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By Katherine F Touzinsky

Entitled
MORPHOLOGICAL PLASTICITY OF INVASIVE SILVER CARP IN DIVERGENT MIDWESTERN RIVERS

For the degree of Master of Science

Is approved by the final examining committee:

Reuben R. Goforth
Chair
Tomas O. Höök
Jon J. Amberg

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Approved by Major Professor(s): Reuben R. Goforth

Approved by: Linda S. Lee (ESE) and Robert K. Swihart (FNR) 11/11/2015
Head of the Departmental Graduate Program Date

MORPHOLOGICAL PLASTICITY OF INVASIVE SILVER CARP IN TWO DIVERGENT MIDWEST RIVERS

A Thesis

Submitted to the Faculty

of

Purdue University

by

Katherine F Touzinsky

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

December 2015

Purdue University

West Lafayette, Indiana

I dedicate this work to my Nana and Papa. Thank you for the past three and a half years of carp-related newspaper clippings and patiently listening to updates on my miniature battle to save the Great Lakes from bigheaded carp invasion. The support I received from you during graduate school was a short but important chapter in a lifetime of encouragement and love. My darling Papa, you will be greatly missed.

ACKNOWLEDGEMENTS

I am so thankful that throughout my career at Purdue I have found myself surrounded by so many brilliantly inspiring and supportive advisors, mentors, and friends. I have many thanks to give.

This thesis started as a hare-brained idea that quickly became a fascinating academic pursuit. I want to dedicate special thanks to **Dr. Reuben R. Goforth** whose enthusiasm for learning through exploration is infectious and whose priorities are centered on his student's growth. The flexibility and support I've received within the Goforth lab have been priceless. I would also like to thank the whole fisheries group in the Forestry and Natural Resources Department, especially **Dr. Tomas Höök**, for intellectual guidance in moving this work forward. Additional thanks to **Dr. Linda Lee** and **Christal Musser** for their tireless efforts with the Ecological Sciences and Engineering Program, for bringing me to Purdue, and for providing a creative and inspiring learning environment for all students in the program.

This thesis involved the capture, dissection and analysis of hundreds of bigheaded carp and I would be amiss not to thank those who got their hands dirty in the name of science: the **Dave Wahl Laboratory at University of Illinois Urbana-Champagne**, Purdue students **Brandon Benninger** and **Wes Goldsmith**, and **Dustin Houston**, for opening his bowfishing tournaments and collaborating on my extension project "Winning

Back Our Wabash: Cook ‘em Up and Clean ‘em Out”. A special thanks to lab manager **Megan Gunn** for consistent support and many hours of help with all stages of my thesis. I also owe thanks to the **Purdue Student Sustainability Fund** for funding the extension project and to **Angela Archer** for helping with the BDHC fry and support in applying to the NOAA Knauss Fellowship. The Knauss Fellowship opened the door to a future career, and I want to thank **Dr. Julie Rosati** and **Jeff Lillycrop** at the US Corps of Engineers Engineer Research and Development Center for supporting me as I finished my degree.

I would like to thank my wonderful family – Ann, Steve, Daniel, and James— for listening me talk a little too long about bigheaded carp during holiday breaks and for consistent support and encouragement when I needed it, each and every one of you are a blessing in my life. And finally, a big thank-you to **Michael Chambers** for flying all the way from the High Sierra to spend a full week in Illinois dissecting hundreds of carp with me, and for never looking back.

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ABSTRACT

Touzinsky, Katherine F. M.S., Purdue University, December 2015. Morphological Plasticity of Invasive Silver Carp in Divergent Midwestern Rivers. Major Professor: Reuben Goforth.

In the past decade, silver carp (SC; *Hypophthalmichthys molitrix)* have incited a great quantity of scientific research because their establishment and success in the Midwestern U.S. has led to concerns that they could invade the Great Lakes Basin. These previous studies have identified phenotypic plasticity in SC behavior and spawning as they invade novel environments. Although divergent habitats have been shown to elicit morphological plasticity in multiple fish species, similar research has not been conducted for SC despite their observed plasticity in other traits. I examined SC collected from two hydrogeomorphically divergent rivers, the Illinois River and middle Wabash River (MWR), as examples of rivers that support SC populations at different invasion stages. I compared differences in SC body shapes through geometric morphometric analysis and life history characteristics through population demographics between rivers. Middle Wabash River silver carp (MWRSC) were in better condition, lived longer, attained greater total lengths, and had higher GSIs than Illinois River silver carp (IRSC). Morphometric analysis revealed a significant divergence in body morphology between MWRSC and IRSC, whereby MWRSC had deeper body sections and narrow, tapered

heads while IRSC had shallower bodies and deeper heads. Principle component analysis indicated that contrasts in morphology were most strongly associated with river, as opposed to other factors such as sex, hybrid status, and time sampled. While I do not assert causal evidence for the difference in shape based on specific environmental characteristics of the two rivers, I speculate that IRSC and MWRSC are undergoing different selection pressures due to population demographics and environmental characteristics of the two rivers. Regardless of the specific causal factors, it is clear that body shapes were different between the two rivers, suggesting that location-based selective agents are driving phenotypic outcomes in invasive SC.

CHAPTER 1. LITERATURE REVIEW

1.1 Introduction

Aquatic invasive species (AIS) are a substantial threat to global freshwater biodiversity, and their introductions have resulted in widespread and catastrophic consequences for aquatic ecosystems (Conover et al. 2007; ACRCC 2014). For the past decade, bigheaded carps (BHDC), including silver (*Hypophthalmichthys molitrix;* SC), bighead (*H. nobilis;* BHC) carps, and their hybrids, have become one of the most devastating AIS in the U.S. They are thus a major focus of invasive species research and management due to their rapid spread, establishment, and domination of the Mississippi River Basin (MRB) and its tributaries (Patel et al. 2010) and their potential to become established in the Great Lakes Basin (GLB). BHDC populations in the MRB typically comprise a complex hybrid swarm resulting from gene flow between the two species (Lamer et al. 2015). Herein, SC refers to populations with silver carp phenotype but unknown or known establishment of hybrids. When it is necessary to differentiate within SC, I refer to individuals with no hybrid characteristics as pure silver carp (PSC) and fish that have been identified with hybrid characteristics as hybrid silver carp (HSC). As BHDC populations continue to invade new river systems, current control efforts are highly focused on developing physical and chemical controls and identifying the most vulnerable tributaries that need protection (ACRCC 2014; USACE 2014). Scientists and habitat management officials must have an understanding of BHDC capacity to adapt to novel environments to better tailor containment strategies and communicate the risks of unintentional introduction to the public.

My study focused on populations of SC in two hydrogeomorphologically divergent rivers: the middle Wabash River (MWR) and the Illinois River. The study was designed to be a preliminary investigation to assess potential phenotypic plasticity in SC by analyzing two descriptive components of their success: population demographics and body morphology. The status of these two rivers is of particular interest because both serve as a pathway of introduction into the GLB. The MWR is a part of the northeast front of BHDC invasion and can be characterized as relatively well connected to its floodplain (Pyron and Lauer 2004). The Illinois River has been anthropogenically altered for navigation purposes through channelization, dams, and levees, and the resulting change in flow has caused a shift in fish assemblage and an increase in phytoplankton production (Bunn and Arthington 2002; Koel and Sparks 2002; Rolls et al. 2012). Populations of BHDC were detected in the lower Wabash River several years prior to the Illinois River (Nonindigenous Aquatic Species Website 2013), but Illinois River silver carp (IRSC) population numbers have increased exponentially, and in some reaches they compose 95% of the total biomass of the river (Chick and Pegg 2001; MIRCA 2002).

Previous studies have analyzed BHDC population demographics between tributaries in the MRB, and there have been numerous reports about shifting BHDC population demographics and the expression of unexpected traits and behavior in newly invaded habitats that are consistent among similar ecosystems (Stuck et al. 2015; Coulter et al. 2013; Deters et al. 2012; Aliyev 1976). BHDC meet many of the life history requirements of an ideal biological invader, including r-selected life history strategy, associations with disturbance, native origins in diverse continents, and broad phenotypic acclimatization to a wide ecological range (Sax and Brown 2000; Elton 1958). It is highly likely that they will continue to expand their range throughout the U.S. as they optimize fitness across rivers that have differing hydrology and ecology. While many studies have captured changes in population demographics, there have been relatively few quantitative analyses of phenotypic plasticity between watersheds. It is because of their ability to establish and display a range of life history and phenotypic plasticity that I advocate for continuous ecological evaluations of BHDC plasticity to ground-truth current computational models and predictions and re-evaluate protective measures for uninvaded tributaries in the MRB and GLB.

In addition to life history demographics, fish plasticity is often expressed in body shape. Fish morphology is often associated with adaptive plasticity based on environmental demands that have resulted in observed consistencies between ecology and morphology, even at the population level (Park et al. 2013). Landmark-based geometric morphometrics is well-established as a tool for capturing and validating dissimilarities in body structures and can quantify the plastic component of evolutionary adaptation in fisheries by analyzing differences between individuals that are otherwise undetectable (Chen et al. 2010; Yong et al. 2011; Doadrio and Perdices 1997; Dwivedi and Dubey 2013). By studying SC populations from two hydrologically distinct watersheds, I aimed to understand and quantify the degree of morphological plasticity that they exhibit between rivers. While I could make no conclusions as to the cause for any observed morphological differences, I nonetheless hypothesized that differences in local environmental demands and life history strategies may have strong influence on SC body shape.

This thesis is written in two parts: a literature review and a scientific study. The first chapter outlines the current literature on the historical presence of BHDC in both their native environments and in the U.S., the large body of modeling studies to understand which habitats are vulnerable to future introductions, and the characteristics of invasive species that have contributed to their successful establishment in the U.S. In addition, I review the proposed methodology for investigating the plasticity of SC between the MWR and Illinois River. The second chapter is written in journal format and contains the introduction, methodology, results, and discussion of this thesis on SC morphological plasticity.

1.2 Invasive Bigheaded Carps in the United States

BHDC were introduced to the U.S. in the 1960's to early 1970's for aquaculture, food markets, and as a form of algal control in sewage plants and farm ponds (Shelton and Smitherman 1984; Kolar et al. 2005; Cremer and Smitherman 1980). The first wild caught SC were collected in the White River, Arkansas, in 1974 (Kolar et al. 2005). Since that time, BHDC populations have become rapidly established in the MRB, with notable spread beginning in the 1990's and exponential population increases in some areas since then. BHDC monitoring in Navigation Pool 26 of the Mississippi River revealed exponential growth in BHDC populations from a harvest of 5,000 kg in 1994 to 50,000 kg in 1997 (Chick and Pegg 2001, Kocovsky et al. 2012). Since then, BHDC have been caught in 28 U.S. states as they spread throughout MRB tributaries (Baerwaldt et al. 2013) and are currently posing a threat to the Laurentian Great Lakes. The Great

Lakes provide a critical freshwater supply, a pathway for shipment of goods and services, and a diverse ecosystem that supports commercial, recreational, tribal, and sport fisheries. BHDC's potential for economic devastation has led to drastic public measures, and the White House Administration has taken unprecedented political and public action to control and halt the expansion of the species' ranges through the assembly of the Asian Carp Regional Coordinating Committee (ACRCC). The ACRCC is a group of academic and government researchers and policy makers that have coordinated a large variety of measures to combat the spread of BHDC. These measures include management plans and ground-up research to understand the biology of BHDC within the MRB and to apply that knowledge to management strategies for BHDC control (ACRCC 2014). In addition, these studies have provided the groundwork for much of our current knowledge about BHDC populations in the U.S.

BHDC establishment and spread in the U.S. is tied to several characteristics that have been well documented in the literature. These characteristics include diverse origins, r-selection, diverse phenotypic selection, and association with disturbed habitats (Sax and Brown 2000; Elton 1958). Despite being associated with reservoirs in their native ranges (Kolar et al. 2005), BHDC have utilized adaptive plasticity to demonstrate high establishment success in novel environments in the U.S. and pose a substantial threat to the biointegrity of North American large rivers and the GLB.

1.3 Tracking the Future Spread of Bigheaded Carps

The demand for research aimed at preventing BHDC from becoming established in the GLB continues to increase and a wide variety of studies have attempted to identify the potential of BHDC to spread into novel environments using computer modeling.

