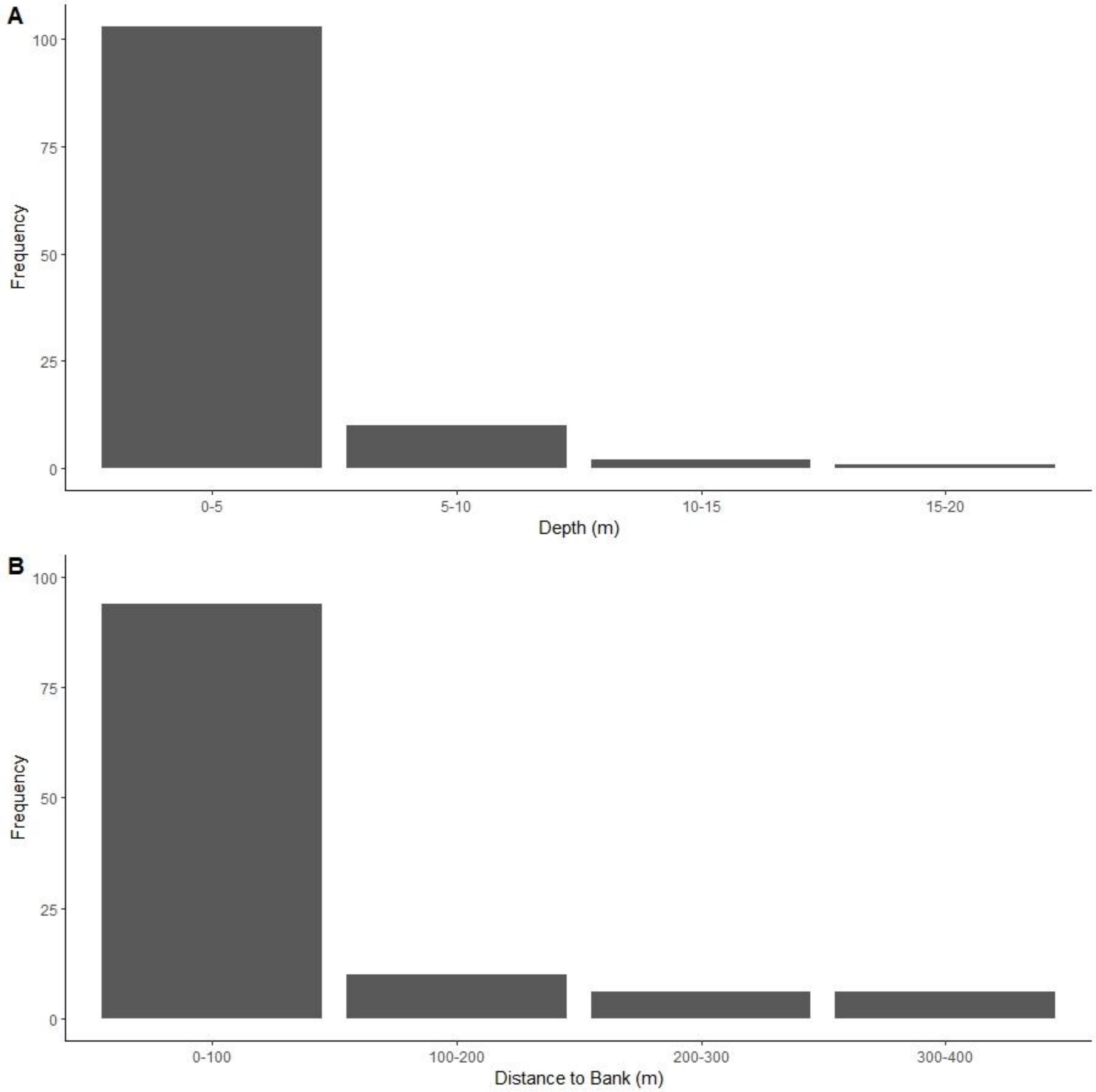

Figure 2.2. Distribution of depth (A) and distance to bank (B) at 116 Grass Carp winter locations (n = 53 Grass Carp) on Truman Reservoir, Missouri, 2017 - 2019.

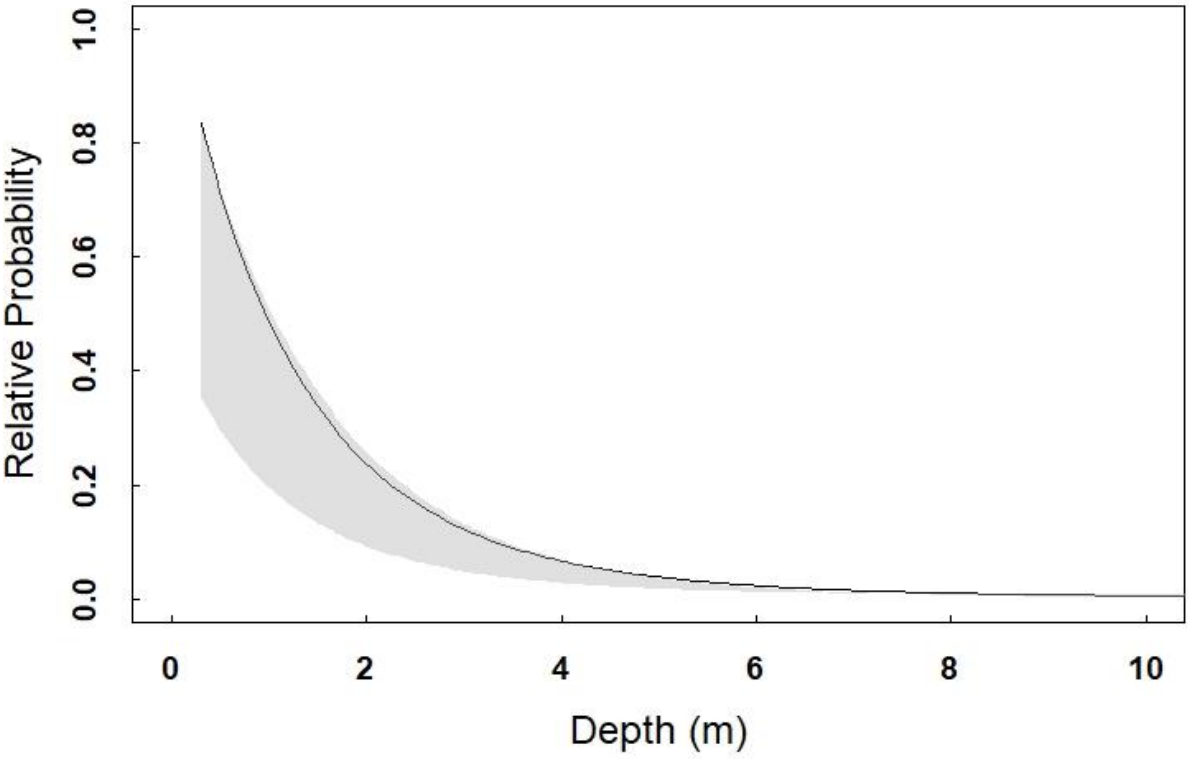

Figure 2.3. Relative probability of winter habitat selection as a function of depth for Grass Carp on Truman reservoir, Missouri over the 2017-2018 and 2018-2019 winters. Grey polygon represents the 95% credible interval.

