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Differential Movement Response of Silver Carp to Individual and Environmental Conditions in the Illinois and Wabash Rivers

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DIFFERENTIAL MOVEMENT RESPONSE OF SILVER CARP TO INDIVIDUAL AND ENVIRONMENTAL CONDITIONS IN THE ILLINOIS AND WABASH RIVERS

by

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Knowledge about the spatial dynamics of invasive species is essential to predict, restrict, and prevent their spread to new areas. Invasive Silver Carp (*Hypophthalmichthys molitrix*) populations are expanding on all fronts and are threatening to establish in the Laurentian Great Lakes. Understanding their movement patterns is vital to prevent their populations from spreading further and to improve management efficiency. This study looked at multiple factors to understand which have an influence on the movement of invasive Silver Carp in two different river systems. Chapter 1 examined the relationship between individual and environmental factors—including length, body condition, temperature, and discharge—and movement in invasive Silver Carp in the Illinois River. Several different movement metrics were examined—including range, upstream and downstream distance per detection, upstream and downstream movement rate, and total movement—to see if they were affected by any of these factors. Chapter 2 examined multiple morphological metrics—including geometric morphometrics, total length, caudal peduncle depth, and caudal fin aspect ratio—related to the movement of Silver Carp in the Wabash River to see if Silver Carp with similar movement have similar morphology. For both chapters, acoustic telemetry was used to track the movement of Silver Carp. For analysis, multiple generalized linear models were used. For Chapter 1, temperature and discharge were the most commonly included predictors across movement metrics. For Chapter 2, no morphological metrics were identified as predictors of movement. Quantifying the effects of individual and environmental factors can aid in the control and containment of this invasive species and may help to manage populations in at-risk environments. This study demonstrated that factors, like temperature and discharge, can be used to determine when individuals are more likely to expand the invasion front of Silver Carp in the Illinois and Wabash rivers. Which specific individuals are the largest threat to the invasion front can be predicted by individual factors like length, but not body shape.

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CHAPTER 1

INDIVIDUAL AND ENVIRONMENTAL FACTORS EFFECT ON MOVEMENT IN THE ILLINOIS RIVER

INTRODUCTION

Identifying factors that influence animal movement is necessary to understand their distribution and impacts on their environment (Morales et al. 2010). This is especially important when considering invasive species, which can disrupt their invaded ecosystem and outcompete local species. However, the negative impacts of invasive species is partially dependent on what habitats they use and when. Knowledge about the spatial dynamics of invasive species is essential to predict, restrict, and prevent their spread to new areas (Sakai et al. 2001, Jud and Layman 2012).

The spatial dynamics of invasive species can be understood by identifying which factors drive their movement. Individual factors such as length and body condition can strongly influence movement (Schrank and Rahel 2006, Guy and Brown 2007). For example, if managers and conservationists know that individuals with particular characteristics within an invasive population are more likely to move and expand the invasion front, they can deploy selective harvest methods to target those mobile individuals. In addition to movement, individual variables relate to other factors that can influence the invasion ecology of a species. In invasive fishes, length and condition can positively influence reproductive potential (Marteinsdottir and Begg 2002, Barneche et al. 2018) which influences timelines for population growth, establishment, and spread. The same individuals that represent the highest reproductive potential due to their larger size, may also move more as they seek food and habitat (Brett and Glass 1973, Gowan and Fausch 1996, Schrank and Rahel 2006, Radinger and Wolter 2014). Fish with low body condition have shown to be more mobile than “fatter” fish (Gowan and Fausch 1996, Hilderbrand and Kershner 2004, Lamer et al. 2019). However, others have observed equivocal or opposite trends (Schrank and Rahel 2006, Heim et al. 2016, Branco et al. 2017). How body condition affects movement is species dependent due to different behaviors (territorial, seasonal migrations, etc.) and different resources (stable or shifting). It is important to know if larger or better conditioned individuals move more since they typically have a greater reproductive potential.

Although movements can be linked to individual characteristics (Bacheler et al. 2021, Eldøy et al. 2021), perhaps more often fish movement is linked with specific environmental conditions with temperature and discharge often identified as the most important for riverine species (Guy and Brown 2007). Fish rely on temperature cues to migrate, spawn, and feed (Lee et al. 2003, Achord et al. 2007, Keefer et al. 2009) resulting in daily and seasonal movements in many species. For example, cold temperatures can reduce swimming speeds, fish activity, and migration rates (Lee et al. 2003, Keefer et al. 2009). Specific river conditions, such as high discharge, are also often linked with movement (Taylor and Cooke 2012). Knowing what environmental factors affect the movements of invasive species can determine when a specific deterrent should be used and when it might be optimal to take specific control actions such as harvest.

Understanding the spatial dynamics of highly mobile invasive species is necessary to control their spread. One species in particular, Silver Carp (*Hypophthalmichthys molitrix*), has established reproducing populations within the Mississippi River Basin and its populations are currently within 65 river km of the Great Lakes (Tucker et al. 1996, Lubejko et al. 2017, Jeffery et al. 2019). Their invasion success in the U.S. has been made possible due to their quick growth, high fecundity, rapid dispersal, lack of predators, and limited competition with natives (Kolar et al. 2007, Prechtel et al. 2018). Bigheaded carp, a subgroup within Invasive Carps that includes Silver Carp and Bighead Carp (*H. nobilis*), now represent up to 46-78% of the fish biomass in the lower Illinois River, a Mississippi River tributary (Coulter et al. 2018b). A future invasion of Silver Carp into the Great Lakes has the potential to negatively impact native species, aquatic food webs, and fisheries resources worth up to $4 billion annually (Lodge et al. 2006, Cudmore et al. 2012, Zhang et al. 2016). Reductions in abundance via harvest or removal have been shown to partially reverse the negative impacts of Silver Carp (Tsehaye et al. 2013) and can reduce propagule pressure to limit spread. Therefore, additional insights about the movements of these fish can aid in controlling the spread and negative impacts of Silver Carp by removing the individuals that are the highest risk of expanding the invasion front.

Previous analyses of Silver Carp movement distance and rate have found positive relationships with water temperatures and water levels (Coulter et al. 2016, Lubejko et al. 2017). The greatest movement distances occurred in late spring and early summer, a period of potential increased risk of moving into novel areas. However, high individual variation in the movements of Silver Carp have also been observed, with sedentary and mobile individuals occurring in the population (Prechtel et al. 2018, Coulter et al. 2022). If mobile individuals are also in better condition or of larger size, movements by these individuals could increase the likelihood of the successful establishment and spread of Silver Carp. Currently, information on how body condition relates to Silver Carp movement is unknown and only a few studies have sought to examine the influence of size (Prechtel et al. 2018, Coulter et al. 2022). This study aims to determine how individual factors, body condition, and size affect Silver Carp movement and whether the influence of environmental drivers outweighs these individual factors. These results will increase the effectiveness of existing management strategies in the Illinois River and similar systems.