Specifically, quantitative studies have been used to predict suitable areas for establishment by modeling current expansion rates and various forms of information about BHDC from the literature (Chen et al. 2007; Cuddington et al. 2014), individual movement and tracking (Currie 2011), the environmental suitability of an area (Long et al. 2014; Goodwin et al. 1999; Ruesink 2005), and ecological niche modeling (Herborg et al. 2007; Kocovsky et al. 2012: Iguchi et al. 2004; Roura-Pascual et al. 2004). Studies have also employed georeferenced data sets and high-resolution computing tools to create sophisticated models for niche-generation at low cost and high speed (Herborg et al. 2007). For example, species distribution modeling (SDM) is an approach that uses empirical data from distribution patterns around the U.S. and a dataset of habitat predictor variables to describe distributions (Ferraz et al. 2012). These studies aim to contribute to preventing new introductions, which is the best way to avoid damages or control costs associated with an invasive species' introduction and establishment. When leveraged with control in currently invaded ecosystems, prevention policies can be one of the most powerful tools to manage invasive species (Olson 2006). They are also highly important because prevention measures (as opposed to control) contribute to roughly half of the federal expenditures (U.S.) made to manage invasive species (National Invasive Species Council 2001). However, it is increasingly apparent that BHDC can exhibit phenotypic plasticity in novel environments and have exhibited local adaptations that differ from ecological traits observed in their natural habitats (Coulter et al. 2013; Deters et al. 2012; Aliyev 1976). Confidence in these models is essential, and ecological research is needed to substantiate predictions and assure that wise project decisions can be made.

By updating existing knowledge on BHDC population demographics and pairing it with quantitative analysis of morphological plasticity, this study began to address the degree to which these models must update ecological data inputs to avoid the assumptions that BHDC maintain consistent behaviors among ecosystems, and that historical fitness and ecological factors will predict future population success. Ideal invaders typically exhibit considerable phenotypic plasticity and genotypic variation (Sax and Brown 2000; Elton 1958; Baker and Stebbins 1965; Sutherland 2004; Catford et al. 2009). Increased understanding of the potential for BHDC phenotypic plasticity through changed behavior and/or divergent traits from historical populations will provide a better picture of their capabilities to invade novel environments that may have previously been considered out of range and will help agency personnel prevent future introductions.

1.4 Bigheaded Carps as Ideal Invaders

Biological invasions have provided both ecologists and evolutionary biologists with an improved understanding of the limits to organismal adaptation and survival in novel environments. Historically, the literature on biological invasions has been focused primarily on the traits of invading species and environmental characteristics that increase vulnerability to invasion (Elton 1958; Baker and Stebbins 1965; Brown & Lomolino 1998; Sax and Brown 2000). Characteristics of successful invaders include four primary characteristics: 1) native origins from large and diverse continents (Darwin 1859), 2) broad phenotypic acclimatization to a wide ecological (and often geographic) range (e.g. Baker 1965; Forcella & Wood 1984; Moulton & Pimm 1986; Crawley 1987; Rejmanek 1996), 3) r-selected life history strategies (Crawley 1987), and 4) associations with anthropogenic habitats and disturbances (Baker 1965; Stebbins 1965).

1.4.1 Widespread Origins

BHDC are members of the fish family Cyprinidae, which is the largest family of vertebrate animals and includes almost exclusively freshwater fishes (Durand et al. 2002). BHC are native to eastern China, eastern Siberia, and North Korea, where mean annual air temperatures range from -4°C in the Manchurian Plain to 24°C in southern China (Kolar et al. 2005). SC are rather ambiguously reported to have origins in the large rivers of eastern China, eastern Russia, and southern reaches of Asia, as well as large lakes and rivers in China, northern Vietnam, and Siberia (Kolar et al. 2005). Both species have been widely and successfully introduced throughout much of eastern Asia.

In addition to being highly successful invaders within eastern Asia, both SC and BHC have been introduced to freshwaters around the world. The first known introductions from China to Taiwan were recorded in the early 18th century (Froese and Pauly 2004). SC have been imported or spread into over 88 countries and have currently established recruiting populations in 23 countries (Kolar et al. 2005). Most of these introductions were the result of aquaculture practices, although a substantial proportion of introductions resulted from biological control, fisheries, and “unknown” vectors. Their popularity in the aquaculture industry undoubtedly compounds the threat of invasion, as continual escapement from fish farms will provide a vector for introduction. In the U.S., 22 pathways for introduction have been identified, including intentional stocking, unsecure aquaculture facilities, domestic live transport, and illegal distribution, among many others (Conover et al. 2007; USACE 2014; Kocovsky et al. 2012). Studies are currently underway to develop alternatives for these pathways that would block or discourage the introduction of these species, but these alternatives are both socioeconomically complicated and costly (USACE 2014). Their success and establishment in so many watersheds is further testament to their substantial ability to acclimate to novel environments, and the broad variability of their native ranges is undoubtedly a contributing factor in their success.

1.4.2 Broad Tolerance/Plasticity

BHDC possess the inherent plasticity to acclimate to a wide variety of environmental conditions. They have expressed plasticity in a variety of ways, including behavioral changes not seen in native ranges, different life history strategies during stages of invasion, and opportunistic feeding. A consistent trend in the literature is that while BHDC may exhibit a certain behavior for the majority of their native range, they are capable of high biological plasticity in novel environments. For example, BHDC typically utilize lentic habitat like slow-moving rivers, lakes, and reservoirs for most of their adult lives in their native ranges, and previous literature has indicated that both species (especially SC) require river habitat for spawning (Kocovsky et al. 2012; Kolar et al. 2005; Coulter et al. 2013). Spawning requirements for BHC and SC have been documented to correlate with discharge and turbidity because BHDC egg buoyancy and exogenous feeding development require rivers of a minimum length of >100 km and a threshold velocity of 0.7 m/s for spawning (Krykhtin and Gorbach 1981, Kolar et al. 2005, Leslie et al. 1982). However, newer studies describe multiple and unpredictable spawning regimes, and while spawning is positively correlated with an increase in discharge and turbidity, it is often not a requirement for spawning to occur (Deters et al. 2013; Aliev 1976). Moreover, Coulter et al. (2013) found that BHDC in the MWR exhibited protracted spawning that was uncorrelated with rises in the hydrograph. Other studies have found that BHDC in the Lower Missouri River did not use tributaries or confluences of tributaries, as has been documented in previous studies on the Illinois River and Yangtze River in China (Kelly Baerwaldt, Fish Biologist USACE, personal communication, 2010; Deters et al. 2013; Chang 1966; Huet 1970). These findings may demonstrate even greater potential for plasticity in and successful establishment by BHDC.

In addition to variable conditions for spawning, many previous studies on BHDC population demographics have revealed differences in growth, age, condition, length, and GSI between and within river systems. These studies include the middle Mississippi River (Williamson and Garvey 2005), the Gavin’s and Interior Highlands reach of the Missouri River and its tributaries (Wanner and Klumb 2009; Hayer et al. 2014(a)), and the La Grange and Peoria reaches of the Illinois River (Irons et al. 2007; Garvey et al. 2012; Stuck et al. 2015). Preliminary comparison of studies on BHDC aligns with previous literature on the subject (Feiner et al. 2011) and suggests that invasion stage has been largely correlated with success, and establishing or newly established populations display higher fitness, faster growth, and more reproductive potential than central populations.

BHDC have broad environmental tolerance, thriving in variable temperatures and salinities, and they are also highly opportunistic planktivores (i.e., they are able to adjust their food ingestion to match what is most available; Sparatu and Gophen 1985). BHDC can endure extremes in temperatures for spawning (a highly temperature-sensitive activity) from 14-15°C in the Lower Volga River, Russia, to 26-30°C in the Yangtze River (Chang 1966; Opuszynski and Shireman 1995). SC display similar tolerance ranges, with upper lethal temperatures for larvae around 46.5°C and overwintering temperatures of 0°C (Kolar et al. 2005). Both species can tolerate brackish waters, and BHDC larvae display some form of osmoregulation. While reports of salinity tolerance have been conflicted, both species have nonetheless displayed an ability to utilize estuarine areas, a specialization that may allow BHDC to occupy and spread to new habitats (Schildhauer 1986).

1.4.3 R-selection

High fecundity, rapid growth rates, large reproductive output early in life, high dispersal capability, and high density are all life history traits commonly exhibited by r-selected species (DeGrandchamp et al. 2008). The fecundity of BHDC is remarkable and has been well studied because of their significance in the global aquaculture industry. Depending on the size and distribution of the fish, fecundity has ranged from 145,000 - 2,000,000 eggs per female fish between 3.18 kg and 8.51 kg (Singh 1989). One study used hydroacoustic survey transects to measure the density of BHDC in the Illinois River and found on average 2,800 BHDC per river mile (4,666 pounds/mile), comprising over 63% of the total biomass of native and invasive fishes in the river (Roth and Secchi 2012). The BHDC population in the Illinois River is growing exponentially (Chick and Pegg 2001; Tsehaye et al. 2013) and has been recognized as one of the densest in the world (Sass et al. 2010). Growth and maturation is related to water temperature and is very rapid relative to other fish species of similar size. In captivity, SC displayed a 17-fold increase in weight in 78 days (Stott and Buckley 1978). SC in some reaches of the Mississippi River have been known to exhibit much faster growth rates compared to those found in the Amur River, Russia, and Gobind Sagar Reservoir, India (Williamson and Garvey 2005). High dispersal capability in BHDC can be assumed because of the interconnectedness of the MRB that effectively exposes over 40% of the U.S. to BHDC invasion. If BHDC are able to become established in the GLB, the environmental consequences are expected to be severe (Schrank et al. 2003; Irons et al. 2007; Sampson et al. 2009; Tsehaye et al. 2013).

1.4.4 Association with Habitat Disturbance

Previous literature has shown that ecosystems in the U.S. that are vulnerable to the establishment of invasive species typically correlate with anthropogenic disturbances and degradation of river habitat (Kolar and Lodge 2001; Calkins et al. 2012). The spread and success of invasive plants, animals, fish, and other organisms have depended on the movement of humans and the trade of goods and services around the world as vectors for introduction into new habitats (Olson 2006), and for many years human land use has compounded the threat of invasive species by pervasive habitat degradation (Hobbs 2000; Klug et al 2014). The Illinois River watershed drains portions of land in Illinois, Wisconsin, and Indiana and has major environmental issues with siltation, nutrients, suspended solids, and flow alterations attributed to agriculture and widespread dredging, dam, and wing dyke construction for navigation and flood control (USACE 2002; USACE 2000). Annually, 13.8 million tons of sediment are delivered from the watershed area to the Illinois River and 8.6 million tons outflow from the Illinois River to the Mississippi River (IEPA 1996). It is highly likely that the altered flow regime and anthropogenic impacts are associated with the major success of BHDC carp establishment in the Illinois River.

The four primary characteristics of ideal invaders provide an accurate summary of BHDC life history and their capacity for success in the U.S., and there are many studies that document the demographics of carp, their behavior in the field, and their effects on native fish species. BHDC can invade a wide variety of habitats, and I will now describe how this study aimed to quantify their capacity for plasticity.

1.5 Assessing Silver Carp Traits in Divergent Rivers

As previously discussed, BHDC have established hugely successful populations under various selective factors within MRB tributaries. They have also been shown to exhibit unexpected behaviors that vary from historical observations within their native ranges (Coulter et al. 2013; Chapman and George, 2011; Williamson and Garvey, 2005). In Robin Waples seminal paper (1991) outlining evolutionarily significant units, four important factors are identified as important for determining the genetic diversity of a species in a specific habitat: genetic traits, phenotypic traits, life-history traits, and habitat characteristics. These four characteristics are crucial to providing a comprehensive understanding of organism's behavior within changing ecological systems. I attempted to address three of these factors: 1) phenotypic traits through adult body morphology, 2) life history patterns through population demographics, and 3) a brief qualitative analysis of the ecological and hydrological characteristics of the Illinois River and MWR. Two of these factors, phenotype and life history, are known to be affected by the environment, and understanding environmental versus genetic effects on these traits is a major question in evolutionary biology (Endler 1986). However, genetic analysis falls outside of the scope of this paper, although it is an ideal subject for further study.

1.5.1 Phenotypic Plasticity – Geometric Morphometrics

A well-known expression of plasticity among fish populations is body shape. Fish morphology is most often associated with adaptation to different environmental demands that result in predictable relationships between ecology and morphology, even at the population level (Park et al. 2013). These morphological differences can be driven by predation pressure (Domenici et al. 2007; O'Steen et al. 2002), resource use (Larson 1976; Franchini et al. 2014), and the hydraulic environment (Drinan et al 2012; Scarnecchia 1988; Statzner 2009; Myers and Belk 2014) and allow for increased success in a particular habitat. Landmark-based geometric morphometrics is used to validate differences between body structures and quantify the differences between individuals that are often invisible to the eye. The field of morphometrics has grown substantially over the past decade. Pioneer studies began with emphasis on allometry, or biological scaling (Huxley 1932), and were expanded to include comparisons between populations of organisms in different geographic areas (Templemen 1935). The scope of study grew to take into account environmental and organismal variables, and researchers developed a large number of statistical techniques to properly analyze their data (Caldrin and Friedland 1999). The use of digital imagery techniques enabled researchers to design software and studies that could seamlessly perform accurate calculations by eliminating redundancy and unevenness of body form. For this study, I focus on using landmark analysis, a form of geometric morphometrics that employs trigonometric functions to represent coordinate systems with particular landmarks points to quantify deformations among individuals (Zelditch et al. 2004). I aimed to generally link these deformations to environmental and population variables within the analysis.