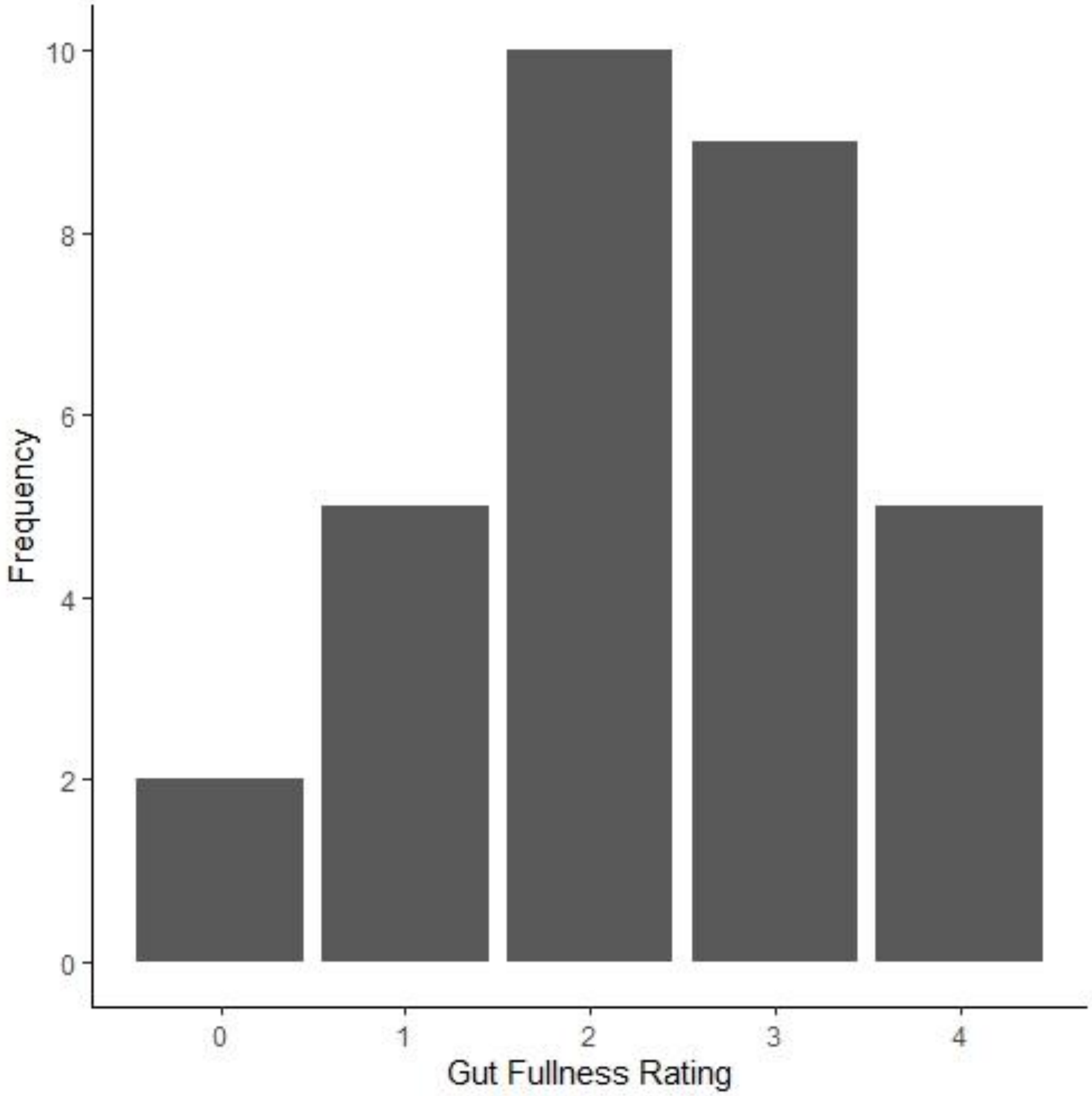

Figure 2.4. Distribution of gut fullness ratings given to 31 Grass Carp captured between 18 February 2019 – 22 February 2019 and 11 March 2019 – 12 March 2019 on Truman Reservoir, Missouri. Fullness ratings: 0 = no material present, 1 = 1-33% full, 2 = 34-66% full, 3 = 67-99% full, 4 = 100% full.

Chapter 3: Spawning Movement Ecology of Diploid and Triploid Grass Carp in a Large Reservoir

Introduction

Originally brought to the United States to control aquatic vegetation, Grass Carp are an invasive species of herbivorous Asian carp that have been documented in 45 states (Nico et al. 2020). Grass Carp have spread throughout the continental U.S. by a combination of natural dispersal and intentional stockings. Grass Carp have had ecological consequences on many of the waterways they have invaded (De Silva et al. 2009; Grabowska et al. 2010; Ireland et al. 2010). They have the ability to alter or significantly deplete aquatic vegetation communities in systems they are introduced to (Bain 1993; Pípalová 2006), which has direct impacts on fauna that rely on vegetation like birds, fish, and invertebrates (Jones et al. 2017a). Aquatic vegetation is an important source of food and shelter for native organisms that use aquatic resources for at least a portion of their life and severe depletion would be detrimental (Gertzen et al. 2017). In systems where Grass Carp cannot reproduce, direct impacts of foraging hypothetically would only last the lifetime of the invaders. However, it is plausible long-term effects on aquatic plant communities would persist and require an extensive period of time to recover even after Grass Carp are removed. When introduced to systems in which they have the potential to successfully reproduce, established populations pose a serious threat if they cannot be controlled.

Grass Carp inhabit lakes and ponds, but they require fast flowing rivers to reproduce (Jones et al. 2017a). Grass Carp are broadcast spawners and require at least 50 km of unimpeded river to allow eggs to drift for 16 - 60 hours before hatching (Stanley et al. 1978; NatureServe 2020). Turbulent waters at the confluence of rivers and below dams are often used as spawning sites as they allow eggs to remain suspended in the water column for fertilization before moving downstream (Deters et al. 2013). Currently, reproducing established populations exist in the Illinois, Missouri, Mississippi, and Ohio River Basins (Nico et al. 2020). Establishment in reservoirs is also probably widespread, but not widely investigated (D. Chapman, U.S. Geological Survey, personal communication). In North America reproducing populations have been documented above Truman Reservoir, Missouri and Lake Texoma at the Oklahoma – Texas border (Hayer et al, U.S. Fish and Wildlife Service, unpublished data; Hargrave and Gido 2004). These populations are probably established, with multiple age classes captured (D. Chapman, personal communication) with conditions suitable in upstream tributaries for spawning. Reproduction has also been documented in tributaries to Lake Erie (Embke et al. 2016), but a population likely is not established yet (Jones et al. 2017b). Persistence in these lake systems is reliant on adult fish being able to migrate into tributaries suitable for successful spawning. In each of these systems, sufficient unimpeded river length above the lake allows eggs to drift and hatch before settling in the lake proper. The conditions needed for spawning are relatively well known, but the movements of Grass Carp from lacustrine habitat into tributaries to spawn is not well studied. Being able to predict when fish are moving into tributaries could help in determining the most opportune time to remove fish before they have had the chance to move to sites upstream to spawn.