I examined the relationship between individual and environmental factors—including length, body condition, temperature, and discharge—and movement in invasive Silver Carp in the Illinois River. I examined several different movement metrics—including range, upstream and downstream distance per detection, upstream and downstream movement rate, and total movement—to see if they are affected by any of these factors. This study encompasses multiple years of telemetry data (2012–2020) for a whole river ecosystem, bounding broad scales of time and space. My hypotheses are Silver Carp with longer bodies and lower relative weight will move more for all movement metrics. Increased temperature and discharge are expected to increase distance per detection and movement rate but have no effect on range or total movement.

METHODS

Study Area

The Illinois River is a 439 km-long, impounded tributary of the Mississippi River. It is formed by the confluence of the Kankakee and Des Plaines rivers in northern Illinois and drains southwest into Pool 26 of the Mississippi River. Within the section that was studied, the Illinois River is separated by five lock and dam structures (La Grange, Peoria, Starved Rock, Marseilles, and Dresden) and is divided into six pools (Figure 1.1). These dams can restrict the movement of fishes (Coulter et al. 2018, Lubejko et al. 2017). The current location of the invasion front of Silver Carp is Dresden Island Pool, 76 river km (rkm) from Lake Michigan via a canal system. The Illinois River is an ideal site to study the movement of Silver Carp considering its importance as an invasion front.

Telemetry

I used acoustic telemetry previously collected from an acoustic telemetry array in the Illinois River from the years 2012 through 2020. Eight-hundred sixty-eight Silver Carp had telemetry detections and accompanying length and weight measurements. Silver Carp were captured and released in all six Illinois River pools (Lubjeko et al. 2017, Coulter et al. 2018) and implanted with acoustic tags (model V13 or model V16; Vemco).

Surgical procedures followed those described in Lubejko et al. (2017) and Coulter et al. (2018). Aseptic conditions were always maintained in the field. Once collected, fish were held *in situ* in net pens. Individuals were anesthetized with carbon dioxide gas in a tank containing river water and buffered with sodium bicarbonate to maintain pH. After signs of equilibrium loss, weight and length measurements were taken. Each fish was placed ventral side up on a V-notched surgery board with river water pumped over the gills. The scales were removed around the incision site, which was positioned posteriorly to the pelvic fins and anterior to the anus, with a sterile scalpel. An incision roughly two times the width of the transmitter was made. Each transmitter was soaked in ethanol for at least two minutes prior to insertion. Transmitters were pushed through the incision and forward. The incision was closed with 2-3 interrupted sutures (Ethicon Inc. Somerville, NJ; vicryl CP-1 absorbable, monofilament). The fish was then placed in a tank filled with river water or an *in situ* net pen. Once it regained normal swimming behavior, it was released. All tools were immersed in 70% ethanol between each surgery.

During all years, an array of up to 54 stationary receivers (model VR2W or model VR2tx; Vemco) was used to monitor movements of tagged individuals. The receivers were placed every 25–30 rkm, including within the lock chamber of each lock and dam. Locations and number of receivers in each pool are available in Coulter et al. 2018. Receivers were placed as either a bottom set where receivers were attached to rebar stands on the bottom of the river with the hydrophone pointing upward, or were attached to stationary objects (e.g., barge mooring cells).

Detections within 48 hours of tagging were omitted from data analysis due to potential influence from tagging effects (Frank et al. 2009). False detections, possible mortalities, or shed tags were identified as described in Coulter et al. (2018) and removed from the dataset before analysis. Any fish that had been detected on only one day, had less than two detections per month, or never moved were removed for further analyses. Fish with a range of zero were removed due to uncertainty if lack of movement, a failure to detect the fish, or mortality had occurred. Only the first three months of data from each fish were used to minimize the chance that body condition measured at the time of tagging would not change. Additionally, fish lacking or with apparent inaccurate length or weight data were removed. In total, there were usable data from 257 of the 868 Silver Carp evaluated.

Data Analysis

Multiple metrics of movement were calculated for each tagged fish, including range (maximum rkm - minimum rkm), upstream and downstream distance per detection (rkm) between consecutive detections, upstream and downstream movement rate (rkm/day) between consecutive detections, and total movement (sum of distance per detection). Range evaluates how much of the river a fish uses as habitat and shows how far upstream or downstream a fish may travel overall. The other metrics describe rate of movement and reveal which fish move the most within the range. Total movement reveals whether a fish is sedentary or mobile and the extent of river use. Movement distance per detection (upstream or downstream) quantifies smaller movements throughout the recorded time that allows us to see specifically when a fish is moving or staying in the same place. Movement rate is the average daily speed at which a fish moves (e.g., meandering or making a directed movement). To determine whether any of the movement metrics were related and to show they provide different measures of movement, a correlation matrix was run on them. Movement metrics represent minimum estimates of movements because individuals may move outside of the study area or beyond the ranges of the stationary receivers (Coulter et al. 2016).

Total length (mm) and relative weight (W_r) of individual fish plus environmental conditions, temperature (°C), and discharge (m^3/s), were used as predictors of movement metrics. Relative weight was used as a measure of body condition (Murphy et al. 1990), using a standard weight equation for Silver Carp (Lamer et al. 2019) and weight and length at tagging. Daily water temperature measurements were collected from the U.S. Geological Survey river gauge at Florence, IL (USGS 05586300). River discharge data were collected from the U.S. Geological Survey river gauge at Henry, IL (USGS 05558300) near the center of the study area.

A generalized linear model was used to evaluate relationships between individual fish and environmental variables and movement range. All other movement metrics had multiple data points per fish, so tag number was added as a random effect and generalized linear mixed-effect models were evaluated (glm and glmer in Package 'lme4'). The full model for range included predictors of body condition (W_r), total length (mm), starting temperature (°C), change in temperature (°C), and change in discharge (m^3/s). The family used for all models was "gamma." Starting temperature and change in temperature were uncorrelated ($r = -0.02$) so both were included in the full model. Starting discharge and change in discharge were correlated ($r = -0.53$) so only change in discharge was included. Change in temperature and discharge was calculated as the change between each detection. The full models for all other movement metrics included body condition, total length, temperature, change in temperature, discharge, and change in discharge as well as a random effect of individual fish. For these other movement metrics, mean temperature on day of detection, instead of measurement at the start of detections, was used since multiple data points were included. Distance per detection and movement rate were associated with directionality (negative values were downstream movement while positive values were upstream movement). To keep this directionality, upstream and downstream movements were analyzed separately. All possible combinations of predictors were modeled and Akaike's Information Criterion with small sample size correction (AICc) was calculated for each model. Model averaging (conditional average) was performed across all candidate models with ΔAIC < 2 for each movement metric. All analyses were done in R Studio (v. 1.3.1093).