Threespine stickleback (*Gasterosteus aculeatus*) population studies have been of particular importance in the past decade because they have provided excellent case studies of morphometric variation among intraspecific populations through their ability to facilitate evolutionarily adaptive traits between habitats (Walker 1997; 1997; Caldrin and Friedland 1999; Hendry 2011; Kaeuffer et al. 2012; Kitano et al. 2007; Kristjansson 2005; McCairns and Bernatchez 2012). Interpreting these patterns of variation within wild populations is often difficult, as environmental variation and possible neutral selections result in conclusions that can be dangerously close to misinterpretation. The challenge lies in separating the phenotypic response to environment from the genetic response (McCairns and Bernatchez 2012). Through geometric morphometrics, my study attempted to address the plastic component of evolutionary adaptation and made no claim to understanding the genetic divergence of fish between the two river systems.

Environmental effects can strongly influence phenotypic displays, and in particular, water flow, velocity, and frequency of flooding select for certain body types depending on the species niche within the water column (Langerhans 2008; Myers and Belk 2014). As previously mentioned, both the Wabash River and the Illinois River have had a long history of overcoming anthropogenic disturbance, but the Illinois River has suffered irreversible changes through the impoundment and control of the river system for commercial navigation purposes (Lian et al. 2012), while the Wabash River remains relatively well connected to its floodplain (Pyron and Lauer 2004). Hydrodynamic characteristics of fish body types have been shown to link high swimming performance (e.g. low drag or high critical swimming speeds) to high velocity habitats, while higher drag morphs utilize a wide range of habitats (Li et al. 2009; Sagnes and

Satzner 2009; McLaughlin & Grant 1994; Bourke et al 1997; Dynes et al 1999; Boily and Magnan, 2002). In terms of specific body structure, the shape of the highest performing fish body type often depends on the niche that the fish occupies and the factors (in addition to flow) to which it is reacting. For example, Scharnweber et al. (2013) found that when exposed to predators throughout growth, shallow-lake roach (*Rutilus rutilus*) developed a slender body, a more posterior dorsal fin, and relatively shallow anterior body that was the most advantageous for flight during high-energy swimming bursts, or "C-starts." Other studies have found that the streamlined, fusiform body type reduces drag and allows for prolonged swimming (Gosline 1971; Langerhans 2008). However, it has also been found that fish with deeper body forms have the advantage in swimming performance that is attributable to a wide range of selective factors such as muscle mass (Crucian carp, *Carassius carassius*; Domenici et al. 2008), a slower rate of growth (common carp, *Cyprinus carpio*; Li et al. 2009), the presence of predators (Langerhans et al. 2004; Hendry et al. 2006), and a niche within structurally complex habitat or the need for unsteady or burst swimming behaviors (Langerhans and Reznick 2007; Myers and Belk 2014).

1.5.2 Life History Characteristics – Growth, Condition, Length-Weight Curves

As previously outlined in this chapter, life history characteristics of BHDC populations have been particularly well studied as their density in the MRB and tributaries increased exponentially over the past few decades. Through the ACRCC, many Federal agencies like the U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, and U.S. Environmental Protection Agency have coordinated studies and literature reviews to give a state-of-the-science for current BHDC knowledge and provide information on their biological characteristics in the MRB and on the borders of their ranges (MRWG 2015). In addition to this new work in U.S. habitats, both species are important to aquaculture and have been well studied in culture experiments for many years. BHDC can exhibit fast growth rates in productive waters, with BHC attaining 2.7 kg in <1 y (Waterman 1997) and SC attaining 5.4 kg in 1 y (Henderson 1979). According to the literature, growth rates of BHC collected from the lower Missouri River in 1998-1999 were higher than those of fishes stocked from Poland (Schrank and Guy 2002), but smaller than those collected by Nuevo et al. (2004) from the Mississippi River around the same time. SC collected from the middle Mississippi River grew much faster than those in the Gobind Sagar Reservoir, India (Tandon et al. 1991) and the Amur River, Russia (Nikolskii 1961; Williamson and Garvey 2005). More recent studies have found that SC in the tributaries of the Missouri River in South Dakota grew much more slowly than those found farther south in the middle Mississippi River, but they reached much larger lengths, with an asymptotic length (or maximum mean length) of 1,223 mm (Hayer et al. 2014) as opposed to 778 mm in the middle Mississippi River (Williamson and Garvey 2005). The BHDC populations in the Illinois River have been declining in condition and growth rate over the past decade and have possibly surpassed carrying capacity (Irons et al. 2011; Garvey et al. 2012; Tsehaye et al. 2013; Stuck et al. 2015). There are several explanations for these differences in growth rates and asymptotic lengths, including density dependence (Kolar et al. 2005; Williamson and Garvey 2005), length of growing season, system productivity (Schrank and Guy 2002), and study-specific aging techniques (DeVries and Frie 1996). A summary of available life history demographics for selected rivers through time is presented in Table 1.1. These demographics present a general decline in growth and condition in well-established populations in the Illinois River, and an increase or general stability in growth of newly established populations like the Mississippi River in the early 2000's (Williamson and Garvey 2005) or the Missouri River (Wanner and Klumb 2009; Hayer et al. 2014a).

Table 1.1 A summary of findings for growth characteristics, GSI, and length-weight ratios for silver carps sampled from river systems in the US.

		Von Bertalanffy Coefficients			Log $_{10}$Length – Log$_{10}$Weight coeff			Gonado-somatic Index		Total	
River & Reach	***Sampling Year***	L_{inf} ***(mm)***	***K***	T_0 ***(yrs)***	***b***	***a***	R^2	***Female***	***Male***	***N***	***Reference***
Lower Wabash River	2011	774	0.55	-0.45	__	__	__	__	__	251	Stuck et al. 2015
Illinois River											
Illinois River, *La Grange*	1990-2006	__	__	__	3.12	-5.3	0.81	__	__	500	Irons et al. 2007
Illinois River, *La Grange*	2010-2011	__	__	__	3.03	-5.1	.95	0.61-1.39	0.21-0.9	582	Garvey et al. 2012
Illinois River	2011	874	0.25	-0.61	__	__	__	__	__	605	Stuck et al. 2015
Missouri River											
Gavin's Point	2003-2007	__	__	__	3.70	-6.9	0.97	__	__	7	Wanner and Klumb 2009
Interior Highlands,	2003-2007	__	__	__	3.13	-5.4	0.93	__	__	68	
South Dakota Tributaries	2009-2012	1,223	0.17	NA	__	__	__	__	__	334	Hayer et al. 2014
Big Sioux	2009-2012	__	__	__	3.21	-5.5	0.98	__	__	__	
Vermillion	2009-2012	__	__	__	2.9	-4.8	0.98	__	__	__	
James River	2009-2012	__	__	__	3.11	-5.2	0.96	__	__	__	

Table 1.1 continued.

River & Reach	***Sampling Year***	***L_{inf}***	***K***	***T_0***	***b***	***a***	***R^2***	***Female***	***Male***	***N***	***Reference***
Mississippi River											
MMR	2003	778	0.63	.16	3.11	-5.3		0.01-0.13	__	69	Williamson & Garvey 2005
Confluence of MMR and Illinois River,	2004-2005	867	0.41		3.27	-5.7		0.02-0.15	__	26	Williamson & Garvey 2005

1.5.3 Habitat Characteristics – Study Area

Analyzing habitat characteristics is important because distinctive habitat features often explain unique adaptations between local populations (Waples 1991). Again, I caution that inferences on phenotypic plasticity based solely on habitat characteristics must be backed by a wide variety of biological information to support any definite conclusions. Because my study did not involve detailed genetic analysis, I only made general observations between habitat characteristics and any observed local adaptations in BHDC. I did not quantitatively analyze the differences in flow regime between the Illinois River and the MWR, but there have been a few studies that have explored each river's unique characteristics, and I review them below.

The Illinois River is a major tributary of the MRB with a watershed area of 72,701 km^2 (Lian et al., 2012). It is heavily utilized for navigation, and the Chicago Sanitary and Ship Canal (CSSC) supports regional commerce by connecting the GLB and MRB (Changnon and Changnon 1996). The CSSC is responsible for a high rate of flow diversion from Lake Michigan and has a strong influence on the low flow of the upper portion of the Illinois River (Lian et al. 2012). In addition to the canal, six drainage districts and seven locks and dams have been constructed along the Illinois River, ranging in head from 1.5-12.2 m (USACE 2004). To accommodate commercial navigation traffic, a channel depth of at least 2.74 m must be maintained throughout, and rock wing dams, bank revetments, and channel training structures have been constructed along the river to reduce dredging requirements by limiting bank erosion and forcing flow into the main channel of the river (USACE 2002; USACE 2000). These channel modifications have resulted in unnatural timing of high and low water levels in addition to significantly altering flow regimes (Lian et al. 2012; Koel et al. 2002). In addition to its utility for shipping, the Illinois River's connectivity to the GLB via the CSSC has also served as a regional conduit for AIS transfer from the GLB to the MRB, including zebra mussels (*Dreissena polymorpha*) and round goby (*Negobius melanostomus*). BHDC were detected in the Illinois River in 1998 (USGS 2012), and the river is now recognized as the most direct mode of introduction from the MRB to the GLB. It has thus become the focus of aggressive and expensive prevention measures, most notably the electrical fish barriers (Jerde et al. 2011; Moy et al. 2011).

The Wabash River is the Ohio River's second largest tributary. It drains a watershed area of 85,340 km^2 and encompasses the longest stretch of free-flowing river (i.e., 662 km) east of the Mississippi River (Gammon 1998; White et al. 2005; Heimann, 2011). There are numerous dams on Wabash River tributaries, although only one dam exists on the main stem at river kilometer (rkm) 662 to form J. Edward Roush Lake (Pyron et al. 2006). According to Pyron and Lauer (2004), the Wabash River has remained relatively unchanged and connected to its floodplain, although water clarity and quality has been affected by anthropogenic activities such as agricultural discharge and point source pollution. The Clean Water Act of the early 1970's and the Payment-In-Kind program of 1983, along with increased awareness of agricultural runoff, have alleviated some of the historical issues with pollution loadings (Pyron et al. 2006; Gammon 1998). The Wabash River is characterized by relatively shallow water depths for most of its length and high flow variation, with riffle-pool sequences upstream and extensive runs with relatively few distinct riffles downstream (Pyron and Lauer 2004). BHDC were first documented in the Wabash River in 2003 (Chapman and Hoff 2011). A comparison of Wabash and Illinois River characteristics is provided in Table 1.2.

Table 1.2 Hydrogeomorphic characteristics of the Illinois and Wabash Rivers

Characteristic	**Wabash River**	**Illinois River**
Drainage Area *(km^2)*	85,340	72,700
Length *(km)*	810	439
Mean total discharge *(cms)*	1000	657
Mean discharge at sample site gauges, 1989-2014 *(cms)*	Henry, IL 419 (USGS 2015)	Lafayette, IN 222 (USGS 2015)
Median annual sediment load *(million metric tons/Mt)*	11.5 (Heiman et al. 2011)	5.9 (Heiman et al. 2011)
Median annual streamflow *(m^3/s)*	967 (Heiman et al. 2011)	765 (Heiman et al. 2011)
First silver carp detection	2003 (USGS 2015)	1989(USGS 2015)

1.6 Addressing Current Needs

BHDC have been extremely successful in becoming established in the MRB, and it is expected that they will continue to push their range boundaries eastward, westward, and northward towards the GLB and surrounding tributaries. BDHC have been well studied at various stages of their invasion because of their enormous success and devastating ecological effects on invaded river systems, and new studies are revealing a surprising amount of variation in life history strategies throughout invasion stage and emerging plasticity in behavior between river systems. Body morphology is a well-known approach to quantifying plasticity by mathematically capturing the population diversity based on both individual characteristics and environmental factors. I sought to quantify the degree of plasticity that BHDC are capable of through geometric morphometrics so that future range expansion modeling efforts and prevention measures can be updated to include a wider range of plasticity, if necessary. Of all river systems studied in BHDC assessments thus far, the MWR and Illinois River provide excellent case study river systems because they vary in both stage of invasion for SC populations and hydrogeomorphic conditions. If SC populations are undergoing plastic adaptation, then it is highly likely that any trends would be captured through morphometric analysis between these two river systems.