Sterile triploid fish are often used in vegetation control in lakes and ponds and are also used in Grass Carp telemetry studies of movement and habitat selection (Nixon and Miller 1978; Bain et al. 1990; Beyers and Carlson 1993; Chilton and Poarch 1997; Maceina et al. 1999; Kirk et al. 2001; Olive et al. 2010; Weberg et al. 2020). The production of triploid fish began in the late 1970s to replace fertile, diploid fish and are commonly stocked to control aquatic vegetation and used in studies to determine movements and habitat selection (Mitchell and Kelly 2006). Producing triploid fish involves shocking eggs with heat, cold or pressure to cause an additional set of chromosomes to be retained (Cudmore and Mandrak 2004). These genetically altered fish in turn do not have the capability of reproducing naturally. To date, only two published studies of Grass Carp movements report using diploid Grass Carp as well (Nixon and Miller 1978; Harris et al. 2020). Triploid fish are often used in studies because they cannot reproduce and contribute to populations in natural systems. Further, many states require that only triploid fish be produced and in turn are much easier to acquire by researchers (Cudmore et al. 2017). An important assumption for studies that aim to generalize their findings for established populations is that triploid fish behave similarly to reproductively viable diploid fish. However, if triploid fish do not develop fully mature gonads, it would be reasonable to assume they might not exhibit similar spawning related behaviors. Triploid females produce rudimentary gonads (Doroshov 1986) and males have only been observed to spermiate when induced artificially (Allen and Wattendorf 1987), indicating reproductive cues are absent or severely diminished in triploid fish. No study has made direct comparisons of movement behaviors in diploid and triploid fish to determine if they behave similarly enough to assume one group behaves like the other.

In this study, I tracked diploid and triploid Grass Carp on Truman Reservoir, Missouri to determine when and what cues trigger fish to migrate upstream in lake tributaries and to determine if there are significant differences between the two groups. Predicting when fish begin movements into tributaries could be advantageous in management by means of harvest or proposed seasonal barriers (ACRCC 2020). Determining whether diploids and triploids behave similarly in spawning related migrations is essential in deciding whether triploids should continue to be used in telemetry studies as surrogates for diploid behavior. I hypothesized that there would be significant differences in movements between diploids and triploids, as triploids are sterile and do not need to make large migrations upstream which requires high energy usage swimming upstream against current. Diploids would be the only group to make large upstream movements during appropriate spawning conditions and would do so with other fertile fish.

Methods

Tagging and telemetry

I stocked 50 Grass Carp (25 diploid, 25 triploid) implanted with VEMCO acoustic transmitters into Truman Reservoir (Study Site section in Chapter 2) on 20 January 2017, and 36 (18 diploid, 18 triploid) on 29 October 2018. Total length of diploid fish ranged from 570-905 mm and weight from 2.16-10.45 kg. Total length of triploid fish ranged from 550-840 mm and weight from 1.78-6.66 kg. All fish were deemed mature as they were > 50 cm total length, the minimum threshold for maturation (Cudmore et al. 2017). Details about origin of fish and implantation of tags can be found in Chapter 2.

I actively began tracking fish in March of 2018 and 2019 as fish began movements upstream that I assumed were associated with spawning preparation. I continued to track fish through July until temperatures reached the maximum spawning threshold (> 30 °C; Cudmore and Mandrak 2004). I attempted to relocate fish at least once every two weeks. Tracking was limited primarily to the Osage River and its tributaries where spawning has been documented (Hayer et al., unpublished data), and where all but three fish that were actively tracked and confirmed to still be alive were located. The Osage River arm was divided into lake proper and tributary at rkm 73 where the channel stayed within its banks and flow was observed most of the year (Fig. 3.1). This point was marked by a bridge with a large riprap structure that dispersed water downstream over a much larger area laterally in more lacustrine habitat. The channel downstream of this point rarely had turbulence and water velocities do not exceed 0.6 m/s, the minimum threshold expected for spawning (Stanley et al. 1978). During March - April I concentrated tracking activities in the main body of the lake to track upstream progression. As fish made larger movements upstream in late April-July, I moved into the tributary proper. The river was searched in segments by traveling upstream from boat launch sites near where I believed fish to be located, before starting a downstream search after moving as far upstream as was possible for a day's track. Some sections of the river were searched over consecutive days if it was believed a fish was moving through the area or a rise in river levels would trigger more fish to initiate an upstream migration. When a fish was encountered, I continued to track the fish for 30 - 60 minutes to determine if it was moving up or downstream. I then continued downstream in search of other fish.

Tracking during this portion of the study spanned > 60 rkm, not including off-channel habitat and other tributaries I encountered. As such, to supplement active tracking data and provide continuous monitoring of large-scale movements, I deployed passive acoustic receivers (VR2; VEMCO, Bedford, Nova Scotia, Canada) throughout the arms of the lake I believed could be conducive to spawning. I deployed 9 passive receivers from March - August 2018 on the Osage, South Grand, and Tebo arms (Fig.

3.1). I did not detect upstream movements for fish on the South Grand and Tebo arms and as such I only deployed receivers on the Osage River and its tributaries in 2019. I deployed 14 receivers in both the lake and tributary proper from March - August 2019. Nine receivers were deployed in the tributary proper ~5 rkm apart in the Osage River while four remained in the lake proper where they were deployed to collect winter habitat data prior to March. I also used data from four stationary receivers that the Missouri Department of Conservation deployed on the Osage River between rkm 73 - rkm 161 (Fig. 3.1). Two receivers were also located on the Sac River, a tributary to the Osage, to detect fish that might be using this waterbody as well (Fig. 3.1). Receivers were only deployed in the river if a test tag located at both banks on either side the receiver could be detected.

Movement data

I quantified Grass Carp locations in rkm upstream from the dam to track large-scale upstream movements. For locations in wider parts of the reservoir or adjacent coves, rkm upstream from the dam was determined based on the closest section of the Osage River channel. This method assumes the shortest distance a fish could have traveled but the distance is likely greater as fish could follow the shoreline and likely not travel down the middle of the reservoir. Although this method may miss smaller scale movements, it is still capable of capturing large scale upstream and downstream movements, which was my primary goal. Time between detections was irregular, making it difficult to compare movement behavior across individual fish. Therefore, I rediscretised individual fish movement to regular 12-h time steps using the package 'adehabitatLT' (Calenge et al. 2009) in R (R core team 2019). I used 12-h steps because consecutive detections at different locations were rarely < 12-h and intervals greater than this may miss quick movements associated with the start of a potential spawning run. Each movement step was then binomially categorized to indicate whether that step was part of a larger upstream migration (1) or not (0). To be considered part of a migration, upstream movement had to persist for ≥ 36 h at a speed ≥ 1 rkm/12 h. These criteria were chosen to ensure upstream movement was deliberate and not random movements often observed during other portions of the year. The step immediately prior to upstream movement was also included in migration events.

