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COMPARISON OF BIGHEADED CARP REPRODUCTION IN TRIBUTARIES OF THE ILLINOIS AND WABASH RIVERS

A Thesis

Submitted for the Requirements for the Degree of

Master of Science

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ABSTRACT

Understanding environmental conditions that support bigheaded carp (*Hypophthalmichthys sp*.) reproduction in tributary rivers provides key predictions of their invasion throughout the United States. Past research, primarily in larger order rivers, identified factors such as discharge, temperature, and turbidity as main environmental drivers of bigheaded carp reproduction. I used the variable hydrologic conditions between the Illinois and Wabash Rivers to compare environmental conditions between tributaries of each basin, determine which conditions influence bigheaded carp reproduction in tributaries, and predict tributaries likely to support bigheaded carp reproduction. Three tributaries of the Illinois and Wabash Rivers were sampled for ichthyoplankton from March-September 2016-2020. I compared tributary conditions, such as discharge, water temperature, chlorophyll *a*, and total phosphorus between each basins. Between basins, I found Wabash tributaries had higher discharge, whereas Illinois tributaries had higher dissolved oxygen. The Sangamon and Little Wabash had the highest peak larval densities, with highest overall peak densities in the Illinois River basin. Bigheaded carp reproduction in Wabash tributaries was positively influenced by discharge, whereas reproduction in Illinois River tributaries was positively related to temperature and discharge. Additionally, I found that tributaries can support similar reproduction to mainstem rivers likely due to increased hydrologic variation. I used drainage area to predict tributaries susceptible to bigheaded carp reproduction, such as the Grand and St. Joseph Rivers, in the Lake Michigan basin. Expanded monitoring of these tributaries is needed as they can serve as sources of recruitment to basin-wide bigheaded carp populations and their size is comparable to Great Lakes tributaries.

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INTRODUCTION

One of the most problematic groups of invasive fishes currently in the U.S. are the bigheaded carps (*Hypophthalmichthys* sp.), which include Bighead Carp (*Hypophthalmichthys nobilis)* and Silver Carp (*Hypophthalmichthys molitrix*). Bigheaded carp are pelagic planktivores introduced into the United States in the 1970’s for the biological control of zooplankton and phytoplankton in aquaculture ponds, where flooding lead to their eventual escapement into the Mississippi River basin (Kolar et al. 2005). This escapement caused concern as bigheaded carp display high growth and reproductive rates and are thought to compete with native fish for planktonic prey (Sampson et al. 2009; DeBoer et al. 2018). The phytoplankton and zooplankton that bigheaded carp consume are not only an important food source for native filter feeders (Sampson et al. 2009), but also the larval and early juvenile stages of many native fish species (Nunn et al. 2012). Additionally, bigheaded carp are highly fecund (Williamson and Garvey 2005), one of the many contributors to their rapid population expansion throughout the United States.

Currently, one of the greatest unknowns concerning bigheaded carp range expansion is their potential impact to the Laurentian Great Lakes. The Laurentian Great Lakes account for nearly US$7 billion in yearly revenue from sportfishing (Krantzberg and De Boer 2008; Tsehaye et al. 2013). With populations of bigheaded carp as close to Lake Michigan as the Dresden Pool of the Illinois River and their eDNA occasionally found within the Chicago Area Waterway System (Song et al. 2017), there have been many questions about the possibility of bigheaded carp becoming established in the Great Lakes and impacting this multi-billion dollar industry. Should bigheaded carp reach the Great Lakes, there is a debate on their ability to become established in these environments with some studies suggesting there are a lack of suitable offshore habitats to support population establishment due to declining phytoplankton densities in

Lake Michigan (Vanderploeg et al. 2012; Alsip et al. 2019) with Lake Erie showing more favorable food availability (Anderson et al. 2015). In addition to the suitability of foraging habitat, there must also be sufficient spawning habitat and conditions to support establishment and expansion of bigheaded carp populations within the Laurentian Great Lakes. Bigheaded carp require long stretches of turbulent water to maintain eggs in suspension to promote hatching (Garcia et al. 2015), indicating that the Great Lakes themselves offer little potential to support reproduction compared to their tributaries. Within their invasive range, bigheaded carp show highly plastic reproductive traits (Coulter et al. 2013) compared to within their native range (Deters et al. 2013); therefore, additional research is needed to identify conditions that facilitate successful reproduction of non-native populations of bigheaded carp.