RESULTS

Silver Carp (N = 257) used in this study during 2012 through 2020 had a mean total length of 636 ± 5.3SE mm and a mean Wr of 102 ± 0.71SE (Table 1.1). Throughout the time covered by this study, water temperatures ranged from 0 to 32°C while discharge ranged from 273 to 9167 m3/s (Table 1.1). Most movement metrics were not correlated (r ≤ 0.1) supporting the use of multiple metrics of movement that could respond to different environmental predictors. Only movement distance and rate of the same direction (i.e., upstream or downstream) were correlated (r > 0.5). Ranges of Silver Carp varied from 0.10 to 223.7 rkm, with an average of 17 ± 1.7SE rkm (Table 1.1). The range averaged model showed all factors affected range and suggested that the most influential factors on increased range of a Silver Carp in the Illinois River was lower temperatures and a greater change in temperature (Table 1.2). Total movement ranged from 0.16 to 360 rkm, with an average of 44 ± 16SE rkm (Table 1.1). The total movement averaged model showed all factors affected total movement and suggested that the most important factors on increased total movement was shorter length and lower temperature (Table 1.2). Downstream distance per detection ranged from 0.016 to 260 rkm, with an average of 11 ± 0.86SE rkm (Table 1.1). The downstream distance per detection averaged model showed length, temperature, and discharge affected downstream distance per detection. The model suggested that the most influential factor on increased downstream distance per detection was lower temperature (Table 1.2). Downstream movement rate ranged from 0.00045 to 120 rkm/d, with an average of 4 ± 0.40SE rkm/d (Table 1.1). The averaged model showed body condition and discharge had the largest effect downstream movement rate (Table 1.2). Upstream distance per detection ranged from 0.016 to 92 rkm, with an average of 4 ± 0.79SE rkm (Table 1.1). The upstream distance per detection averaged model showed length, temperature, change in temperature, and discharge affected upstream distance per detection. The averaged model suggested that the most important factors on increased upstream distance per detection was shorter length and lower temperature (Table 1.2). Upstream movement rate ranged from 0.0019 to 43 rkm/d, with an average of 2 ± 0.41SE rkm/d (Table 1.1). The upstream movement rate averaged model showed length, temperature, change in temperature, and discharge affected upstream movement rate. The averaged model suggested that the most influential factors on increased upstream movement rate was shorter length, lower temperature, and greater change in temperature (Table 1.2).

DISCUSSION

Individual and environmental factors are drivers of Silver Carp movement and can be used to predict when invasive fish may spread into new habitats and how they can be efficiently managed. Despite most studies with Silver Carp only relating movement to environmental characteristics (DeGrandchamp et al. 2012, Lubejko et al. 2017, Coulter et al. 2018), all the individual and environmental factors tested were included in at least one of the final models in the analysis. The effects and combinations of factors differed depending on the type and context of movement quantified, with factors influencing downstream movements being the most different from other predictors. Overall, temperature and discharge were the most commonly included predictors across movement metrics, consistent with much of the previous work regarding Silver Carp (Larson et al. 2017, Sullivan et al. 2017, Coulter et al. 2022). Length and Wr also affected movement and are likely doing so in different ways because length and Wr were not correlated (r = 0.036). Understanding these environmental and biotic relationships is ultimately important when inferring how movement will influence programs of prevention and control for invasive species (Keller and Sandiford 2014). This information can possibly be used to predict when invasive fish may spread into new habitats and inform efficient management.

Environmental drivers of movement are factors that can possibly be used to predict when invasive fish movements may allow spread into new habitats. Lower temperatures appear to produce higher risk for invasive Silver Carp to spread across the river ecosystem, which is counter to expectations where fish are expected to move more when it is warm (Lee et al. 2003, Kolar et al. 2007, Keefer et al. 2009). Perhaps thi temperature-dependent movement pattern is related to reproduction. Silver Carp spawn in spring in the main channel starting at ~18°C (Kolar et al. 2007), so we expected to see and indeed saw increased movements at cooler spring temperatures and more individuals in the population moving to spawning sites. Given that these types of movement appear across so many river systems (DeGrandchamp et al. 2008, Coulter et al. 2016, Lubejko et al. 2017, Sullivan et al. 2017), managers may be able to exploit this behavior during cooler months when fish are moving to spawn. Also, it is possible that the temperature-dependent movement pattern is due to increased movement during cool fall months when fish move to overwintering areas. Coulter et al. (2017) saw this pattern in the lower Illinois

River as fish moved into Swan Lake backwater. As for discharge, the effect on movement was usually positive across all models but the effect on models was slight, as most coefficients were small. Discharge has been shown to be an influential environmental factor in many studies (Peters et al. 2006, Taylor and Cooke 2012), including ones on Silver Carp (DeGrandchamp et al. 2008, Calkins et al. 2012). It is likely that these results vary from our study since we used discharge data over three months and may have been less robust to detect a short-term discharge effect.

Individual covariates are sometimes overlooked in movement analyses, especially if the examination of individual covariates is not the study goal. In past studies, length is most often included as it is easiest to measure, while other factors such as sex (especially in monomorphic species) and condition are more difficult to quantify during the short handling window telemetry surgeries may offer. However, there is a growing recognition of the importance of individual variation in behavior (Shaw 2020) that can sometimes relate to possible individual covariates. Smaller and/or poorer condition fish tended to move more during the observation period, likely driven by density-dependent factors (Coulter et al. 2018b, Baines et al. 2020). No previous work has related Silver Carp movement to condition but several studies have examined the influence of length on movement with mixed results, including a positive association with total length and movement in mobile individuals and a negative relationship in sedentary individuals (Coulter et al. 2018b, Prechtel et al. 2018, Coulter et al. 2022). Condition and length may have influenced movement metrics differently since condition reflects the health and development of reproductive organs of an individual while length is closely related to age.

Our results identified specific individuals that may pose an increased risk of spread based on their movements which could allow managers to target “high risk” individuals in control efforts. Removal of this species for commercial harvest or population reduction/management often uses entanglement gears that may inadvertently target those fish our study found to be moving less (higher condition, larger size). Removal of large individuals could provide immediate benefit by preventing them from spawning immediately, but removing small individuals may prevent multiple spawning periods, hence reducing their long-term spawn potential (Tsehaye et al. 2013). Methods such as the “Modified Unified Method” or Dozer Trawls that are less size selective could be used by managers seeking to remove multiple sizes of individuals (Hammen et al. 2019). Quantifying the effects of individual and environmental factors can aid in the control and containment of this invasive species and may help to manage populations in at-risk environments.

CHAPTER 2

MORPHOLOGY EFFECT ON MOVEMENT IN THE WABASH RIVER

INTRODUCTION

Morphology can provide valuable insight into the movement patterns of animals due to its influence on locomotion and habitat use (Kolok 1992; Robinson and Wilson 1994; Snorrason et al. 1994; Lauder and Drucker 2004). Swimming performance is one of the most important factors affecting the survival of a fish, and one of the greatest influences on fish swimming performance is body morphology (Ohlberger et al. 2006; Hanson et al. 2007). Certain morphologies enhance swimming abilities both within and among species leading to better predator avoidance, successful migration or invasion, defense of territories or offspring, and improved access to habitats (Pettersson and Hedenström 2000; Blake et al. 2005; Hanson et al. 2007). There are three main ways body morphology can affect swimming performance: the ability to perform precise maneuvers, the power of acceleration, or the energetic cost of sustained swimming (Webb 1984).