I quantified river conditions based on data from the Osage River gage at rkm 116.7 (USGS gage 06918250). Temperature (°C), discharge (m^3/s), and gage height (m) are measured every 15 minutes at this location. Discharge indicates the volume of water moving through that section of the Osage River channel at any point in time. I used this gage as it was in the Osage River above Truman Reservoir and was located between the beginning of fish migrations into the river and their furthest upstream detection. Therefore, I believe the conditions at this gage were representative of those fish experienced at other points in the river. River conditions were assigned to each carp movement step based on its time-synoptic gage reading, and the difference of these variables from the last step were calculated to represent change over time (Δtemperature, Δdischarge, and Δheight). These variables were included as they are believed to be primary drivers of Grass Carp spawning (Shireman and Smith 1983; Cudmore and Mandrak 2004).

Analysis

I used generalized linear mixed models (GLMM) to determine the probability of carp migrating upstream as a function of river conditions and Julian day (fixed effects) with individual fish included as a random effect to account for individual-level variation. Using a logit link function with a binary response (upstream movement/not upstream movement), models took the form:

Equation 1

$$\log\left(\frac{p}{(1-p)}\right) = \beta_0 + \beta_1 T_{ij} + \beta_2 D_{ij} + \beta_3 H_{ij} + \beta_4 \Delta T_{ij} + \beta_5 \Delta D_{ij} + \beta_6 \Delta H_{ij} + \alpha_i$$

where the log-odds (p = the probability of upstream migration occurring) of an individual, *i*, being in an upstream migration is the function of parameters (*T* = temperature, *D* = river discharge, *H* = river gage height, ΔT = change in temperature between 12 h steps, Δ*D* = change in discharge between 12 h steps, Δ*H* = change in river gage height between 12 h steps) for that movement step, *j*, plus the random effect, α_i, the variation between individual fish. I considered the quadratic forms of all river condition variables in my models as I believed there was a nonlinear response to these variables. Ten *a priori* models were developed to determine what combination of environmental variables were most effective in determining upstream migrations (Table 3.1). I used an information theoretic approach to identify the most supported models from the full set of models (Burnham and Anderson 2002). I used the Akaike Information Criterion (AIC: Burnham and Anderson 2002) to identify the best approximating models before verifying if parameter estimates were informative using 85% confidence intervals, based on recommendations of Arnold (2010) for distinguishing informative parameters when using AIC model selection.

Results

Of the 86 fish that were stocked, only eleven were detected making directional, upstream movements during the spawning season from late April-July in 2018 and 2019. At least 20% of the fish experienced tag loss or mortality (see Chapter 2) and 10% of them were never detected. In 2018, two of the seven fish (both diploid) believed to still be alive with known locations before the spawning season (March – August) made migrations upstream into the Osage River proper. Two fish resided in the lake proper after upstream movements began on 20 May 2018. One fish remained in the Sac River, a major tributary to the Osage River, but was not detected making upstream movements. It is possible one fish made a migration run up Barker Creek on the Tebo arm in 2018, but only one passive receiver was deployed, and directionality cannot be determined. No fish were detected by receivers on the South Grand and Tebo tributaries. In 2019, 10 of the 42 Grass Carp known to be alive made migrations upstream into the Osage River. Fourteen of the fish not detected making upstream movements were detected in the lake proper after migrations began on 27 April 2019. Four fish were detected after 27 April 2019 in the tributaries proper but cannot be confirmed to have made upstream movements. The other 14 fish had no detections after 27 April 2019. Three of the fish residing in the tributaries proper after 27 April 2019 were detected during the spawning season on the Sac River. Two of these fish were located in the lake proper before the earliest upstream migrations were detected and movements upstream coincided with events that triggered other fish to move up the Osage River. The furthest upstream receiver was only 6.5 rkm into the Sac River, making it difficult to determine if strong upstream movements on the Sac River persisted. As such, the two fish detected on the Sac River with perceived upstream movement were omitted from further analysis. I only included the 2019 spawning season in further analysis as limited detections made migration inferences difficult in 2018.

Ten Grass Carp (5 diploid, 5 triploid) made spawning related movements in the spring and summer of 2019 (Fig. 3.2). Two fish (both diploid) were from the group stocked in January 2017 and the other eight were stocked in October 2018. The two fish from the initial stocking also made upstream migrations in 2018. Total length of migrating fish at stocking ranged from 685 - 800 mm and weight ranging from 3.38 - 5.99 kg (Table 3.2). Upstream migrations were detected between 27 April 2019 and 01 July 2019 (Fig. 3.3), with river temperatures ranging from 15.4 - 25.4 °C. Migrations were associated with rising river level events, with a median of 0.09 m/12 h (-0.22 – 2.6 m/12 h).

Five fish initiated upstream migrations in the lake proper (2 diploid and 3 triploid), and the other five began their migration above rkm 73 in the river proper (3 diploid and 2 triploid; Fig. 3.2). Migrations began as far downstream as rkm 13 and as far upstream as rkm 107.6 (Table 3.3). Six fish (4 diploid and 2 triploid) made one upstream migration, 3 fish (2 diploid and 1 triploid) made two migrations, and one diploid made three migrations. Of the fish that made multiple migrations, all but one returned downstream (13.9 – 64 rkm) before their next migration. The one fish that did not return downstream before beginning its next migration was a triploid that began where it ended its last migration and could have been resting as there was only a three-day lapse between events. Total distance traveled during migrations ranged from 13.9 – 108.1 rkm (Table 3.3).

Effects of river conditions

Ten individual fish with fifteen unique movement events were incorporated into the GLMMs. The most supported model included the quadratic forms of temperature and Δheight (Table 3.1). This model had an AIC weight of 0.99, indicating there is a 99% probability of being the best approximating model in the set of candidate models (Symonds and Moussali 2011). The coefficient values for the quadratic forms of temperature and Δheight were informative based on 85% confidence intervals (Table 3.4). The highest probability of fish engaging in upstream migration occurred between 18 – 21 °C, and when river water levels were rising at a rate >1.5 m in a 12 h period (Fig. 3.4.).

Discussion

Between 2018 and 2019, ten unique tagged Grass Carp exhibited upstream migrations, potentially related to spawning, on the Osage River above Truman Reservoir. Only 24% of the fish actively tracked in 2019 were observed making upstream migrations. I focused on the Osage River and as such it is possible upstream movements were missed on other tributaries of the reservoir for fish that did not move up the Osage River. This may also be due to record flooding during the 2019 spawning season (May – August), which likely caused fish to disperse into backwaters and connected waterways and remain undetected if they did indeed attempt to migrate for spawning. Movements that were detected on the Sac River could have been spawning related, however, Grass Carp spawning has not been observed on the Sac River, possibly because it is regulated by an upstream dam in which rising hydrographs do not always coincide with rain events that cause water rises on nearby tributaries (Hayer et al., unpublished data). Multiple fish made a second or third upstream movement, in which they began downstream from the end of their last migration. Grass Carp are capable of spawning twice in one year, but it is rare (Shireman and Smith 1983). Asynchronous development of oocytes has been observed in Grass Carp (Shireman and Smith 1983), indicating fish that made multiple migrations could have not been ready to spawn during their first migration or they did not encounter other individuals to spawn with.