CHAPTER 2. MORPHOLOGICAL PLASTICITY OF INVASIVE SILVER CARP IN TWO DIVERGENT MIDWEST RIVER SYSTEMS

2.1 Introduction

Aquatic invasive species (AIS) are substantial threats to global freshwater biodiversity, and the consequences of their introductions and subsequent establishment are often catastrophic for invaded ecosystems (Conover et al 2007; ACRCC 2014). Aquatic habitats are especially vulnerable to AIS invasions due to their widespread anthropogenic degradation (Rahel 2002; Alcaraz et al 2002), and the Mississippi River Basin (MRB) has been particularly impacted by numerous aquatic invaders (Patel et al. 2010). Some of the most significant effects have resulted from the introduction and establishment of bigheaded carp (BHDC), including silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis* (Patel et al. 2010). BHDC are highly invasive fishes that have become established throughout the middle and lower MRB, and the direct connection from the Illinois River to Lake Michigan through the Chicago Area Waterway Systems (CAWS) has led to considerable concern about their establishment in the Laurentian Great Lakes. Successful establishment of BDHC in the Great Lakes would endanger diverse ecosystems that currently support commercial, recreational, tribal, and sport fisheries worth billions of dollars in revenue for both the U.S. and Canada (Ricciardi et al. 2011; Cudmore et al. 2012). It would also allow BHDC to expand their range into viable Great Lakes tributaries (Kocovsky et al. 2012; Cooke and Hill 2010; Stuck et al. 2015).

Many strategies and management plans have been conceived in response to ongoing concerns about BHDC range expansion, as well as long term solutions for controlling these AIS (ACRCC 2014). These plans include the development of physical and chemical control tools and the identification of vulnerable pathways by identifying waters at high risk of invasion and establishment (ACRCC 2014; USACE 2014). Modeling studies are critical tools for predicting potential BHDC range expansion and establishment in areas of interest such as the Great Lakes Basin (GLB; Chen et al. 2007; Cooke and Hill 2010; Cuddington et al. 2014; Goodwin et al. 1999; Ruesink 2005; Kocovsky et al. 2012, etc.). These studies predict suitable areas for establishment utilizing various information about BHDC, including data from previous studies in both native ranges and MRB tributaries (Chen et al. 2007; Cuddington et al. 2014; Oh 2014), individual movement and tracking (DeGrandchamp et al. 2008; Currie 2011), the environmental suitability of an area (Goodwin et al. 1999; Ruesink 2005), and ecological niche modeling (Herborg et al. 2007; Kocovsky et al. 2012; Iguchi et al. 2004; Roura-Pascual et al. 2004). Such models are quick, relatively inexpensive, data-driven tools that allow fisheries managers and agencies to make decisions on prevention measures. Prevention is one of the most cost effective management techniques for invasive species (Olson 2006), and therefore, confidence in these models is essential. However, because these models are based on historical and/or observational data about BHDC, it is necessary to substantiate data inputs with ongoing ecological field research.

Successful establishment of BHDC and other AIS can be affected by many factors, including intraspecific competition, recruitment, food resources, and hydrologic condition. Recent literature has demonstrated that BHDC on the boundary of their range expansion (i.e., edge populations) exhibit population characteristics different from core populations in the middle and lower MRB (Stuck et al. 2015; Hayer et al. 2014a). For example, the Illinois River currently sustains what are likely the highest SC densities in the world (Sass et al. 2010), and collective BHDC populations are undergoing intense density dependent population regulation and limited food resources there (Schrank et al 2002; Sampson et al. 2009; Irons et al. 2011). In a recent study that directly compared Illinois River fish with lower Wabash River (LWR) fish, SC densities in the LWR were found to be 3X less than those in the Illinois River, and LWR fishes are also larger, exhibit higher condition, grow faster, and live longer than Illinois River silver carp (IRSC, Stuck et al. 2015). Edge populations also face stage dependent challenges as invasion progresses (Crooks 2005). As an example, SC densities are increasing in northern Missouri River tributaries on the northwestern most range of BHDC expansion, and individuals in these populations exhibit faster growth rates than fishes from native ranges (Hayer et al. 2014a). However, these SC are typically smaller than fishes found in other reaches of the upper MRB and could possibly be limited by the comparatively harsh conditions of prairie stream ecosystems.

In addition to displaying stage dependent changes in demographics, invasive BHDC have also exhibited unexpected plasticity in multiple traits among invaded ecosystems (e.g., Coulter et al. 2013; Deters et al. 2012; Aliyev 1976). For example, phenotypic plasticity in spawning behavior related to hydrology was documented in both the middle

Wabash River (MWR, Coulter et al. 2013) and tributaries of the lower Missouri River (Deters et al. 2012) that contradicts expected spawning requirements based on studies within the species' native ranges (Yi et al. 1998; Schrank et al 2002; Zhang et al. 2000; Kolar et al. 2005). The consistent phenotypic responses exhibited by BHDC across invaded ecosystems suggest that they are able to express traits differentially to increase invasion success across rivers that are drastically different in hydrology and ecology. These examples make a strong case for continued research to understand the plasticity of life history and ecology of BHDC and other AIS in invaded ecosystems because such plasticity, while being highly adaptive from an evolutionary perspective, also allows for rapid acclimation to a much wider variety of environmental conditions than may be recognized based solely on the expression of traits in a given species' native range (Sax and Brown 2000).

Differences in body shape are another common expression of phenotypic plasticity among fish populations. The landmark-based, geometric morphometrics approach to assessing differences in body morphology allows users to capture and validate disparities between body structures, and it can quantify the plastic component of adaptation with applications in fisheries management by analyzing differences between individuals that are otherwise undetectable (Chen et al. 2009; Yong et al. 2012; Doadrio and Perdices, 1997; Dwivedi and Dubey, 2013). As an example, the well-studied threespine stickleback species complex demonstrates the considerable role that morphological plasticity has played in tropic radiation among geographically separated populations (Walker 1996; 1997; Caldrin and Friedland 1999; Hendry 2010; Kacuffer 2012; Kitano et al. 2007; Kristjansson 2005; McCairns and Bernatchez 2012). This species complex has provided excellent case studies of morphometric variation between intraspecific populations through their ability to facilitate environmentally adaptive traits between habitats. While there are many studies on interspecific and intraspecific populations of fish, there is a paucity of information on the morphological plasticity of invasive fishes.

While morphological plasticity and adaptation are important factors contributing to evolution and persistence of species in their native ecosystems, they are also mechanisms that can facilitate AIS expansion and establishment in novel environments. As previously discussed, invasive BHDC have exhibited surprising phenotypic plasticity that has allowed these species to continue spreading through the hydrogeomorphically diverse MRB and, more recently, the Ohio River Basin. The potential for their establishment in Great Lakes tributaries hinges on their ability to adapt to novel environments that, in general, have more variable flow conditions, lower water temperatures, and lower productivity than much of the MRB they currently inhabit. Past studies on various fish species have demonstrated that morphological adaptation of BHDC to these novel conditions is highly possible, although similar studies of morphological plasticity in BHDC have not been published to date. Recognizing BHDC potential for morphological adaptation to variable hydrogeomorphic regimes would make evaluating the likelihood of establishment in GLB tributaries, upper Mississippi River reaches, and other non-invaded freshwaters much more powerful.

The Illinois River and MWR are largely contrasting hydrogeomorphic environments in which BHDC have become established. The first reported occurrences of SC in these rivers were temporally similar, but IRSC population densities increased very rapidly (Chick and Pegg 2001), and in some reaches of the Illinois River, SC compose over 95% of the total biomass (MIRCA 2002). IRSC have been intensely studied over the past decade given that the Illinois River is the most direct connection between the MRB and GLB. As mentioned before, densities of silver carp in the LWR are considerably less than those in the Illinois River, and establishment has taken considerably longer. The Wabash River forms the northeast front of BHDC invasion and is one of two MRB tributaries through which invasion of Lake Erie may occur (Hayer et al. 2014b; ACRCC 2015; Sass 2010). The Illinois River and MWR are of particular interest because they are hydrogeomorphologically divergent rivers with established BHDC populations that threaten to invade the GLB. The Illinois River has been irreversibly affected by channelization, levees, and dams for commercial navigation purposes that have resulted in hydrological and channel alterations from lotic to lentic habitats (Bunn and Arthington 2002), shifts in fish assemblages (Koel and Sparks 2002), and increases in phytoplankton production (Rolls et al. 2012). In contrast, the MWR is controlled but still relatively well connected to its floodplain compared to most midwestern rivers (Pyron and Lauer 2004). It is characterized by riffle-pool sequences during summer low flows and a swift, shallow channel that strongly contrasts the Illinois River (Gammon 1998). Past studies of potential relationships between fish body morphology and environmental factors have demonstrated that morphological changes often improve swimming performance among diverse habitats (Li et al. 2009; McLaughlin & Grant 1994; Bourke et al. 1997; Dynes et al. 1999; Boily and Magnan, 2002). It is therefore possible that the hydrogeomorphological differences between the Illinois and Wabash Rivers have selected for divergent SC body shapes in resident fishes.

The rivers are hydraulically connected through the MRB and are separated by roughly 530 rkm (NREL 2015). Despite this large spatial separation, BHDC can move over large distances (DeGrandchamp et al. 2008), and gene flow between the two rivers may occur. Any diversification between IRSC and WRSC populations can be considered a plastic response to the environment and not a neutral process owing to geographic isolation (Scharnweber et al. 2013).

I examined the potential for SC to express trait plasticity between the Illinois and MWR as examples of hydrogeomorphically divergent, invaded rivers. I did not seek to establish causality for specific environmental characteristics to elicit plasticity in SC traits. Rather, my goal was to evaluate differences in body morphology and population demographics to demonstrate proof of concept that divergent novel river habitats elicit differential plastic expression of these traits in invasive SC. I hypothesized that SC would exhibit body shapes specific to the river from which they were captured. Specifically, I expected MWRSC to have deeper bodies and more streamlined, fusiform shapes associated with greater swimming performance in higher velocity habitats compared to IRSC that inhabit generally deeper, lower velocity habitats. And because the MWRSC are an edge population, expected MWRSC to be in better condition, have longer lifespans, exhibit higher growth rates, and have higher gonadosomatic indexes (GSI) than IRSC (Weber et al. 2015; Hayer et al. 2014b; Stuck et al. 2015). Such demonstrated plasticity in SC between these divergent rivers would stress the importance of considering phenotypic plasticity as a factor when estimating range expansion and establishment success for BHDC and other AIS.

2.2 Methods

2.2.1 Data Set

Fishes used in this study were collected during summer 2013. Collection efforts for IRSC were coordinated with researchers from the University of Illinois, and fishes were collected using multiple gear types, including electrofishing, trammel nets, hoop nets, and gill nets in the Peoria Pool near Henry, IL (estimated rkm 312-315). BHDC are notoriously difficult to capture using traditional sampling gears (Conover et al. 2007; Stancill 2003; Wanner and Klumb 2009). It has therefore been suggested that non-traditional methods (e.g., bowfishing) may be more efficient in capturing large numbers of BHDC, although standardization issues must be considered for calculating some metrics such as relative abundance (Conover et al. 2007; Wanner and Klumb 2009). Because I was only interested in measuring the morphology of a subsample of adults and their associated life history characteristics, I decided to focus on data collected from fishes that were captured during bowfishing tournaments in both rivers. ILSC were collected at the Illinois Bowfishing Association’s Directors Tournament near Starved Rock State Park (estimated rkm 381-393) in July 20, 2013. The locations and densities of SC in the Wabash River are sporadic and highly dependent on the hydrograph (Goforth et al. 2011), so efforts to capture fishes using traditional gears (e.g. electrofishing and gill nets) were relatively limited. Collection efforts were therefore focused on two bowfishing tournaments: Americus, IN, in August (rkm 519) and Attica, IN, in September (rkm 473). A summary of the total counts of fish collected can be found in Table 2.1.

Immediately following collection at the bowfishing tournament weigh-ins, SC were euthanized using MS222 and a photograph was taken of the right side of each specimen with a ruler for scale reference. Photographs were captured with a Nikon L105 fitted to a stationary camera stand to ensure that each specimen's photograph was captured a consistent plane. Specimens were then measured for total length (mm), weighed (kg), sexed, gonads were removed and weighed, and finally, they were assessed for hybrid characteristics. Fishes were classified as pure silver carp (PSC) if they displayed no hybrid characteristics, and as hybrid silver carp (HSC) when the degree of overlap between the pectoral fin and the origin of the pelvic fin base was >0.2 cm and/or when twisted or clubbed gill rakers were present (Kolar et al 2005; Lamer et al 2010). Gonads were removed, blotted dry, and weighed (g). Postcleithrum bones were removed, cleaned, and placed in a dry envelope for aging at a later date (Johal et al. 2001).

Previous studies have used pectoral fin rays to estimate BHDC age (Williamson and Garvey 2005; Shrank and Guy 2001), but many aging structures yield similarly accurate results in adult carps depending on the research needs (Johal et al. 2001). I used postcleithra as aging structures because they are both accurate and time-efficient during removal and analysis (Seibert 2013; Stuck 2012; Johal et al. 2000). Dried postcleithra were transverse sectioned from the middle of the postcleithrum using an Isomet low speed saw (Buehler, Lake Bluff, IL) with a diamond wafering blade and mounted to glass slides (Johal et al. 2000). Each section was polished using increasingly fine grade of sandpaper to a thickness between 0.3 to 0.5 mm and photographed under magnification using a Nikon SMZ1500 stereomicroscope (Nikon Instruments, Inc., Melville, NY, USA). The photographs were adjusted for clarity and contrast between opaque and hyaline zones in the growth rings. Two independent readers counted annuli on each specimen and discrepancies were fixed by a third independent reader.