Body length, caudal peduncle depth, and caudal fin aspect ratio are the morphological characters that are most likely to affect the energetic cost required for sustained swimming. Optimal characteristics for efficient swimming include longer body length, a narrow caudal peduncle, and a high caudal fin aspect ratio (Boily and Magnan 2002; Sambilay1990; Webb 1982). Body length has been shown to be a morphological factor that can influence movement in fish (Schrank and Rahel 2006; Guy and Brown 2007). Caudal fin characteristics especially can be used as an indicator of swimming speed across many fish species (Sambilay 1990). Boily and Magnan (2002) found that a low aspect caudal fin was an indicator of poor swimming in Yellow Perch. Additionally, several different highly active species, such as tuna, have all converged to have a similar body form, a narrow caudal peduncle and a low caudal fin aspect ratio. This suggests that these features help provide better swimming performance, by increasing thrust or reducing drag (Webb 1984; Blake et al. 2009; Feilich and Lauder 2015). Similar morphology in other species could make those fish more efficient swimmers.

Invasive Silver Carp populations are expanding on all fronts and are threatening to establish in the Laurentian Great Lakes, which could cause devastating effects to that ecosystem (Huxel 1999) and associated fisheries (Lodge et al. 2006). Understanding their movement patterns is vital to prevent their populations from spreading further and to improve management efficiency (Coulter et al. 2018). Silver Carp show a leptokurtic distribution of movements with many individuals remaining in one location while others are mobile (Coulter et al. 2016; Coulter et al. 2022; Prechtel et al. 2018). Mobile individuals may be of particular interest to managers as these individuals may pose the highest risk for spread. Differences in behavioral type may be partially driven by morphological differences. Other species have shown varying behavior may affect morphology (Mittelbach et al. 2014). The relationship between morphology and movement has not been studied in Silver Carp and may provide additional knowledge that can be used in management and eradication efforts.

In this study, I examine if multiple morphological metrics relate to the movement of Silver Carp and if Silver Carp with similar movement have similar morphology. My objectives are to determine the geometric morphology of Silver Carp, track their movements, and see if morphology and movement are related. My hypothesis is that the fish that move more will have longer length, narrower caudal peduncle, and lower caudal fin aspect ratio. These carp are expected to have both greater ranges and total movement. Knowing if morphology is related to movement is useful because it could assist management on eradicating the Silver Carp that pose the biggest threat to spreading the invasion front.

METHODS

Study Area

The Wabash River is an 810 km-long tributary of the Ohio River. It flows in a southwest direction across Indiana and its watershed drains most of the state. The Wabash River has only one mainstem dam near Huntington, Indiana, which is located upstream of the study area. The Wabash River flows freely for 660 km from the dam to its confluence with the Ohio River. The focus of this study was on the lower portions of the Wabash River and its tributary, the White River. The Wabash River is unnavigable by large boats and barges due to its abrupt and unpredictable changes in water depth. The lower portions of the Wabash River are dominated by sandy substrates, with few backwater habitats. The Wabash River is different from other rivers where Silver Carp movements have been studied and instead resembles rivers like tributaries of the Laurentian Great Lakes which are susceptible to future invasion (Coulter et al. 2016). An advantage of studying Silver Carp in the Wabash River is there is no compounding impacts of dams on the results. This makes the Wabash River an ideal study site because the results from this research can provide recommendations to similar habitats if the invasion continues to spread or worsen.

Telemetry

An acoustic telemetry array for the Wabash and White Rivers was established in the summer of 2021. This array of stationary receivers (model VR2Ws; Vemco) were deployed and used to monitor movements of tagged individuals. Forty receivers, which were deployed in pairs, were distributed evenly along the Wabash and White River approximately every 25 km. Three hundred adult Silver Carp were collected, tagged, and released from May 2021 through May 2022 from locations dispersed along the Wabash River from Mount Carmel and Hutsonville in Illinois, and New Harmony, Vincennes, and the White River in Indiana. These Silver Carp were captured by using boat electrofishing (Coulter et al. 2018, Lubejko et al. 2017) and were implanted with acoustic tags (Vemco V16-4H, 120 s mean ping interval, Vemco, Bedford, Nova Scotia, Canada) following the 2% rule of transmitter to total weight. Surgical procedures followed those described in Lubejko et al. (2017) and Coulter et al. (2018). Details of surgery are described in Chapter 1. Length (mm) and weight (g) measurements were taken from every fish. Only fish meeting the same criteria for survival as described in Chapter 1 were included in this analysis.

Morphometrics

Morphometric analysis was conducted to measure body conditions that may be linked to individuals with greater range and movement rate. Photographs were taken of each fish before telemetry tag surgery using a setup designed to take the most “natural”, least distorted view of the individual. The setup was built following the guidelines set by Muir, Vecsei and Krueger (2012). Each fish was laid on a fine net over a wooden box to prevent any distortion of the fish when laid down. This allowed the fish body to sink while the head and tail were elevated. An overhead tripod with a Nikon D3000 digital camera with a 50-mm focal length, positioned directly over the fish in a flat plane was used (Muir, Vecsei, and Krueger 2012). After being anesthetized and before surgery, each fish was laid in the middle of the net on its left side with its fins placed in a natural position (Clabaut et al. 2007; Valentin et al. 2008; Farré et al. 2016). A ruler was included in the photograph so that the scale of the landmark configuration can be computed (Webster and Sheets 2010). Three photographs were taken of each fish to ensure the photograph was in focus. A level was used to make sure the camera, tripod, and box were flat. Fish were then released back into the river.

Data Analysis

Morphological differences among fish were determined from geometric morphometric measurements using multiple statistical programs for image processing and analysis. Landmark locations on fish were from Coulter et al. 2019 (Figure 2.1; Table 2.1). Within MorphoJ, Procrustes superimposition, covariance matrix, and principal component analyses were performed. The data were evaluated for outliers and none were found. A regression was performed with centroid size as the independent variable and Procrustes coordinates as the dependent variable. Regression residuals were exported into an Excel spreadsheet to use for further analysis.

Data were pulled from acoustic telemetry receivers in August 2022. The movement metrics calculated for each tagged fish to relate to morphometrics were range (maximum rkm - minimum rkm) and total movement (sum of all distances per detection). Range evaluated how much of the river a fish used as habitat and showed how far upstream or downstream a fish may travel overall. Total movement revealed whether a fish was sedentary or mobile and the extent of river use. Days detected, tagging date, range, and total movement were all uncorrelated ($r<0.5$). Four movement groups were identified based on range and total movement. A frequency histogram was used to determine cut offs for movement groups, with a minimum of ten individuals in each group required for analysis.