The longest upstream migration began at rkm 13.4 before ending near rkm 121.5, which is indicative of lake resident fish initiating upstream movements into tributaries. There was no clear relationship between location and timing of a fish's first upstream movement, as the earliest detected movement upstream was by a diploid residing in the lake near rkm 53.3 on 27 April 2019 and the next fish detected making an upstream movement resided much further upstream at rkm 96 and did not do so until 30 April 2019. This may indicate fish were at different stages of spawning readiness and thus began migrations at different times. However, it may have also been plausible that fish were initiating upstream migrations for purposes other than spawning. Rising river levels and higher flows could have delivered chemical cues downstream associated with flooded vegetation or other indicators to trigger upstream exploration. This may also explain why four fish made multiple migrations upstream when it is only likely for them to spawn once. Without direct confirmation of spawning by tagged individuals, it is impossible to know for sure why fish initiated upstream movements.

GLMMs suggested the probability of a Grass Carp making an upstream migration was strongly influenced by water temperature and rising river levels, with the greatest probability between 18 – 22 °C and river level rises >1.5 m/12 h. I was not able to directly confirm movements were related to spawning, but they coincided with conditions in which spawning has been observed. It is generally believed Grass Carp require water velocities > 0.6 m/s for eggs to remain suspended in the water column (Stanley et al. 1978), however velocities as low as 0.23 m/s have been observed to carry eggs (Leslie Jr. et al. 1982). Water velocity was not provided for the Osage River gage (USGS gage 06918250) until 2020, but water velocities associated with discharge in 2020 are indicative that water velocity in 2019 was > 0.6 m/s when upstream migrations were observed. Spawning in rivers has been observed to coincide with rising water levels (Lin 1935; Krykhtin 1975; Chilton and Muoneke 1992), likely as a result of increased water velocities capable of keeping eggs suspended while moving downstream. Models predicted water rise to play a larger role in determining migrations than discharge, and this may be a result of models including both fish residing in lake and tributary habitat before migrations began. If fish in the lake proper are responding to changing water conditions, they might be more likely to detect changes in water depth than discharge and velocity further downstream in lacustrine habitat.

Upstream movements began at 15.4 °C, which is concurrent with previous observations that movements to spawning sites will begin at cooler temperatures (Cudmore et al. 2017) in preparation to be at sites when the 18 °C threshold is reached (Stanley et al. 1978; George et al. 2017). The highest probability of movement coincided with optimal temperatures for spawning (18 – 22 °C), which may be a further indication these movements were spawning related.

In this study, both diploid and triploid Grass carp made upstream migrations during favorable spawning conditions, contradictory to my initial predictions. Triploid fish are expected to have no influence on the increase of wild populations, with females producing rudimentary gonads (Doroshov 1986) and males only observed to spermiate when induced artificially (Allen and Wattendorf 1987). Therefore, if triploid fish cannot release gametes naturally, then it would not be favorable for fish to expend energy migrating upstream for reproductive purposes. However, triploid fish that are traveling together with a cohort of diploid fish may continue upstream with them during rising river events. This being said, it should be mentioned again that these upstream movements may not have been related to spawning and fish could have been exhibiting upstream dispersal in search of food. Both diploids and triploids initiated upstream migrations similar distances upstream during the first significant water rise when conditions for spawning were favorable, which lasted from 27 April 2019 – 05 May 2019. Therefore, I conclude that diploid and triploid fish behave similarly in making upstream migrations into lake tributaries potentially related to spawning or for other exploratory purposes, including finding food. As such, I suggest triploid fish are suitable surrogates to study Grass Carp movement ecology in lake systems.

Management Implications

The results from this study suggest there is unlikely to be a time when fish moving from the lake will be concentrated in predictable places when moving upstream. Asynchronous movements by fish residing in different areas of the lake mean it is unlikely fish will be concentrated in the same location simultaneously, except perhaps at sites suitable for spawning if that is what these movements are intended for. Migration events may be spread out over multiple days, if not weeks during spring and summer river rise events. The most effective way to manage fish moving upstream may be to determine spawning destinations and if they are concentrating in these areas. If fish aggregate at upstream sites, then control via harvest may be suitable. These sort of harvest efforts have seen increased use to capture Grass Carp in tributaries to Lake Erie, but there have been difficulties in capturing fish in large numbers (ODNR Division of Wildlife 2019). It is unknown whether the low number of fish being caught is due to the present Grass Carp population being small, or if current capture methods are not efficient in removing fish. The use of seasonal barriers to prevent Grass Carp from moving upstream have been suggested (ODNR Division of Wildlife 2019) but concerns of native fish that also make upstream migrations will have to be addressed. To address growing populations of Grass Carp in novel waterways, agencies must determine tributary sites often used by fish and whether these sites are suitable for mass harvest.

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Tables and Figures

Table 3.1. Akaike's information criterion (AIC) model selection results for binomial generalized linear mixed models of Grass Carp spawning movement behavior in the Osage River above Truman Reservoir, Missouri, 2019, including change in AIC compared to lowest value (ΔAIC) and number of parameters (K). AIC weight indicates the relative probability that a model is the best approximating model compared to all other candidate models.

Model[a]	K	AIC	ΔAIC	AIC weight
$T + T^2 + \Delta H + \Delta H^2$	6	879.46	0	0.99
$T + T^2 + \Delta H$	5	888.26	8.81	0.01
$T + T^2 + \Delta D$	5	903.06	23.61	0
$T + T^2 + \Delta D + \Delta D^2$	6	903.48	24.02	0
$T*\Delta H$	5	991.92	112.46	0
$T + \Delta H$	4	997.56	118.10	0
$T + T^2 + \Delta H$	5	997.97	118.51	0
$J + \Delta H + \Delta H^2$	5	998.44	118.99	0
$J * \Delta H$	5	1002.33	122.88	0
$J + \Delta H$	4	1006.92	127.46	0

[a] T= Temperature, ΔH = change in river height over 12 h, ΔD = change in river discharge over 12h, J = Julian day

Table 3.2. Tagged Grass Carp that were detected making upstream migrations on Truman Reservoir, Missouri in 2019. Length and weight of fish at stocking, maximum dispersal indicates distance in river km from stock location to furthest upstream site detected.