Identifying local and catchment scale factors that characterize fish communities and populations (Esselman and Allan 2010) can be useful in explaining seemingly sporadic and inconsistent reproductive events and abundance estimates of ichthyoplankton (Cyr et al. 1992; Michaletz and Gale 1999; Krabbenhoft et al. 2014). Past research has identified several local-scale environmental factors that correlate with bigheaded carp reproduction, such as discharge (Schrank et al. 2001) and water temperature (Kolar et al. 2007). River discharge peaks that coincide with water temperatures between 17 to 30°C have been shown to trigger spawning events in bigheaded carp (DeGrandchamp et al. 2007; Kolar et al. 2007; Kocovsky et al. 2012). Often associated with increased river discharge, high turbidity has also been found to correspond with increased bigheaded carp reproduction (Deters et al. 2013; Hintz et al. 2017). Although not extensively compared to bigheaded carp reproduction, higher dissolved oxygen levels are needed to support larvae survival and development of most species (Werner 2002) and has some correlation to bigheaded carp reproduction (Roth et al. 2021). Adequate food availability is considered one of the most important factors in determining the survival of larvae (Werner 2002) and may influence adult fish reproductive behaviors and habitat selection (Bakun 2010). As planktivorous fish, plankton availability could play a role in determining the spatiotemporal variability in successful reproduction due to changing water chemistry, nutrients, and other environmental conditions. For example, studies have found phytoplankton densities (estimated with chlorophyll *a*) to inversely correlate with river discharge (Biggs 1995; Harvey et al. 1998). Additionally, there has been evidence of fish assemblages and reproduction being influenced by broader catchment scale variation (e.g., drainage area and latitude) rather than reach-scale variation (Wang et al. 2006; Esselman and Allan 2010; Schaick et al. 2020) due in part to catchment characteristics like drainage area correlating with more localized conditions such as discharge (Knighton 2014) and nutrients (Lohman and Jones 1999).

Most previous research on bigheaded carp has focused on high order streams, such as the Mississippi and Illinois Rivers, with various studies examining abundance and reproduction (e.g., Sass et al. 2010; Larson et al. 2017; Parkos et al. 2021). However, there have been relatively few studies (e.g., Camacho et al. 2020; Schaick et al. 2020) focusing on mechanisms of reproduction in smaller order tributaries of these rivers. Smaller rivers, such as tributaries of the Illinois and Wabash Rivers, often experience greater variation in their flow regime than their mainstem counterparts (Figure 1). The flow variation in tributaries shows potential for bigheaded carp reproduction at different times and increased frequency than larger rivers (Camacho et al. 2020). For example, a tributary may experience a greater change in river discharge than the mainstem river at a time when other environmental factors are optimal, which could influence bigheaded carp to select tributaries as spawning habitat over mainstem rivers that are slower to respond to precipitation events. With evidence of protracted spawning by bigheaded carps

(Papoulias et al. 2006; Coulter et al. 2013), tributaries also have the potential to host spawning events outside the typical spawning season as a product of localized precipitation events.

The contrasting hydrology of the Illinois River and Wabash River allows for a comparison of bigheaded carp reproduction under a potentially wide range of environmental conditions. The Illinois River is a 707-km-long river that drains approximately 75,000 km^2 of agriculturally dominated landscape (Groschen et al. 2000) and has been heavily modified by seven locks and dams that facilitate barge traffic (DeBoer et al. 2021). These modifications result in severe channelization and regulated river discharge (Mattingly et al. 1993). In addition to these modifications, alterations in fish populations and communities have been attributed to poor water quality throughout the basin (Pegg and McClelland 2004; Whitten and Gibson-Reinemer 2018). The Wabash River is an 810-km-long river that drains nearly 85,500 km^2 of agriculturally dominated landscape into the Ohio River. However, unlike the Illinois River, the Wabash River is relatively shallow and largely unimpounded. The free-flowing portion of the Wabash River extends for 662 km, the longest stretch of free-flowing river east of the Mississippi River (Gammon 1998). Despite a more natural flow regime, anthropogenic changes to the river have led to many extinctions and regional extirpations of species in Wabash’s extremely diverse fish community (Simon 2006). Though bigheaded carp invaded the Wabash River in a similar timeframe as the Illinois River, their abundance never reached the hyperabundant levels found in the Illinois River, potentially due to the Wabash River having less habitat degradation (Stuck et al. 2015; Shields et al. 2021).