PERMANOVAs were run to determine if movement groups from each movement metric and geometric morphometric residuals were related. In addition to the geometric morphometric residuals, other body measurements were calculated (total length, caudal peduncle depth, caudal fin aspect ratio) and compared among movement groups. Caudal fin aspect ratio was determined by $A=h^2/s$ (h = height of the caudal fin; s = area of fin) (Sambilay 1990). A correlation matrix was performed on body measurements to ensure metrics were not related. Total length and caudal peduncle depth were highly correlated (r=0.76), while aspect ratio was unrelated to total length (r=0.14) or caudal peduncle depth (r=0.14). Caudal peduncle depth was dropped from analyses and length was retained due to ease of measurement. To evaluate differences among movement groups based on body measurements, generalized linear models were created with movement group as the explanatory variable and body measurements as response variables. Gamma(log) models were created using glm() function in stats package. Residuals were checked to determine goodness-of-fit. ANOVA were run on the gamma(log) models to determine if movement group explained body measurements. To evaluate movement metrics in a continuous framework (no movement groups), additional generalized linear models were created. Zero inflated gamma models were created using glmmTMB(). DHARMa residual was used to check goodness-of-fit. ANOVA were run on the zero inflated gamma models to determine if movement explained body measurements.

RESULTS

In total, 75 fish had movement data and morphology photographs. There were 608,235 detections received by the acoustic telemetry array from the 75 individuals. Each individual had an average of 11.6 ± 1.43SE detections. All individuals were detected for 2-277 days with an average of 56.6 ± 3.34SE days. Every month from August 2021 to August 2022 had at least 30 detections. Range movement groups included: group 1 (0 km), group 2 (0.1–10 km), group 3 (11–70 km), and group 4 (71+ km). Total movement groups included: group 1 (0km), group 2 (0.1–15 km), group 3 (16–80 km), and group 4 (81+ km). Averages, minimums, and maximums of movement metrics and body measurements were calculated (Table 2.2). Geometric morphometric analysis showed a wide range of morphologies of Silver Carp in the Wabash River (Figure 2.3).

PERMANOVA showed movement group was a non-significant predictor of geometric morphometric variation for either movement metric, since both range groupings ($F_{1,71}$=0.95, p=0.51) and total movement groupings ($F_{1,71}$=0.73, p=0.83) were non-significant. All body measurements were not different among range groupings (length: t=-1.49, p=0.14; aspect ratio: t=0.30, p=0.77) nor for total movement groupings (length: t=-1.6, p=0.11; aspect ratio: t=0.56, p=0.58). ANOVA also showed body measurements had no significant variation among range groupings (length: $F_{1,71}$=2.0, p=0.16; aspect ratio: $F_{1,71}$=0.06, p=0.81) and total movement groupings (length: $F_{1,71}$=2.3, p=0.13; aspect ratio: $F_{1,71}$=0.22, p=0.64). All body measurements were non-significant for the continuous metrics of range (length: z=-1.1, p=0.29; aspect ratio: z=0.64, p=0.52) or total movement (length: z=-1.1, p=0.29; aspect ratio: z=0.55, p=0.59). ANOVA also showed body measurements had no significant variation among range metric (length: $F_{1,71}$=2.3, p=0.13; aspect ratio: $F_{1,71}$=0.57, p=0.46) and total movement metric (length: $F_{1,71}$=2.3, p=0.13; aspect ratio: $F_{1,71}$=0.57, p=0.46).

DISCUSSION

It is critical to know the factors that affect the movement of the invasive Silver Carp in order to stop the advancement of the invasion front and lessen ecosystem damage. Many factors have been studied in relation to movement, but geometric morphometrics (the interactions among many body morphology characters) have never been examined as a potential predictor of movement in an invasive species. A recent study found that traditional ways to measure morphometrics may be better to distinguish groups of fish than geometric morphometrics

(Martin et al. 2023), which reaffirmed why both geometric morphometrics and body measurements were tested in this study. The combination of geometric morphometrics and body measurements to examine shape and acoustic telemetry to examine movement made this study a thorough examination of how body shape could predict movement. Along with this, the sample size of the study was large, every season was included, and data from detections were captured every month of the study. Data from all seasons were included and a range of environmental conditions was covered, including major variation in discharge (6,590-126,000 ft^3/s) and water temperature (1.0-31.4 °C) (USGS, monitoring location 03378500). These data were sufficiently comprehensive to detect an effect of morphology if one occurred.

Despite quantifying geometric morphometrics as well as individual morphological characters, neither were informative about movement patterns. A wide range of morphologies occurred among Silver Carp in the Wabash River but geometric morphology, length, caudal peduncle depth, and caudal aspect ratio did not provide an explanatory pattern for long-distance movements. Long-distance movements include metrics like home range over an extended period of time, while small-scale movements include daily movements within an individual's home range. Morphology may affect small-scale patterns of movement which were not considered in this study. Previous studies have looked at the effect morphology has on drag (Pettersson and Hedenström 2000; Hanson et al. 2007; Feilich and Lauder 2015). Drag could greatly reduce the swimming ability of a fish (Bushnell and Moore 1991) and may have influenced movement in this study.

Body shape could affect movement if other factors were examined. All the fish in this study were most likely mature. Bigger fish have been known to move more, but mature fish may be engaging in activities like spawning and gathering in the same area (Deters et al. 2013). Our subset of fish was from a relatively small range of sizes. Most carp movement studies (Coulter et al. 2016; Lubejko et al. 2017; Prechtel et al. 2017) had smaller individuals or smaller averages than included in this study. There was no distinct morphological separation seen, but hybridization could have occurred with Bighead Carp (*Hypophthalmichthys nobilis*). Introgressive hybridization between these two species has been seen before (Murphy et al. 2007; Coulter et al. 2020) and could explain morphological variations. Some hybrids may look indistinguishable from Silver Carp but have different physiology or behaviors. Other biotic factors, such as genetics, may affect Silver Carp fitness and be related to how they move. Morphology and movement may not yet be related because Silver Carp are newly introduced to the U.S. Midwest system and have not yet had enough evolutionary pressure to develop an optimum morphology.

Abiotic factors could have had an influence on movement as well. The Wabash River has a very different flow environment than other rivers in the area. The Ohio and Illinois rivers are dammed for navigation during summer and act as pools during this time. The study site within the Wabash River is not dammed and water levels become very low (Pyron et al. 2020). This changes the flow environment and may have influenced the swimming ability of Silver Carp in the Wabash River compared to other environments, where they may have remained stationary for long periods of time. Silver Carp have been shown to prefer low flow areas (Calkins et al. 2012). Silver Carp may be acting differently in the Wabash River than in other systems due to this behavior.

Quantifying the effects of individual factors can aid in the control and containment of this invasive species and may help to manage populations in at-risk environments. The lack of relationship between body shape and movement is an important insight for Silver Carp management. Because body shape isn't a good predictor of the more mobile individuals, indiscriminate gear for removal could be an effective way to eradicate the biggest movers. Other factors, such as reproductive potential, could be the most effective way to target Silver Carp that will contribute the most to the invasion. General invasive species management could use these principles to guide their management as well.