Table 2.1 Total numbers of pure silver carp (PSC) and hybrid silver X bighead carp (HSC) sampled from the Illinois and middle Wabash Rivers from June to September 2013. Number of individuals collected are presented according to gear used for capture (i.e. "bowfished" and "other gears" (i.e., trammel nets, hoop nets, and electrofishing)), sex, and age determined from excised and sectioned postcleithra.

Illinois River (n = 221) – July Sampling

PSC (n=80)				HSC (n=141)			
Bowfished		Other Gear		Bowfished		Other Gears*	
23		**57**		**29**		**112**	
M	F	M	F	M	F	M	F
10	13	**21**	**36**	**23**	**6**	**72**	**40**
(3+) **1**	*(3+)* **4**	*(3+)* **4**	*(3+)* **3**	*(3+)* **4**	*(3+)* **1**	*(3+)* **7**	*(3+)* **5**
(4+)4	*(4+)* **5**	*(4+)* **4**	*(4+)* **14**	*(4+) 12*	*(4+)* **3**	*(4+)22*	*(4+)* 15
(5+) 3	*(5+) 3*	*(5+) 3*	*(5+) 5*	*(5+) 4*	*(5+) 0*	*(5+) 12*	*(5+) 4*
(6+) 2	*(6+) 1*	*(6+) 1*	*(6+) 1*	*(6+) 2*	*(6+) 0*	*(6+) 1*	*(6+) 1*
(7+) 0	*(7+) 0*	*(7+) 0*	*(7+) 0*	*(7+) 1*	*(7+) 0*	*(7+) 1*	*(7+) 0*
		**9 not aged*	**12 not aged*			**29 not aged*	**15 not aged*

Middle Wabash River (n = 143) - June, Ausgust, September Sampling

PSC (n=93)				HSC (n=50)			
Bowfished		Other Gear		Bowfished		Other Gears*	
61		**32**		**48**		**2**	
M	F	M	F	M	F	M	F
24	**37**	**18**	**14**	**37**	**11**	**2**	**0**
(3+) 5	*(3+)* 5	*(3+)* 2	*(3+)* 2	*(3+)* 2	*(3+)* 0	*(3+)* 2	*(3*
(4+) 10	*(4+)* 17	*(4+)* 7	*(4+)* 4	*(4+)* 12	*(4+)* 3	*(4+)* 0	*(4*
(5+) 3	*(5+)* 6	*(5+)* 2	*(5+)* 2	*(5+)* 8	*(5+)* 2	*(5+) 0*	*(5*
(6+) 3	*(6+)* 4	*(6+) 0*	*(6+)* 2	*(6+)* 5	*(6+) 2*	*(6+) 0*	*(6*
*(7+)*1	*(7+)* 4	*(7+)* 1	*(7+)* 3	*(7+)6*	*(7+) 2*	*(7+) 0*	*(7*
**2 not aged*	*1 not aged	*6 not aged	*1 not aged	**4 not aged*	*1 not aged		

*The number of HSC captured using other gear in the Wabash was too low to provide an accurate comparison and was thus not included in the morphological analysis across rivers.

2.2.2 Life History Analysis

I investigated length – at – age, fish condition, and reproductive condition (i.e., GSI) as potential factors influencing body shape in SC in the Illinois River and MWR. Data used for these analyses were taken from fishes captured using different gears and during different sampling months (Illinois: wide variety of sampling gear and bowfishing, July; Wabash: electrofishing and bowfishing, June, August, and September). These differences could result in sampling bias; therefore, life history analysis was only presented as demographics for each population and I did not make statistical comparisons between rivers. Condition was determined based on the linear regressions of total length and weight for each river. (Wanner and Klumb 2009; Hayer et al. 2014a; Garvey et al 2012). GSI was calculated for both males and females (GSI= 100* gonad weight [g]/body weight [g]) (Crim and Glebe 1990) and linear regression was used to describe the relationship between GSI and fish total length (Shrank and Guy 2001).

2.2.3 Shape Analysis

I explored shape variation in bowfished SC from the Illinois River and MWR using morphometric techniques to determine whether fish morphologies differed between the rivers. Morphometric analysis utilizes landmarks selected for a particular species that define a truss, or a set of measures that give an even coverage of both the vertical and horizontal directions of the organism (Wimberger 1990). For SC, I selected a set of ten landmarks from individually homologous anatomic loci that have been highly utilized in fish morphology studies (Figure 2.1; Strauss and Bookstein 1982*;* Bookstein et al. 1985; Ujjania and Kohli 2011; Myers and Belk 2014). The landmarks from the right side of each fish were digitized using tpsDig software (Figure 2.1; Rohlf 2003b). Many fish morphology studies have had issues with dorso-ventral arching of the body as a result of fixation or during the process of death (Franchini et al 2014; Valentin et al. 2008; Fruciano et al. 2011, 2012; Franssen 2011).   Analysis of the data indicated that the upward/downward arching of the caudal peduncle strongly affected morphological assessment in specimens. To avoid confounding non-biological effects due to the bending of specimens, a program within tpsUtil software (Rohlf 2003a) was used to unbend specimens by fitting a quadratic curve through a designated set of landmarks (pictured in Figure 2.1) from the snout to the center of the caudal fin and then straightening the curve. These landmarks were then removed for subsequent analysis. Landmarks were then resized using the reference ruler in the photograph and imported into MorphoJ software for morphometric analysis (Klingenberg 2011). All subsequent analysis was calculated using MorphoJ.

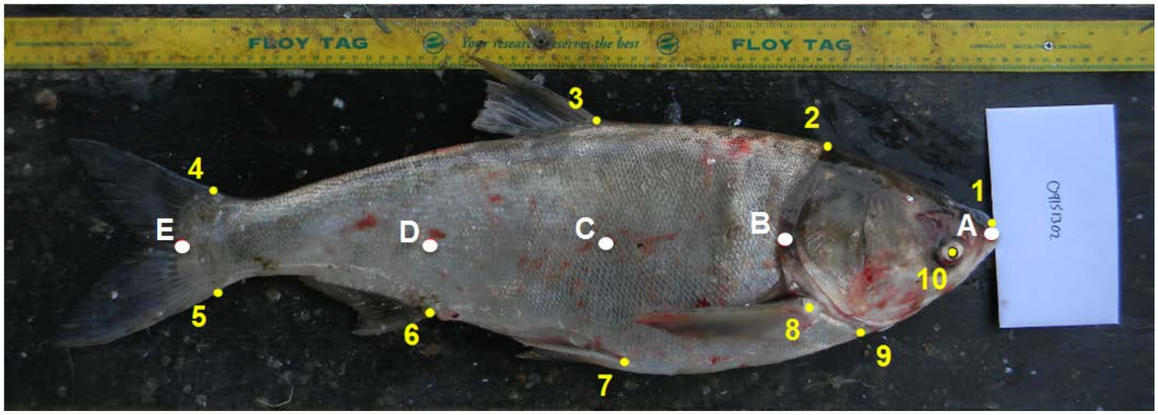

Figure 2.1 Anatomical landmarks on the right side of silver carp and silver carp X bighead carp hybrids that were digitized, in yellow (for descriptions, see Table 2.2). White landmarks were used for unbending specimens using tpsUtil and were located at the anterior tip of the snout (A), the operculum and the lateral line (B), the lateral line between the pelvic and dorsal fin insertion (C), the lateral line above the insertion of the anal fin (D), and the median of the pectoral fin (E).

Table 2.2 Homologous landmarks designating data collection points on photographs of silver carp and silver carp X bighead carp hybrids. Anatomical descriptions are provided for each landmark.

Landmark	Description
1	anterior tip of snout
2	occiput
3	origin of the dorsal fin
4	top of the caudal peduncle
5	bottom of the caudal peduncle
6	origin of the anal fin
7	origin of the pelvic fin
8	origin of the pectoral fin
9	inferior-most point of the operculum
10	center of the eye

Three types of analysis were used for both preliminary analysis within rivers and for testing between rivers: principal component analysis (PCA), discriminant function analysis (DFA), and canonical variate analysis (CVA). Ontogeny often plays a role in the shape of individuals based on the niches they occupy throughout life (Johansson et al. 2005; Svanbäck and Eklöv 2002, Hjelm 2001; 2003; Meyers and Belk 2014). It was necessary to first determine whether total length affected the shape of individuals in my study by regressing principle component (PC) scores against total length. In this case, PC scores were calculated through a multivariate ordination of body shape or a PCA of a covariance matrix of Procrustes coordinates. Procrustes coordinates were created by optimally superimposing each specimen over the average fish shape. PCA maintains Euclidian distances between all specimens so that patterns of variation between groups become evident. These PC scores were used for both preliminary analysis of size effect and to test for any differences in PSC and HSC morphology between rivers (Scharnweber et al. 2013; Kistner and Dybdahl 2014). DFA optimally distinguishes between two groups by analyzing their degree of separation to estimate whether or not they can be reliably distinguished (Klingenberg 2011; Dwivedi and Dubie 2012) and was used to test for within-river effects of gear and month sampled. CVA emphasizes the relative arrangement of multiple groups simultaneously and maximizes the separation of specified groups (Klingenberg 2011). The within-group variation is minimized mathematically to more easily identify the defining characteristics of the group being tested and a group assessment is used to test the probability of correctly assigning individuals to their correct groups based on morphology (Zelditch et al. 2004; Kistner and Dybdahl 2014). I used CVA to analyze the effects of hybrid status and sex on body shape because they are both characteristics possessed by individual fish and therefore should be analyzed together. Using CVA corroborates any patterns observed using PCA, and in addition to testing for effects of hybrid status and sex within populations, a second CVA analysis included river to test for the differences in shape between rivers and to capture the relative importance of the three variables (river, sex, hybrid status), with a Bonferroni correction to account for any increases in Type I error. Eigenvalues are reported as measures of how much variance is concentrated within each of the PC and CVA scores across shape space. If all of the variation is equally distributed across all directions of shape space, the variance will have a minimum variation of zero.

For each CVA, Procrustes and Mahalanobis distances were measured for all possible pairs of groups, and permutation tests of pairwise distances between groups (i.e., 1000 iterations) were used to calculate p-values. Permutation tests are suitable for hypothesis testing, although they are less useful for calculating confidence intervals when compared to bootstrapping methods. However, they nonetheless yield similar results, are often used interchangeably, and can produce more exact achieved significance levels (ASL) (Klingenberg & McIntyre 1998; Klingenberg et al 2002; Zeldich et al 2008). The distances between group mean depends on both the differences in morphospace and the direction of variance within groups. Mahalanobis distances scale for non-isotropic variation between groups by manipulating the distances so that variation is isotropic (Zelditch et al. 2004). This procedure often has a large effect on distances between groups and for this reason I relied only on Mahalanobis distances to interpret my results (Zeldich et al. 2004).

Throughout the morphometric analysis, wireframe diagrams of groups plotted against average shape were used to aid in interpreting the meanings of observed morphological differences in both PC and CVA scores (Dwivedi and Dubie 2012; Sheehan et al. 2005; Cadrin and Silva 2005). Each deformation is exaggerated for increased visibility; the scale is reported within figure captions.

2.3 Results

2.3.1 Length – at – Age

A total of 364 SC were collected from the MWR (MWRSC, n=143) and the Illinois River (IRSC, n=221) to be used in this study (Table 2.1). MWRSC ranged from 456 to 842 mm in total length, with a mean (±1 standard deviation, SD) of 653 ± 6.19 mm. IRSC ranged from 412 to 795 mm in total length with a mean (±1 SD) of 527.0 ± 4.1 mm. For age distributions: the mean age of MWRSC was 5.0 ± 1.49 years (yr) and the mean for IRSC was 4.2 ± 0.86 yr. IRSC and MWRSC ranged from 3-7 years and 2-

12 years in age respectively. When mean length at age was graphed for both populations the overall trend of larger MWRSC is apparent for all ages, although there was high variation within age classes and their standard deviations overlapped (Figure 2.2).