Fish ID	Ploidy	Total Length (mm)	Weight (kg)	Maximum Dispersal (rkm)
9235	Triploid	740	4.83	95.9
9236	Triploid	800	5.81	95.9
9240	Triploid	745	4.98	55.4
9246	Triploid	750	4.51	80.8
9247	Diploid	712	4.19	87.9
9256	Diploid	685	4.47	55.4
9257	Diploid	790	5.99	95.9
9259	Triploid	758	4.78	70.8
52506	Diploid	670	3.42	115.5
52524	Diploid	675	3.38	115.5

Table 3.3. Upstream migrations detected for ten tagged Grass Carp on Truman Reservoir in 2019. Start and end dates indicate when fish were first detected making upstream movements and when they stopped.

Fish ID	Ploidy	Start Date	End Date	Start Location (rkm)	End Location (rkm)	Total Distance Traveled (rkm)
52524	Diploid	27 Apr	03 May	53.3	136.5	83.2
52506	Diploid	30 Apr	04 May	96	134.1	38.1
9236	Triploid	30 Apr	07 May	82.4	136.1	53.7
9247	Diploid	01 May	03 May	82.2	121.5	39.3
9235	Triploid	01 May	04 May	82.4	127.1	44.7
9257	Diploid	01 May	15 May	52.8	121.1	68.3
9256	Diploid	06 May	07 May	82.4	96	13.6
9247	Diploid	07 May	08 May	107.6	121.5	13.9
9246	Triploid	15 May	21 May	13.4	121.5	108.1
9257	Diploid	18 May	20 May	89.8	135.6	45.8
52524	Diploid	20 May	24 May	72.5	121.5	49
9247	Diploid	24 May	25 May	82.4	111.4	29
9259	Triploid	21 Jun	26 Jun	13.4	82.2	68.8
9240	Triploid	23 Jun	27 Jun	73.1	96	22.9
9259	Triploid	29 Jun	01 Jul	82.2	111.4	29.2

Table 3.4. Beta coefficients for the top supported binomial linear mixed model of Grass Carp spawning migration behavior on the Osage River above Truman Reservoir, Missouri, 2019. The model was selected using Akaike's information criterion (AIC). Included are the upper and lower 85% confidence intervals of beta coefficients.

Covariate[a]	β	85% CI
T	2.257	1.715 - 2.799
T^2	-0.058	0.072 - -0.045
ΔH	3.418	2.513 - 4.324
$ΔH^2$	-0.855	-1.225 - 0.484

[a] T= Temperature, ΔH = change in river height over 12 h, ΔD = change in river discharge over 12h

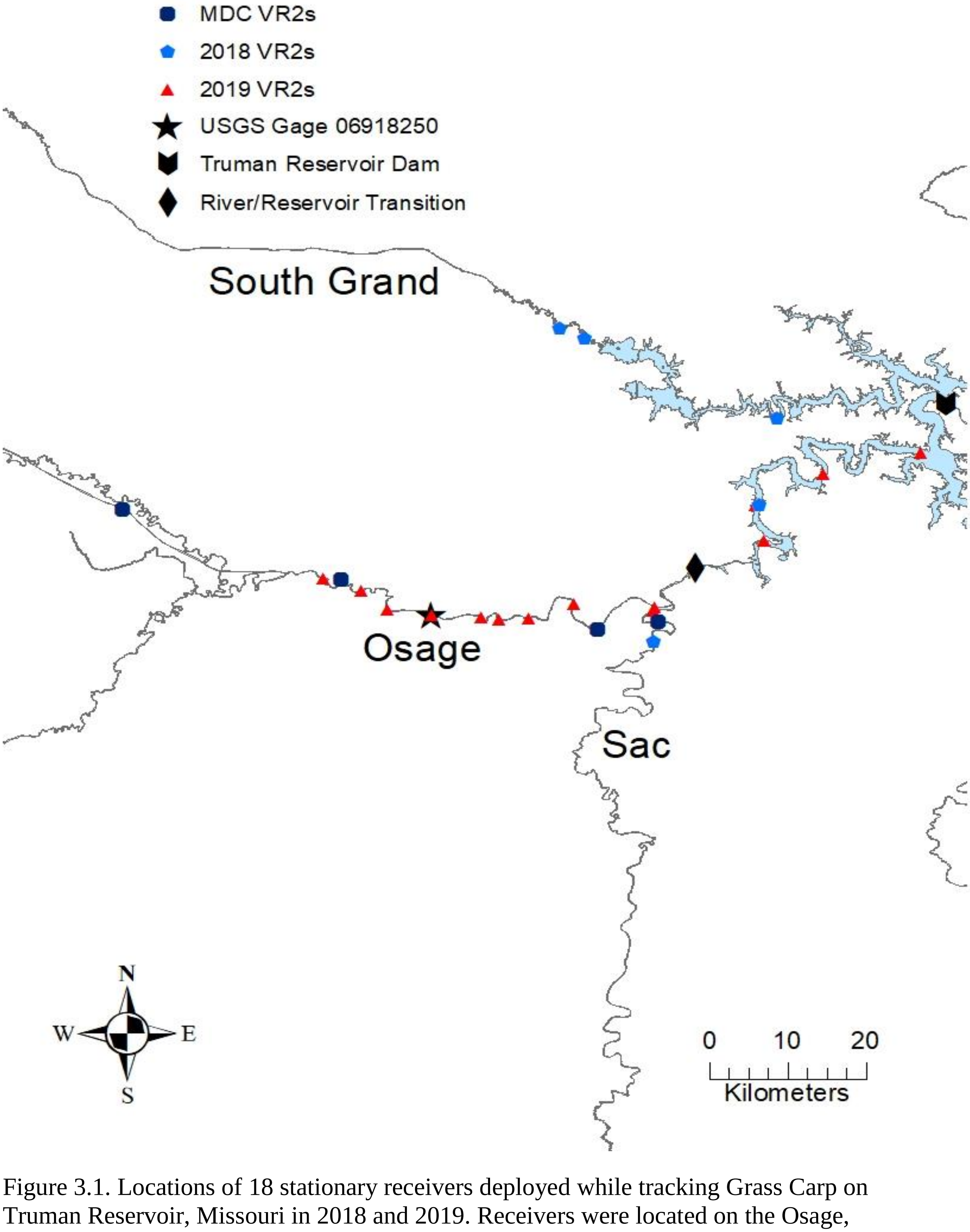

Figure 3.1. Locations of 18 stationary receivers deployed while tracking Grass Carp on Truman Reservoir, Missouri in 2018 and 2019. Receivers were located on the Osage, Sac, and South Grand Rivers. Four Missouri Department of Conservation (MDC) receivers were in place the entirety of the study, and the other 14 were relocated from the lake proper into the tributaries from March-August.