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APPENDIX A

FIGURES AND TABLES

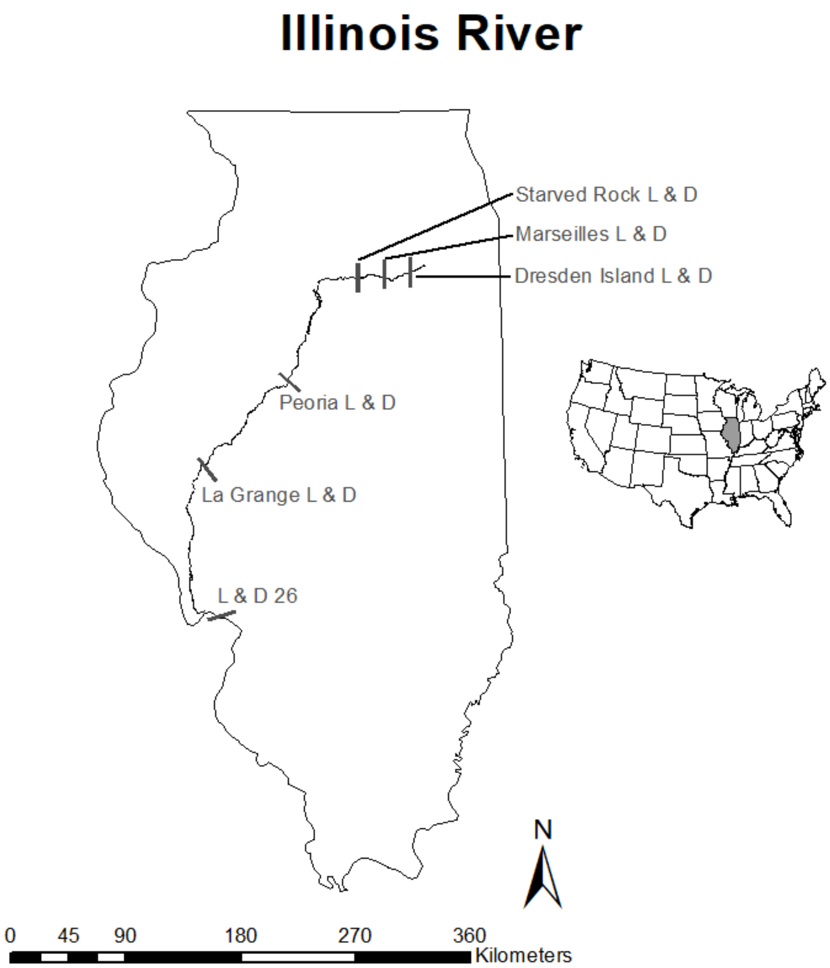

Figure 1.1. Map of the study site, the Illinois River. All lock and dams on the river are marked with a slash and labeled. All these sites were also the locations were the Silver Carp used in this study were collected, tagged, and released.

Table 1.1. The mean, minimum, and maximum of all factors and movement metrics for Silver Carp in the Illinois River.

Factor	Mean	Minimum	Maximum
Body Condition (W_r)	102	77	166
Length (mm)	636	465	827
Temp (°C)	14	0	32
Discharge (m^3/s)	2013	273	9167

Movement Metric (km)	Mean	Minimum	Maximum
Range	17	0.16	224
Total Movement	44	0.16	360
Upstream Rate	1.7	0.16	43
Upstream Distance	4.1	0.16	92
Downstream Rate	4.1	0.16	120
Downstream Distance	11	0.16	260

Table 1.2. Final averaged model results from AICc for the influence of each factor on several different movement metrics of Silver Carp. Estimate with standard error are listed in each box. Dashed lines signify variables that were dropped by AICc.

Movement Metric	W_r	Length	Temp	ΔTemp	Discharge	ΔDischarge
Range	-0.78 ± 0.11	-0.15 ± 0.11	-0.37 ± 0.11	0.25 ± 0.11	0.090 ± 0.11	0.092 ± 0.11
Total Movement	-0.061 ± 0.093	-0.34 ± 0.10	-0.49 ± 0.11	0.069 ± 0.13	0.14 ± 0.13	-0.0002 ± 0.13
Downstream Distance	---	0.0068 ± 0.01	-0.51 ± 0.062	---	0.17 ± 0.076	---
Downstream Rate	0.030 ± 0.023	---	---	---	-0.042 ± 0.02	---
Upstream Distance	---	-0.16 ± 0.063	-0.27 ± 0.084	0.052 ± 0.062	0.021 ± 0.024	---
Upstream Rate	---	-0.39 ± 0.19	-0.74 ± 0.23	0.79 ± 0.27	0.040 ± 0.046	---

Table 1.3. Results from final averaged models. Filled boxes indicate significant or marginally significant results. Plus sign (+) shows increasing the associated factor will increase the given movement metric. Minus sign (-) shows decreasing the associated factor will increase the given movement metric. The spaces are left blank if the factor was not significant.

	Range	**Total Movement**	**Upstream Rate**	**Upstream Distance**	**Downstream Rate**	**Downstream Distance**
W_r						
Length		-	-	-		
Temp.	-	-	-	-		-
Discharge					-	+
ΔTemp.	+		+			
ΔDischarge		-				

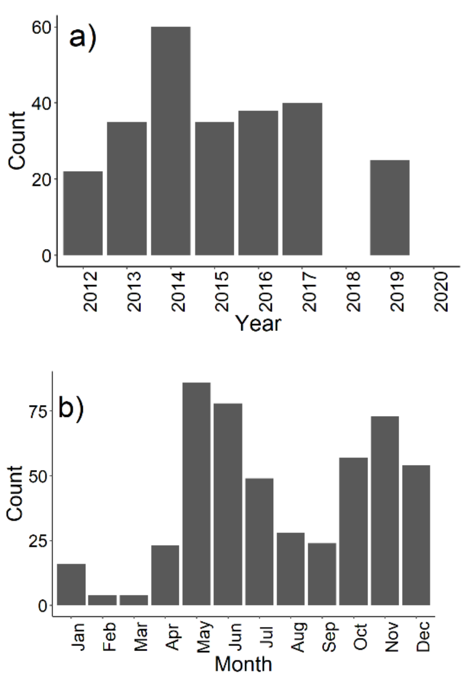

Figure 1.2. a) Number of Silver Carp tagged every year of the study. b) Number of Silver Carp that had detections in a month for all years of the study (2012-2020).

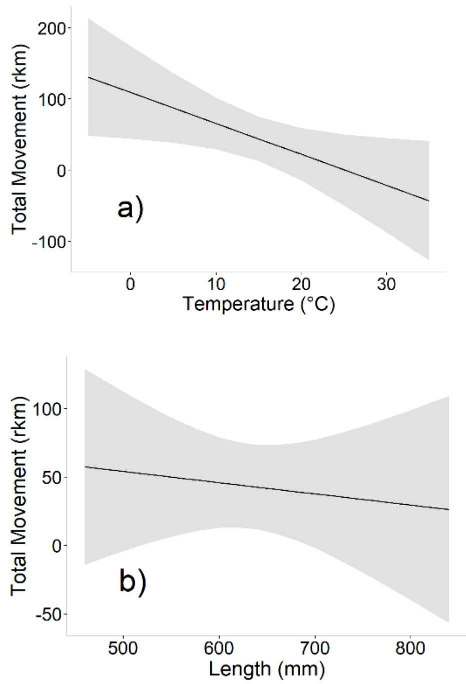

Figure 1.3. Predicted values of total movement given a specific temperature (a) and length (b).