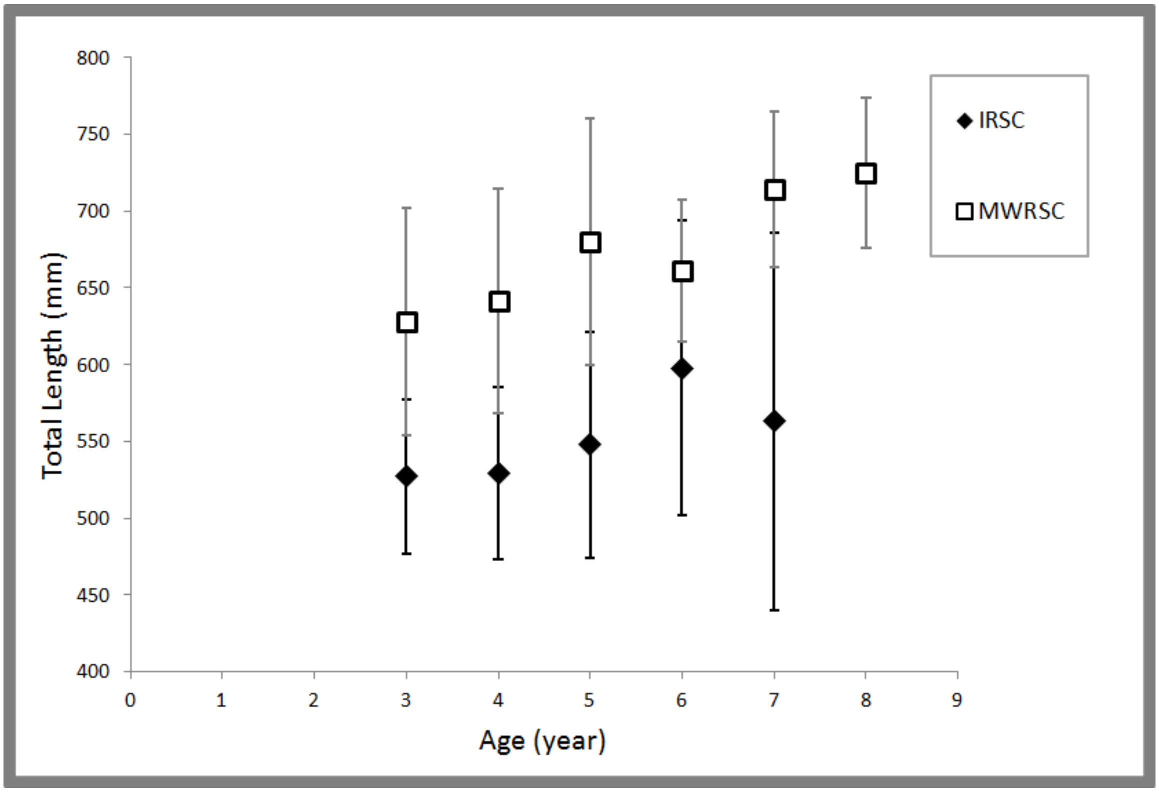

Figure 2.2 Length-at-age and standard deviation for Illinois River silver carp (IRSC) and middle Wabash River silver carp (MWRSC) caught using all gears.

2.3.2 Condition and Gonadosomatic Index

The $\log_{10}$length and $\log_{10}$weight relationships were significant for both PSC and HSC in the Illinois River and MWR (Table 2.3). In the MWR, both HSC and PSC exhibited increases in width relative to length where the in the Illinois River, these trends were less apparent.

Table 2.3 Log_{10} Length-weight regressions for middle Wabash River and Illinois River pure silver carp (PSC) and hybrid silver carp (HSC) collected using all gear types.

Location	Hybrid Status	Slope (b)	Y-intercept (a)	Adjusted R-squared	Sample size (N)	Intercept 95%CI	Slope 95%CI
Wabash River	HSC	3.16	-5.41	0.89	50	0.88	0.31
	PSC	3.03	-5.05	0.95	93	0.39	0.14
Illinois River	HSC	2.84	-4.58	0.89	141	0.43	0.16
	PSC	2.99	-4.99	0.94	86	0.43	0.16

The GSI for adult male and female SC ranged from 0.01 to 17.3% of total body weight (male: minimum=0.01%; maximum=1.22%; mean=0.26±0.20%; female: minimum=0.12%; maximum=17.3%; mean=3.55±3.61%). An ANOVA for female SC revealed that GSI was not related to either hybrid status or sampling gear (F=16.0, df=1, P=0.127 and F=5.0, df=5, P= 0.60, respectively). However, female SC GSI was different among months (F=3.57, df=2, P=0.031), especially for female MWRSC sampled during bowfishing tournaments on August 18 and September 19 (F=50.53, df=2, P=0.001). Female SC gonads were an average of 7.1±4.08% of total body weight in August and 6.4±2.88% in September. In the Illinois River, the majority of female SC measured GSI's between 0.5 and 2.5% and the MWR female SC was more generally distributed across a wider range of GSI (Figure 2.3). The total length of female SC and GSI were weakly correlated in the MWR (adj r^2=0.05, df=1, P=0.06); however, they exhibited a positive relationship in the Illinois River (adj r^2=0.32, df=1, P<0.001). The total length of male SC and GSI were significantly correlated for both MWRSC (adj r^2=0.32, df=1, P<0.001) and IRSC (adj r^2=0.24, df=1, P<0.001).

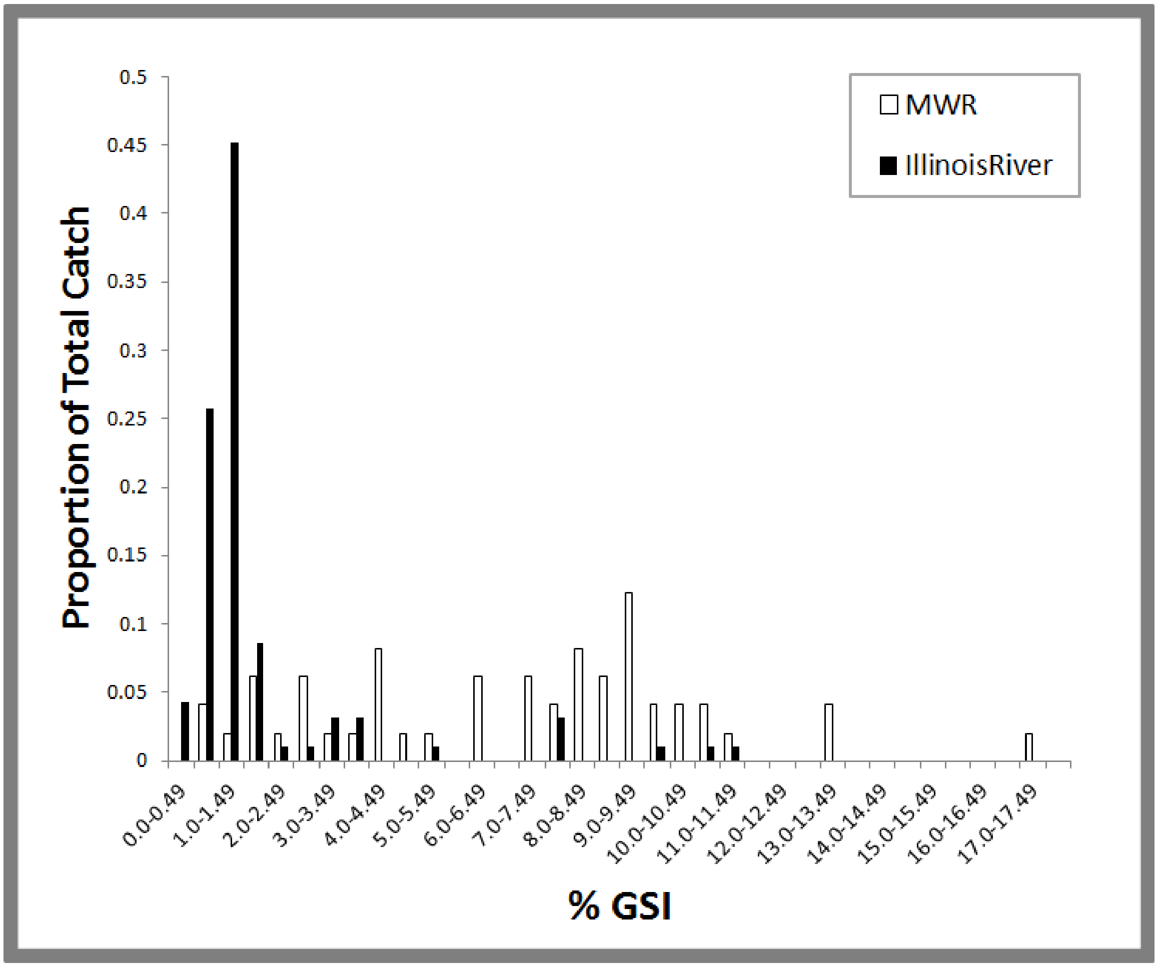

Figure 2.3 Gonadosomatic Index (GSI) frequency distributions for female silver carp collected from the Illinois River and middle Wabash River (MWR) using all gears.

2.3.3 Morphometric Analysis

After separating specimens by river, hybrid status, and sex to isolate the variable of gear, a preliminary DFA analysis found that bowfishing and electrofishing selected for significantly different morphologies for all SC populations in both rivers except for PSC males (Mahalanobis distance= 8.14, P=0.29) and HSC females (Mahalanobis distance= 3.93, P=0.22) in the Illinois River. Because bowfishing tournaments yielded large numbers of specimens in both rivers, subsequent morphological analysis was limited to bowfished SC from both rivers.

A second DFA of bowfished specimens revealed that month sampled in the MWR during the August and September tournaments had no significant effect on body morphology for male PSC and HSC and female HSC (male HSC Mahalanobis distance=2.17, P=0.12; male PSC Mahalanobis distance=3.02, P=0.48; female HSC Mahalanobis distance: 1.25, P=0.84). Female MWR PSC were significantly affected by month sampled (Mahalanobis distance=3.98, P=<0.0001); however, the effect was mostly observed in the width of the caudal peduncle, the location of the pectoral fin, and the anterior tip of the snout. Because changes in landmarks were only observed in female PSC, I grouped fish sampled in August and September, but consider possible effects during between-river comparison. A CVA for both rivers indicated that hybrid status and sex were significant grouping variables and all subsequent morphological analyses separated hybrid status and sex to make direct comparisons between rivers. More information about the distances in morphospace from CVA analysis between groups within each river are provided in Table 2.4.

Table 2.4 Mahalanobis Distances between Hybrid Status and Sex from CVA within the Illinois & MWR *(p-values from 10000 permutation rounds)*

Illinois River Bowfished Carp	Female HSC n=5	Female PSC n=12	Male HSC n=23
Female PSC n=11	3.7397 P=0.0008		
Male HSC n=23	4.3498 P=<.0001	2.8946 P=<.0001	
Male PSC n=11	4.3519 P=0.0001	2.2561 P=0.0149	2.3712 P=0.0001

Table 2.4 continued.

middle Wabash River Bowfished Carp	Female HSC n=8	Female PSC n=34	Male HSC n=35
Female PSC n=34	2.1484 P=0.0004		
Male HSC n=35	2.3634 P=<.0001	2.2832 P=<.0001	
Male PSC n=22	2.552 P=<.0001	2.3301 P=<.0001	1.5446 P=0.0024

A regression of PC score 1 (24% of total variance) against total length revealed no significant correlations between shape and length for male and female IRSC, or male MWRSC and female PSC (Figure 2.4), but there was a significant positive relationship between MWR female HSC total length and PC1 scores (F=10.94, df= 1,9, P=0.009). However, only nine individuals were available for this analysis, and the results could be a false positive; thus, length was not considered a covariate when evaluating morphology.