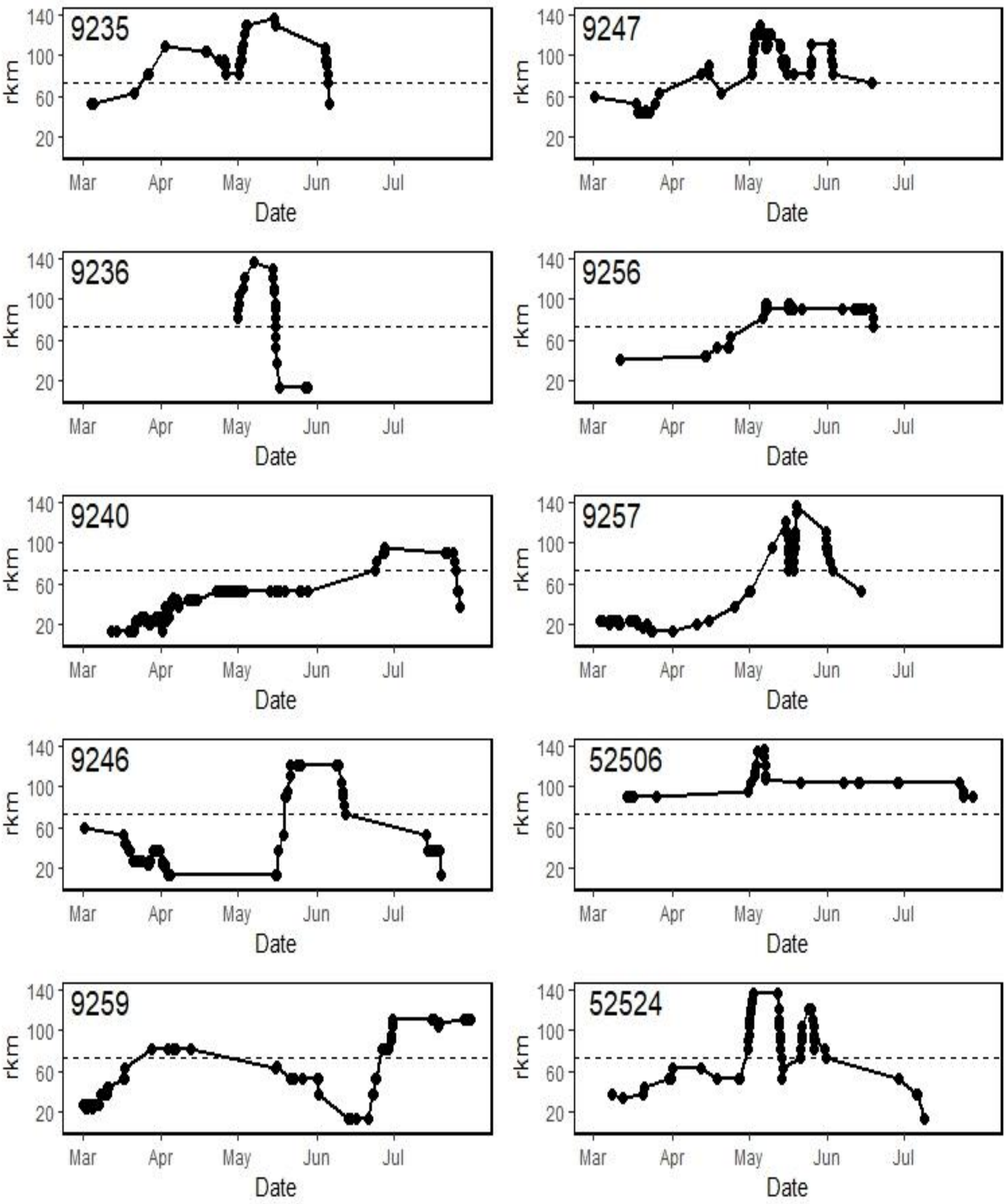

Figure 3.2. Movements of 10 tagged Grass Carp detected making upstream migrations during the 2019 spawning season on the Osage River above Truman Reservoir, Missouri. The left column represents triploid fish and the right represents diploid fish. The y axis indicates distance in river km from the Truman Reservoir dam. The dashed horizontal line indicates the transition from lacustrine to riverine habitat at river km 73.

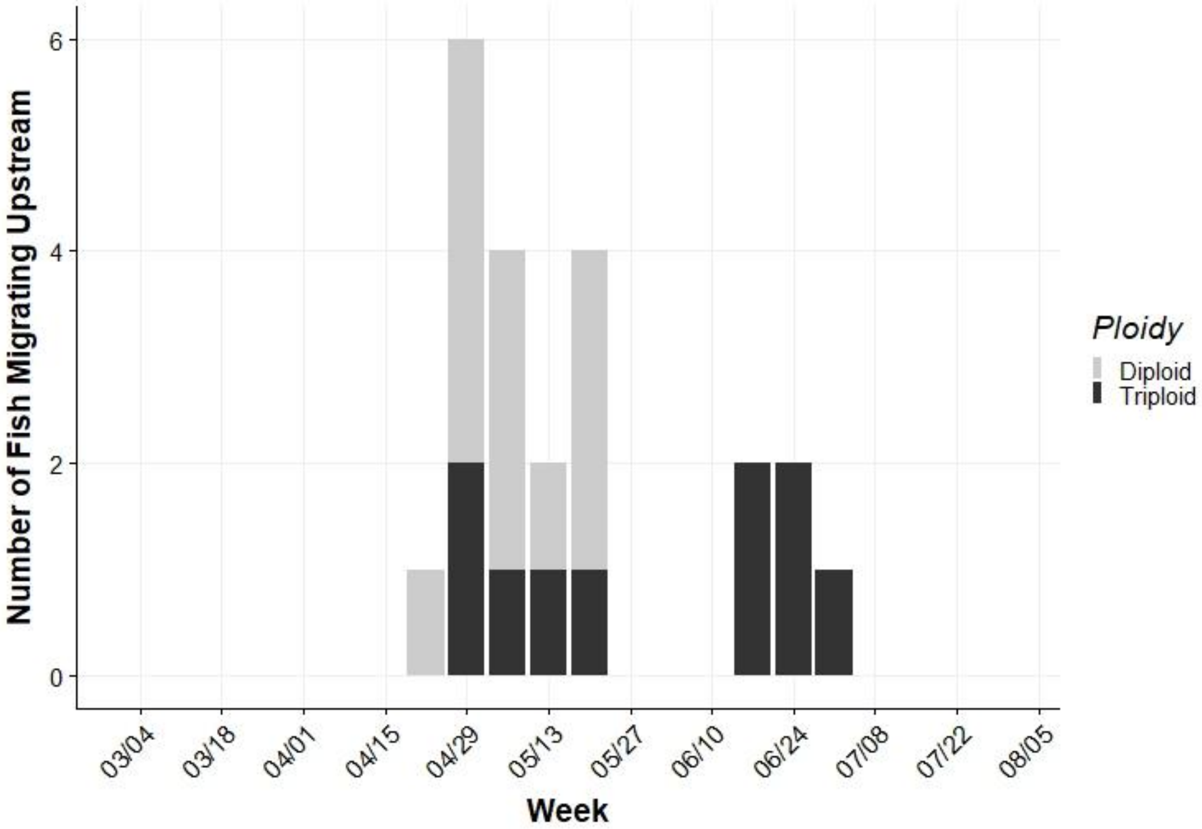

Figure 3.3. Timing of tagged Grass Carp in upstream migrations on Truman Reservoir in 2019. Five diploid and five triploid fish made upstream migrations located on the Osage River arm. Fish were included as being in an upstream migration event if they had at least one 12 h period of the week associated with a movement event.