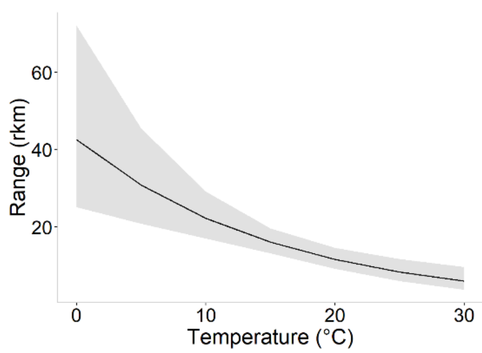

Figure 1.4. Predicted values of range given a specific temperature

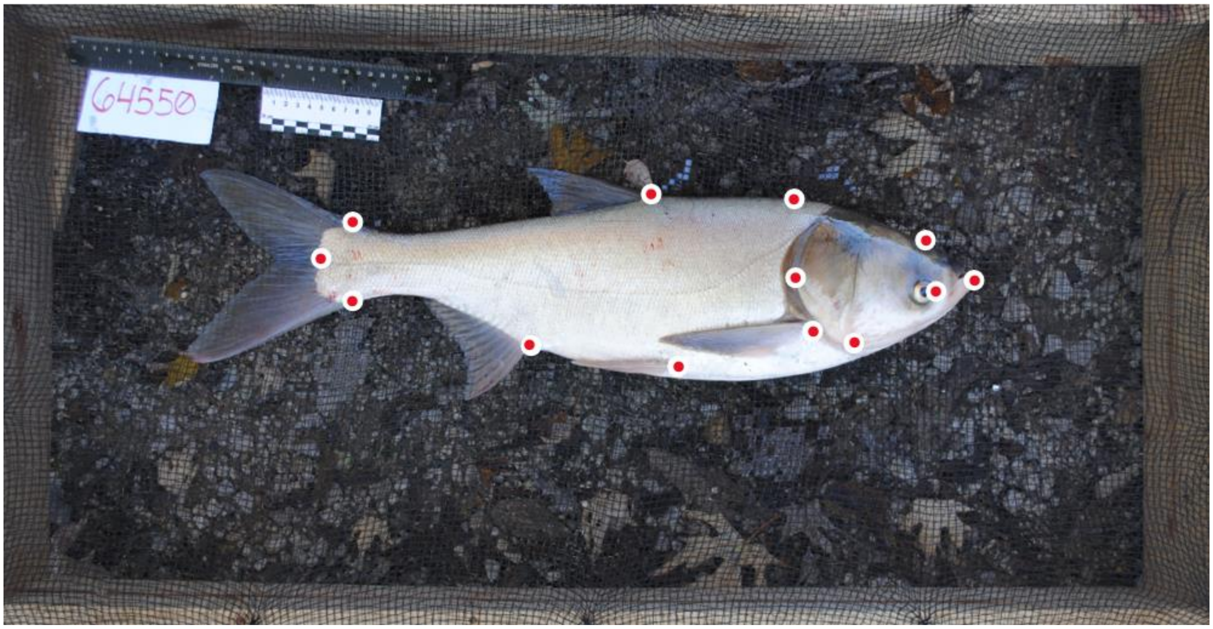

Figure 2.1. Example of morphometric photo of a Silver Carp taken to determine morphology. Dots represent landmark locations used in geometric morphometric analysis.

Table 2.1. Descriptions of landmark locations used in geometric morphometric analysis (Coulter et al. 2018b).

Landmark	Description
1	Anterior point of snout
2	Anterior extreme of bony orbit of eye
3	Top of cranium at midpoint of eye
4	Top of cranium at posterior point of bony opercle
5	Posterior point of bony opercle
6	Doral insertion of pectoral fin
7	Anterior ventral point of bony opercle
8	Anterior insertion of dorsal fin
9	Dorsal origin of caudal fin membrane
10	Posterior of hypural bones at lateral membrane
11	Ventral origin of caudal fin membrane
12	Anterior insertion of anal fin
13	Anterior insertion of pelvic fin

Table 2.2. The mean, standard error, minimum, and maximum of all factors and movement metrics for Silver Carp in the Wabash River (N =75).

Factor	Mean	SE	Minimum	Maximum
Range (km)	27.0	5.46	0.00	204
Total Movement (km)	35.6	7.23	0.00	349
Weight (kg)	3.06	0.08	2.03	5.90
Total Length (mm)	663	5.78	570	823
Peduncle Depth (mm)	67.6	0.76	55.0	87.0
Caudal Aspect Ratio	27.2	0.64	16.2	38.3