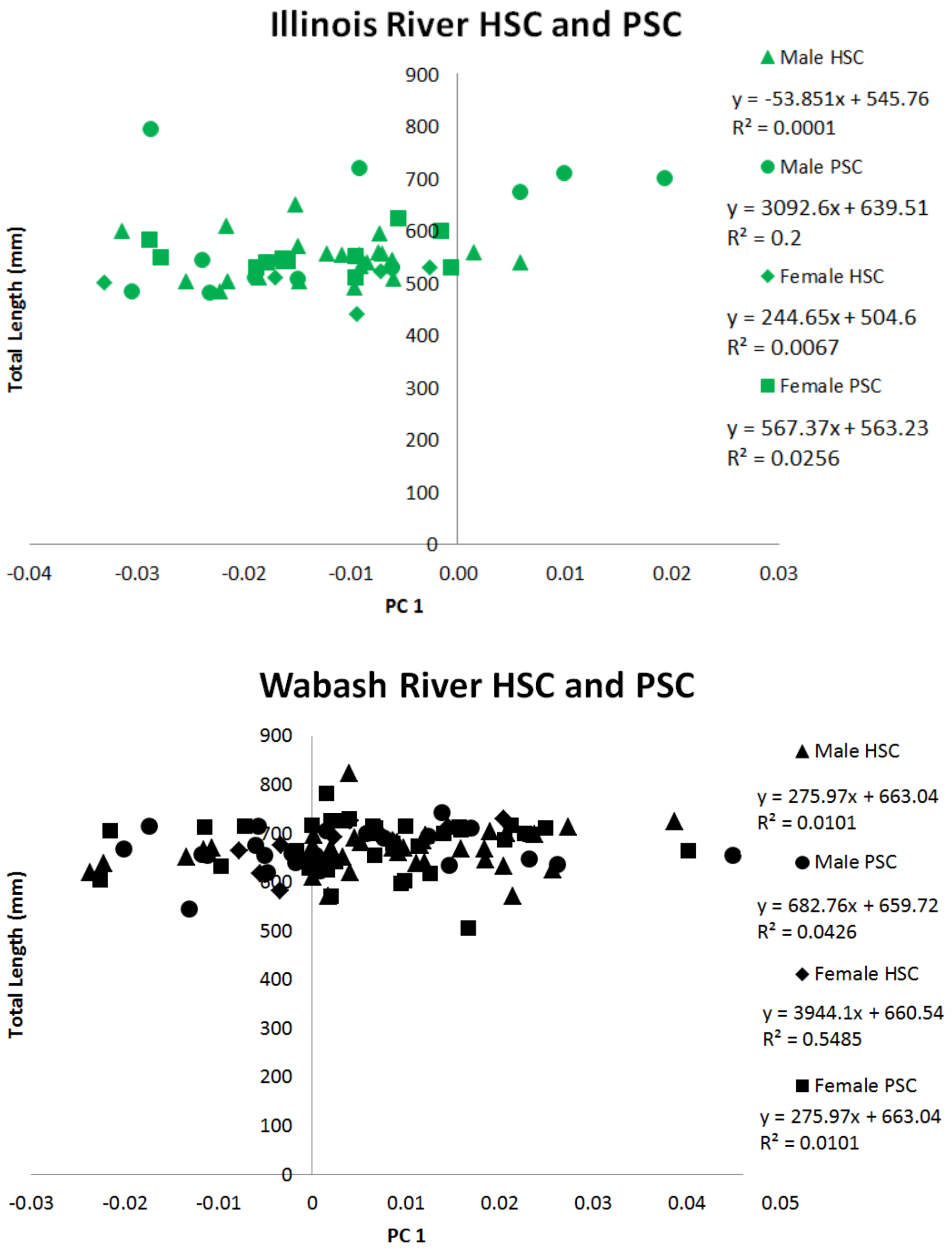

Figure 2.4 Regression analyses of PC 1 scores versus total length (mm) for MWR and Illinois River male and female silver carps (PSC) and silver carp X bighead carp hybrids (HSC).

2.3.4 Patterns of Morphological Diversification between Rivers

Morphometric data were obtained from 161 bowfished SC: 109 from the MWR and 52 from the Illinois River. The first four PC scores accounted for a total of 66.9% of the total shape variation and may therefore represent the majority of the shape differences between groups. Their shape differences are visualized using a wireframe diagram in Figure 2.5. PC1 primarily contrasts body depth, eye position, and steepness of head from the occiput to the anterior point of the snout; PC2 contrasts body depth, higher and steeper occiput/head depth, and length of the caudal region. PC 3 contrasts broad skulls with superiorly located pectoral fins with slim skulls and posterior pectoral fins. Finally, PC4 contrasts a narrowed caudal peduncle, deep head, long operculum, and posteriorly located pectoral fin with a broad caudal peduncle, narrow head, short operculum and anterior pectoral fin. Each PC score was tested against all variables. PC 1 was the only PC score that was significantly different between rivers (ANOVA F=72.475, df= 1, P=<0.0001), and it was not affected by hybrid status or sex. Both PC2 and PC4 were significant with only sex (PC2: ANOVA F=21.243, df=1, P=<0.0001; PC4: ANOVA df=1, F=12.996, P=0.0004), and PC 3 was significant with sex, hybridization, and river (ANOVA sex: F=7.03, df=1, P=0.009; hybrid status: F=10.1, df=1, P=0.002; river: F=33.25, df=1, P<0.0001).

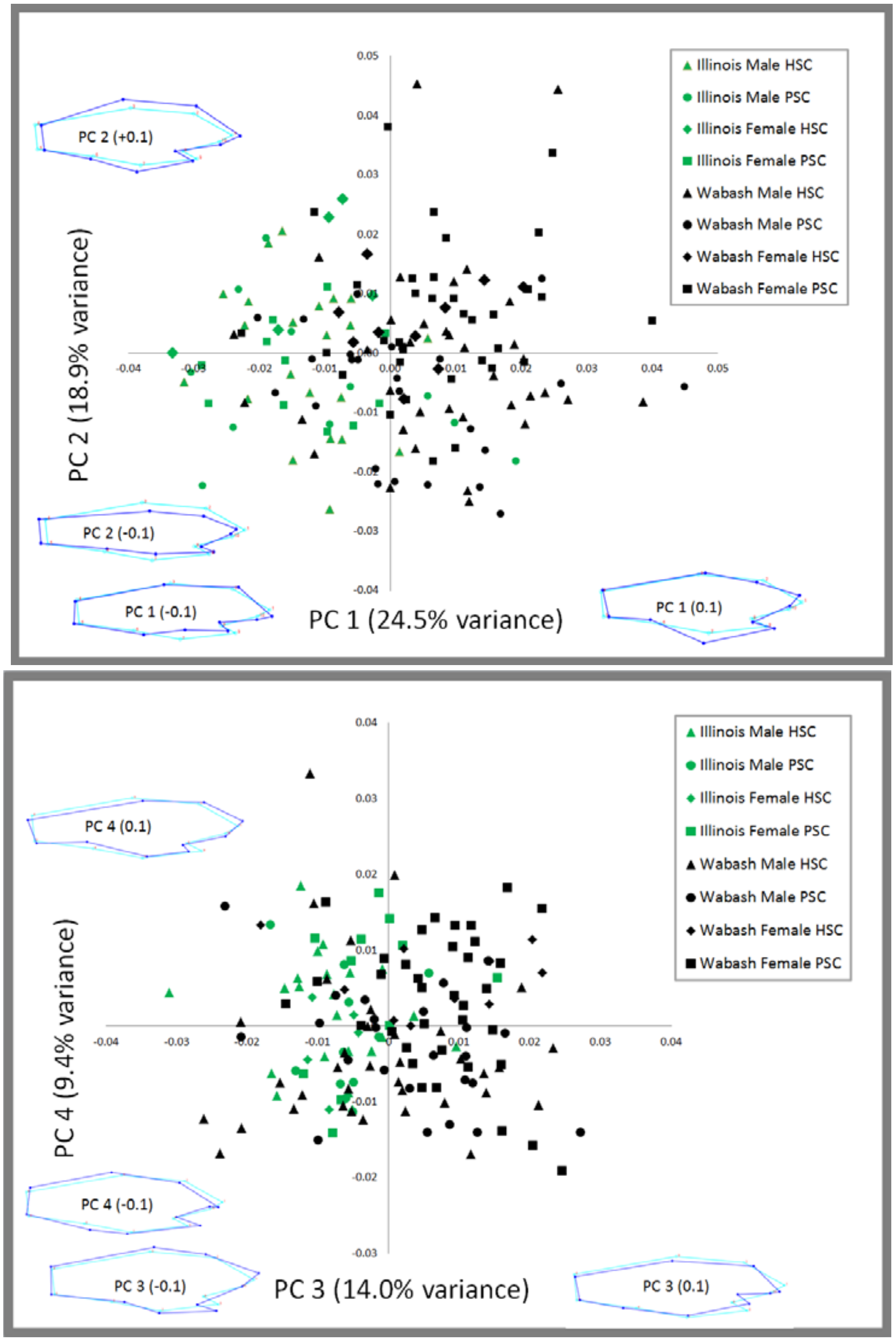

Figure 2.5 PC 1 and 2 (above) and PC 3 and 4 (below) for middle Wabash River (MWR) and Illinois River bowfished pure silver carp (PSC) and silver carp X bighead carp hybrids (HSC) with corresponding wireframe graph at a plus/minus 0.1 scale factor. Fishes from the Illinois River and MWR are most significantly related to PC1, with Wabash Fish exhibiting deeper bodies and narrower heads.

2.3.5 Quantification of Disparity between Rivers

SC differed morphologically between the two rivers. CVA analysis resulted in significant Mahalanobis distances between all groups of fish and their differences are shown in Figure 2.6, and the graphic outputs of MorphoJ showed the highest divergence between the rivers occurring with the location of landmark 7 (origin of the pelvic fin), landmark 8 (origin of the pectoral fin), landmark 9 (inferior most point of the operculum), and landmark 2 (occiput). Mahalanobis distances between rivers ranged from 4.47 between Illinois River female HSC and MWR male PSC to 1.48 between Illinois River female PSC and Illinois River male PSC (Table 2.5).

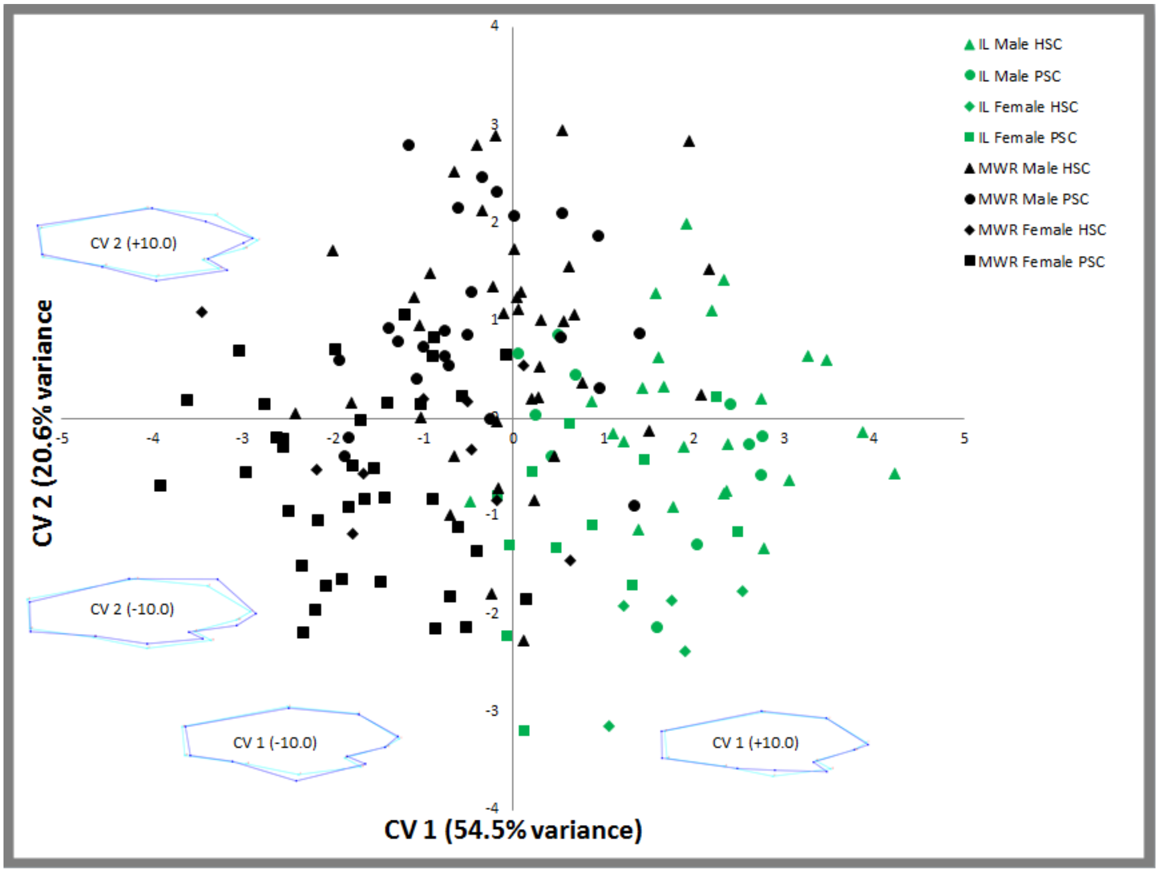

Figure 2.6 CV 1 and 2 for middle Wabash River (MWR) and Illinois River bowfished male and female pure silver carp (PSC) and silver carp X bighead carp hybrids (HSC) with corresponding wireframe graph at a plus/minus 10.0 scale factor.

Table 2.5 Mahalanobis distances among groups in shape space of middle Wabash River (MWR) and Illinois River pure silver carp (PSC) and silver carp X bighead carp hybrids (HSC). Sample sizes are in parenthesis, Bonferroni corrected probabilities are shown with asterisks.

	Female IR HSC (5)	Female IR PSC (11)	Male IR HSC (23)	Male IR PSC (11)	Female MWR HSC (10)	Female MWR PSC (36)	Male MWR HSC (36)
Female IR PSC (11)	3.08*						
Male IR HSC (23)	3.14*	2.32***					
Male IR PSC (11)	3.15***	1.48	1.69				
Female MWR HSC (10)	4.21***	2.99***	3.53***	3.52***			
Female MWR PSC (36)	4.23***	2.83***	3.92***	3.35***	2.04*		
Male MWR HSC (36)	3.79***	2.65***	2.49***	2.36**	2.32*	2.33***	
Male MWR PSC (24)	4.47***	2.64***	3.03***	2.43**	2.56***	2.31***	1.62**

*significant at $p < 0.01$, ** significant at $p < 0.001$, ***significant at $p < 0.0001$

Morphological differences existed between the sexes and between PSC and HSC within each river, but both PCA and CVA analyses between rivers showed that MWRSC had deeper body sections and narrow tapered heads, while IRSC had relatively shallower bodies and deeper heads (Figure 2.7).