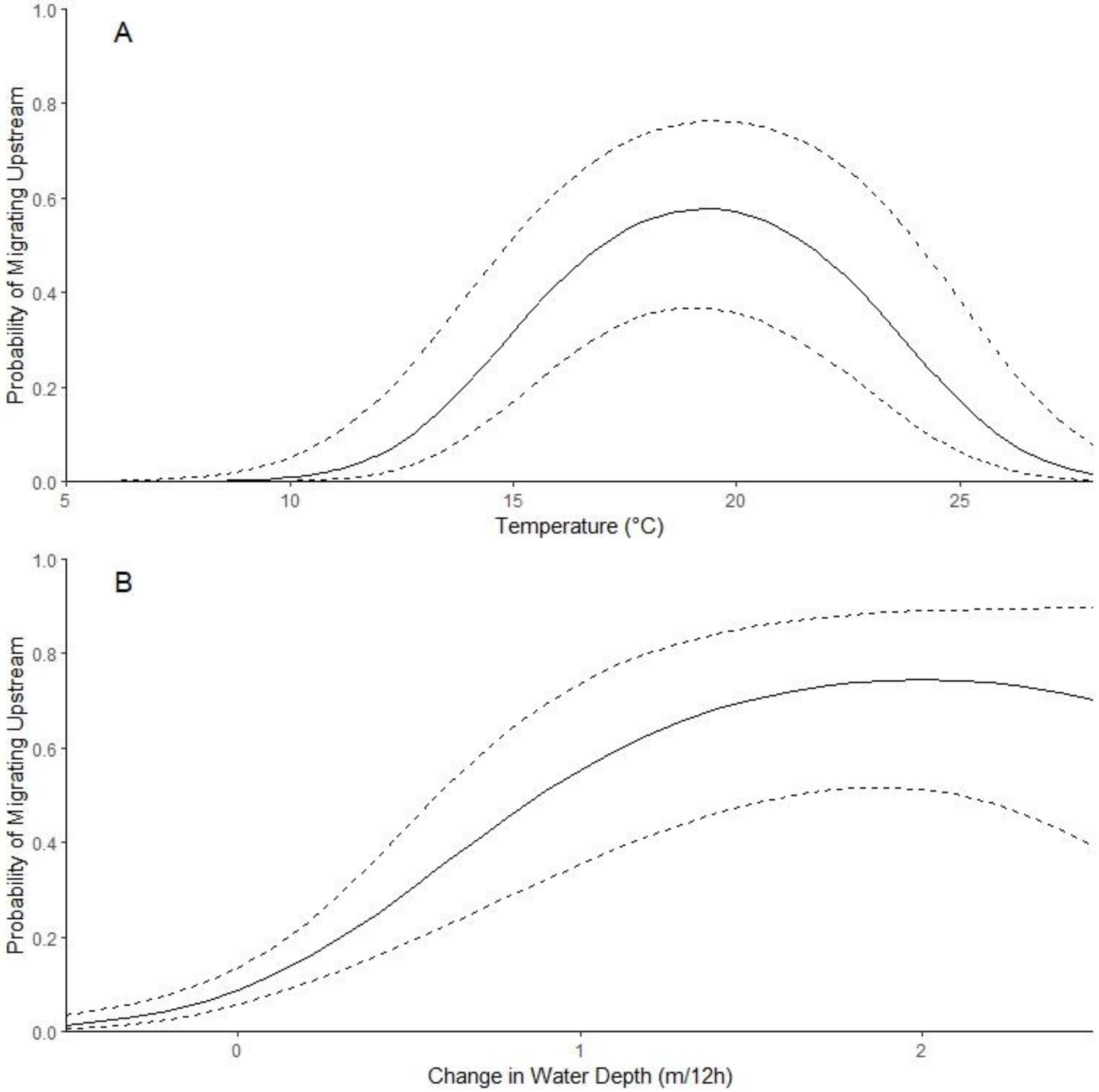

Figure 3.4. Predicted probabilities with 95% confidence intervals of upstream migration by Grass Carp on the Osage River above Truman Reservoir, 2019, based on the fixed effects of a binomial generalized linear mixed model. Plot A indicates the probability as a function of temperature while change in water depth is held constant at 1 m/12h. Plot B indicates probability as a function of change in water depth while temperature is held constant at 18 °C.

Chapter 4: General Conclusions

One of the primary objectives of the work was to determine winter habitat selection and to assess the potential effectiveness of Judas fish in harvest control of Grass Carp in large lakes and reservoirs. I observed Grass Carp using shallow littoral habitats (< 3 m deep), most often within 100 m of the shoreline. Selection of these habitats made it difficult to capture large numbers of fish, as they were dispersed along the bank and would often flee to deeper waters when capture attempts were made. Of the fish that were caught, 94% had food material in their gut, indicating overwinter feeding was present in this system. The use of near shore habitat where inundated vegetation was often found gave Grass Carp the opportunity to feed over winter.

The use of Judas fish to control Grass Carp populations in large lakes and reservoirs is likely not an efficient method as fish disperse in littoral habitat and few are caught per netting attempt. Relocating and trying to capture fish is very time consuming, with no assurances that fish in the area will be caught. Future efforts may wish to try the Judas fish method in tributaries where fish can be located quicker, and netting efforts can be focused in a confined area. Grass Carp in Truman Reservoir and potentially others feed over winter months, and it is probable that winter consumption was underestimated in bioenergetic models predicting vegetation consumption in Lake Erie if it was assumed Grass Carp feed at significantly lower rates in the winter. Habitat selection and diet studies should be further applied to natural lake systems like Lake Erie, where large vegetation beds have the potential to support a substantial Grass Carp population.

I also sought to determine factors influencing migrations related to spawning and whether diploid and triploid Grass Carp made similar migrations. Both diploid and triploid fish had a high probability of making upstream migrations during water rises on the Osage River above Truman Reservoir when water temperatures were between 15 – 25 °C. Four fish made multiple migrations in the same spawning season, which may be an indication that fish were not completely ready to spawn or they did not encounter other fish to spawn with the first time. Migrations ranged from 13.6 – 108.1 river km and were made by lake resident fish as well as fish that remained in the tributary. Change in water depth may be important in initiating migrations, especially in lake resident fish where change in velocity and discharge is less likely to be detected in lacustrine habitat. Migrations made by the 10 Grass Carp in 2019 started and ended at different times, indicating fish likely are not moving upstream in large groups.

Grass Carp should be expected to enter tributaries for spawning related migrations with significant water rises after water temperatures reach 15 °C. Upstream migrations may serve as the best time to harvest lake resident fish that are concentrated in tributaries, as fish may be too dispersed in lacustrine habitat for efficient control. Harvest efforts during spawning periods may still be a difficult task as fish do not appear to migrate upstream at the same time. Both diploid and triploid fish made migrations upstream during the same supposed spawning events, indicating triploids are suitable for movement related telemetry studies.