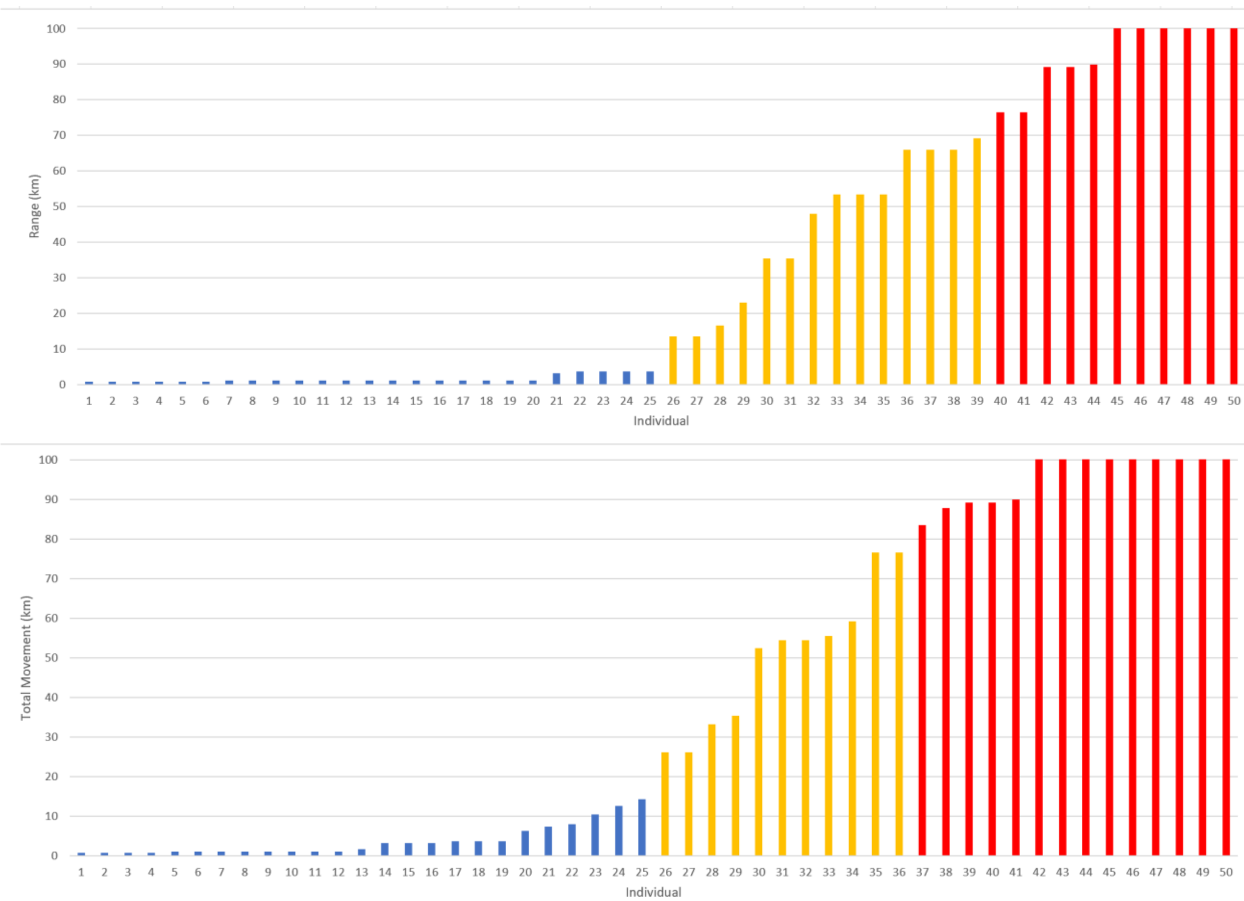

Figure 2.2. Movement groups assigned for all Silver Carp. Twenty-five individuals had zero range and total movement (not represented in these plots). Three other movement groups were created based on histograms and a minimum number of ten individuals per group. Separate groups were assigned for range and total movement.

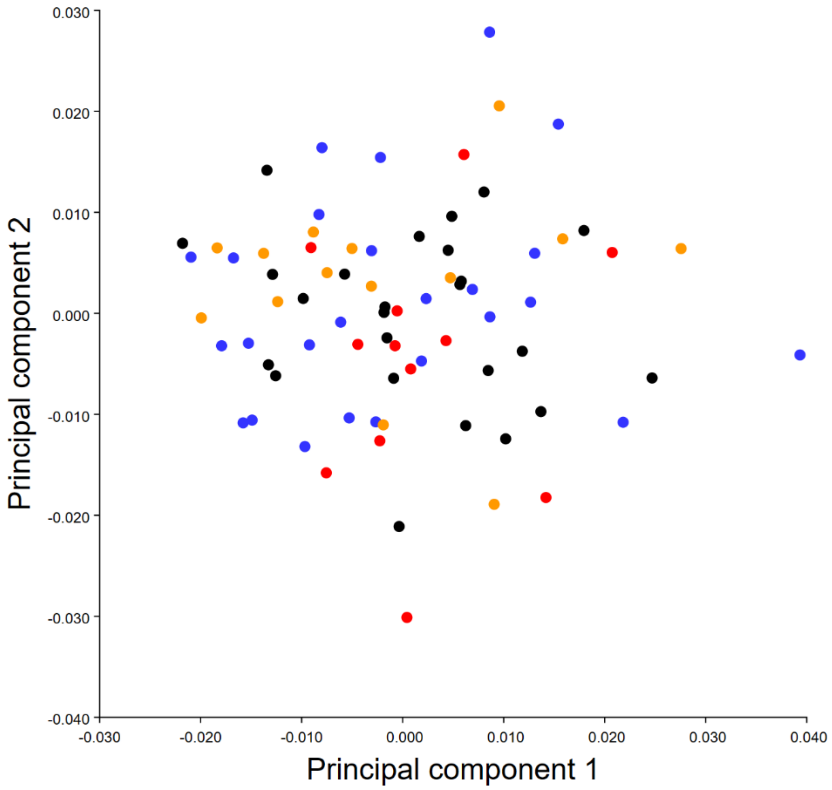

Figure 2.3. Principal component analysis for geometric morphology. PC1 variance explained: 25%. PC2 variance explained: 17%. The large distribution (i.e. not in clusters) shows there are many morphological variations of the Silver Carp included in this study. Black is zero range, blue is small range, orange is medium range, and red is large range. The lack of clustering by color shows range may not be a powerful predictor of morphology.

Table 2.3. Eigenvalues for the principal component analysis for geometric morphology. Eigenvalues that explained less than 10% of variation were not included.

PC	Eigenvalues	% Variance	Cumulative %
1	0.000149	24.7	24.7
2	0.000102	16.9	41.5
3	0.0000946	15.6	57.2

APPENDIX B

SUPPLEMENTAL MATERIALS

Table 1.4. Correlation matrix of movement metrics.

Movement Metric	Range	Total Movement	Upstream Distance	Upstream Rate	Downstream Distance	Downstream Rate
Range	1.00	-0.01	0.07	0.10	0.02	-0.01
Total Movement	-0.01	1.00	-0.02	-0.01	0.04	0.05
Upstream Distance	0.07	-0.02	1.00	0.75	-0.09	-0.05
Upstream Rate	0.10	-0.01	0.75	1.00	-0.06	-0.07
Downstream Distance	0.02	0.04	-0.09	-0.06	1.00	0.53
Downstream Rate	-0.01	0.05	-0.05	-0.07	0.53	1.00

Table 1.5. All models with delta AIC < 2 that went into the average model for all movement metrics.

Group	Model	logLik	AICc	DeltaAIC	AICWeight
Range	Change Temp. + Length + Start Temp.	-938.9	1888.0	0.00	0.30
	Change Disc. + Change Temp. + Length	-938.0	1888.3	0.30	0.26
	+ Start Temp.	-939.5	1889.2	1.20	0.16
	Change Disc. + Change Temp. + Start	-938.5	1889.2	1.23	0.16
	Temp.	-937.7	1889.9	1.84	0.12
	Change Temp. + Length + Start Temp.				
	+ Wr				
	Change Disc. + Change Temp. + Length				
	+ Start Temp. + Wr				
Total Movement	Change Disc. + Change Temp. + Length	1302.1	-	0.00	1.00
	+ Discharge + Temp. + Wr		2586.2		
Downstream Distance	Temp. + Discharge	-1884.2	3778.5	0.00	0.72
	Temp. + Discharge + Length	-1884.1	3780.4	1.89	0.28
Downstream Rate	Discharge	1241.0	2490.0	0.00	0.53
	Discharge + Wr	1240.0	2490.2	0.24	0.47
Upstream Distance	Temp. + Change Temp. + Discharge +	-336.4	687.5	0.00	0.35
	Length	-337.9	688.2	0.79	0.23
	Temp. + Discharge + Length	-337.9	688.2	0.79	0.23
	Temp. + Change Temp. + Length	-339.2	688.7	1.30	0.18
	Temp. + Length				
Upstream Rate	Temp. + Change Temp. + Length	-128.1	268.7	0.0	0.68
	Temp. + Change Temp. + Discharge +	-127.8	270.2	1.5	0.32
	Length				

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