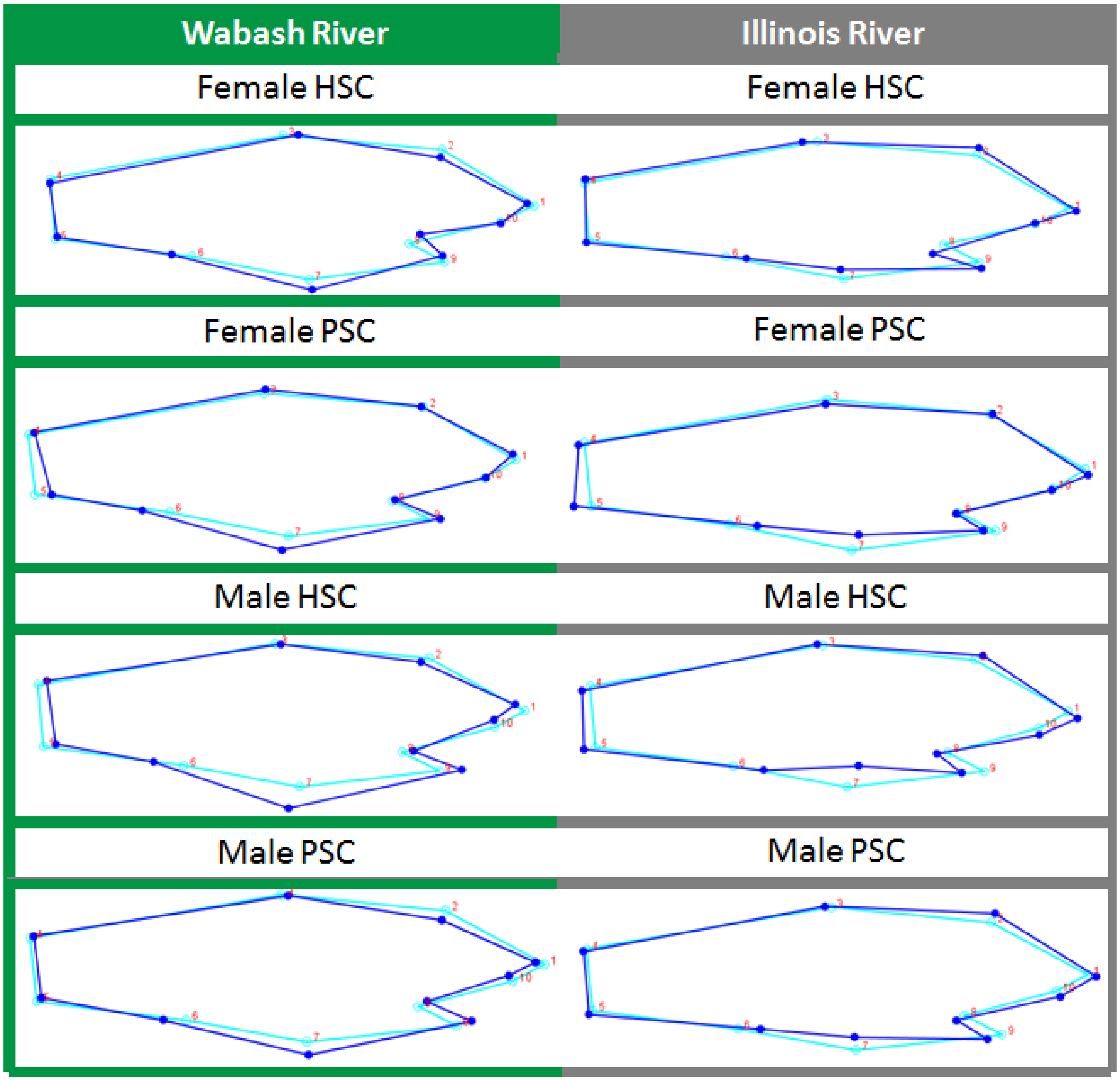

Figure 2.7 Contrast of shape differences between rivers along the axis of CVA1. Fish were grouped within rivers according to sex and hybrid status and compared between rivers. Light blue wireframe is the mean shape of all fish in the sample, while dark blue represents the relative shape change for each group at a scale of plus or minus 0.1. Overall, MWRSC had deeper, more robust bodies and shallower heads, while IRSC had deep heads and narrow bodies.

2.4 Discussion

The results of this study suggest that there is significant divergence in body morphology between IRSC and MWRSC populations. The greatest difference between rivers occurred along the axis of PC 1, which was also the only PC score that exhibited a significant interaction with river sampled. PC 1 contrasted MWRSC having deep bodies and shallow head depths (between the occiput and anterior most point of the nose), with IRSC having shallow bodies and steeply sloped heads. These results can be attributed to several possible factors, and I do not assert causal evidence for the differences in shape based on specific environmental characteristics of the two rivers. However, given previous studies and the results of the life history analysis, I speculate that morphological differences observed in this study between the two rivers were most likely related to population demographics and different environmental characteristics.

2.4.1 Life History Characteristics

The most obvious morphological differences between IRSC and MWRSC were the more fusiform shape of MWRSC compared to the thinner thoracic region and broader head of IRSC. The life history analyses of SC revealed that MWRSC were in better condition, lived longer, attained greater total lengths, and had higher GSIs than IRSC. Increased body depth in MWRSC could potentially be attributed to the better condition and higher GSIs of these fishes because healthier individuals are more likely to have greater muscle mass and larger gonads, especially in females. Length-weight relationships were represented though log a and log b; the variation in log a is a function of the body shape of the respective species being sampled and log b <3 as observed in the Illinois River typically indicates that larger specimens have changed their body shape to become more elongated or that small specimens were in good condition at time of sampling relative to large specimens (Froese 2006). I found IRSC to be more elongated in shape compared to MWRSC, and their condition declined as fish attained larger sizes.

Moreover, the age structure and length frequency distributions of IRSC and MWRSC suggested that SC grew fast in both rivers but achieved greater lengths and lived longer in the MWR. This may reflect, in part, lowered intraspecific competition in the MWR relative to the Illinois River. IRSC have undergone exponential growth since the late 1990s (Chick and Pegg 2001; Tsehaye et al. 2013), and the body conditions and growth rates of IRSC have declined over the past decade due to large population size and crowding (Irons et al. 2011; Garvey et al. 2012; Tsehaye et al. 2013; Stuck et al. 2015). Their density is >3X those of SC in the LWR (Stuck et al. 2015), and populations may be at or reaching carrying capacity based on decreasing length-weight slopes and intercepts over time (Sass et al. 2010: ($\log_{10}$mass=3.122*$\log_{10}$TL-5.29); Garvey et al. 2012: ($\log_{10}$mass=3.03*$\log_{10}$TL-5.09); this study: ($\log_{10}$mass=2.99*$\log_{10}$TL-4.99). This intraspecific competition is likely compounded by competition for food with native planktivorous fishes in the Illinois River, including bigmouth buffalo (*Ictiobus cyprinellus*) and gizzard shad (*Dorosoma cepedianum*) (Irons et al. 2007; Chapman and Hoff 2011; Kolar et al. 2005). In addition to natural mortality, Stuck et al. (2015) suggested that large adult IRSC are being pressured by commercial fishing harvest, a practice that is not yet in place in the Wabash River. These effects likely contributed to differences in SC life history characteristics between the rivers that, in turn, influenced SC body shapes.

Changes in body morphology associated with varied life history characteristics emphasize the need to relate population demographics to invasion stage because degree of establishment is often associated with population plasticity (Bohn et al. 2004; Azour et al. 2015). Differences in growth, age, condition, and length have been previously observed in studies of SC on the middle MRB and its tributaries, including the Gavin's and Interior Highlands reaches of the Missouri River, the upper Mississippi River, the Missouri River tributaries, and the La Grange & Peoria reaches of the Illinois River (Irons et al. 2011; Williamson and Garvey 2005; Wanner and Klumb 2009; Hayer et al. 2014a; Garvey et al 2012; Table 1.1). Irons et al. (2011) analyzed SC populations both before and after the peak population stage, while the middle Mississippi River (Williamson and Garvey 2005) represents an established and reproductively active population. Studies on edge populations in the Missouri River tributaries (Hayer et al. 2014a) and the Gavin's Dam reach of the Missouri River (Wanner and Klumb 2009) were all investigations of newly established SC populations. Changes in life history strategy throughout invasion stages have been documented in other invasive species and often reflect higher fitness, faster growth, and greater reproductive investment in newly established edge populations compared to more advanced invasion stages (Feiner et al. 2011). In general, this study corroborates findings that populations in these ranges display higher growth rates, maximum lengths, GSI, and condition than interior/central populations. The overall good health and vigor of MWRSC individuals may have influenced their robust body shape given that this population is in a much earlier invasion stage compared to IRSC.

2.4.2 Local Environmental Demands

Changes in body shape can substantially affect fish hydrodynamics, and when expressed over divergent river systems, even minor changes could offer substantial advantages (Webb 1984; Ostenfeld et al. 1998; Li et al. 2008). The shape of the highest performing fish in a given ecosystem often depends on the niche that the fish occupies and the environmental factors to which it is routinely exposed (Scharnweber et al. 2013). IRSC and MWRSC are subject to different hydrogeomorphic regimes, with the Illinois River characterized by a highly altered, lentic channel and the MWR characterized by lotic riffle-pool sequences. Water flow can substantially influence intraspecific phenotypic diversity (Langerhans 2008), and there have been many studies linking the expression of a deeper body and more fusiform shape to increased swimming performance (McHenry and Lauder 2006; Webb 1975; Blake 1983; Bioly and Magnan 2002). In addition to water flow, this advantage is attributable to a wide range of factors including muscle mass (Crucian carp, *Carassius carassius*, Domenici et al. 2008), the presence of predators (Langerhans et al. 2004; Hendry et al. 2006), and a niche within structurally complex habitat that results in the need for unsteady or burst swimming behaviors (Langerhans and Reznick 2007; Myers and Belk 2014). While this study did not evaluate niche occupancy of MWRSC, these fishes clearly encountered faster, shallower habitats and more unpredictable flow regimes in the MWR compared to the Illinois River. Given the increased swimming performance associated with the deeper, more fusiform bodies demonstrated for other fishes in moving waters, it would not be surprising if controlled laboratory studies of morphological plasticity in SC revealed their expression of these traits under simulated MWR conditions.

I found that SC populations in both rivers exhibited very fast growth at young ages; e.g., IRSC at age 3 averaged 527 mm total length and MWRSC averaged 629 mm total length. The tradeoff between fast growth and decreased swimming performance has been well documented in teleost fishes (Arnott et al. 2006; Billerbeck et al. 2001; Lee et al. 2010), and it is possible that the combined effects of fast growth and hydrogeomorphic regime could explain some of the variation in head and body depths between MRWSC and IRSC. Li et al. (2008) analyzed the morphological response of transgenic common carp (*Cyprinus carpio)* to a growth hormone (GH) and the effects of these morphological changes on critical swimming speeds (U_{crit}). They found that transgenic carp exhibited shallow bodies and deep heads, while control carp displayed deeper bodies and caudal regions, longer ventral caudal lengths, and shallower head depths. The morphological differences found in transgenic carp are similar to those I observed in IRSC and resulted in a swimming disadvantage (U_{crit} was 22.3% lower than control carp) that may be attributed to increased drag from the deeper heads and shallow bodies of GH carp. The deeper body/narrow heads of control carp allowed for more thrust and greater swimming power through their fusiform shapes (Li et al. 2008; Law and Blake 1996). The deeper heads and shallow, elongated bodies of IRSC could reflect a combination of fast growth and density limitation, while the more fusiform shape of MWRSC affords them increased swimming performance in a lotic environment. As before, I was unable to demonstrate causation for morphological divergence in MWRSC, and additional work is needed to fill the large number of gaps remaining in the current body of field-tested work on BHDC plasticity.

2.5 Conclusions

As BHDC continue to expand their ranges in North America and other global freshwaters, it is important to understand their adaptive capacity in novel environments so that modeling efforts to anticipate their range expansion can yield more reliable results. Increased confidence in model projections through updated information on plasticity in midwestern rivers is critical for fisheries scientists and managers to accurately identify vulnerable tributaries in the MRB and GLB. This study focused on the Illinois River and the MWR as examples to compare establishment of SC in a densely populated and altered hydrogeomorphic regime versus an edge populations in a more natural channel. I found evidence that PSC and HSC exhibit morphological plasticity and differing life history characteristics between the MWR and Illinois River, and this provides strong support for location-based selective agents driving phenotypic outcomes as they progress in their invasion.

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