The aim of this study was to examine bigheaded carp reproduction in tributaries of two hydrologically distinct rivers, the Illinois and Wabash Rivers, to determine the environmental conditions that may influence reproductive success in these systems. Tributary information will be useful in combination with large river research to provide a comprehensive management plan targeting critical areas to prevent the spread of these bigheaded carp species. Several studies have used thermal and hydrologic modeling to predict bigheaded carp reproduction in Great Lakes tributaries (Kocovsky et al. 2012; Murphy and Jackson 2013). However, determining the reproductive potential of Great Lakes tributaries can be aided by the examination of similarly sized Illinois and Wabash tributaries that support bigheaded carp reproduction and the environmental conditions that support them. My objectives in this study were to 1) compare environmental conditions within and among the Illinois and Wabash tributaries and basins, 2) quantify the environmental mechanisms leading to invasive carp reproduction in tributaries of two hydrologically distinct rivers, and 3) use significant environmental drivers of bigheaded carp reproduction to determine reproductive potential in uninvaded environments, such as Lake Michigan tributaries. I hypothesized that hydrological variation would be the most important factor in determining bigheaded carp reproduction followed closely by thermal variation, with Wabash tributaries being primarily influenced by hydrology and the Illinois tributaries being influenced by multiple environmental factors including hydrology due to contrasting basin wide hydrology. Further, tributaries with the greatest overall river discharge, and by correlation greatest drainage area, would likely have the highest bigheaded carp reproduction. Additionally, I also predicted drainage area to be the best indication of tributaries susceptible to bigheaded carp reproduction.

METHODS

Study Sites

Three tributaries each of the Wabash River (Little Wabash, Embarras, and Vermilion) and the Illinois River (Sangamon, Spoon, and Mackinaw) were sampled (Figure 2) from 2016-2020. Tributaries were selected due to their connectivity to basins with established populations of bigheaded carp that are known to support reproduction (Irons et al. 2010; Coulter et al. 2013). Each tributary was sampled at two locations, one lower site near the mouth and one upper site, to investigate the spatial extent of reproduction (Figure 2). Additionally, the mainstem river was sampled upstream of each tributary confluence. Sampling was conducted monthly in April and August-September and bi-weekly from May-July from 2016-2019. There was increased sampling effort (weekly) during June and July of 2020 when conditions favorable for bigheaded carp spawning were present (i.e., rising hydrograph with water temperatures exceeding 17°C, Kolar et al. 2007).

Sampling Techniques

Fish eggs and larvae were collected using active (push) and passive (drift) netting techniques at lower tributary and mainstem sites, while only drift nets were used at upper sites because shallow water conditions precluded the use of push nets. Push nets had openings of 0.5m with 3.0m of 500µm mesh netting and were mounted on a frame at the bow of the boat. Push nets were submerged directly below the surface and driven upstream for five minutes at a speed targeting 10,000 rotations on a General Oceanics flowmeter or approximately 50m^3 of filtered water. Drift nets had rectangular openings of 0.25m height x 0.45m width with 1.0m of 500µm mesh netting. Drift nets were set just below the water surface and fished for time periods determined by water velocities calculated using a Hach FH950 portable velocity meter in order to filter approximately 50m^3 of water. For both net types I sampled left-channel, mid-channel, and right-channel habitats to account for varying habitat types and water velocities. Larval fish and eggs collected in the nets were preserved in 95% ethanol until identification in the laboratory.

Environmental data was collected at each sampling location during reproduction surveys to investigate which conditions facilitate bigheaded carp reproduction. To quantify phytoplankton and nutrient levels, I collected surface water samples to determine sestonic chlorophyll *a* (µg/L) and total phosphorus (mg/L) concentrations during 2019-2020. Water temperature (°C), dissolved oxygen (mg/L), and water velocity (m/s) were determined in the field during each sampling period using a YSI Pro DSS and Hach FH950 portable velocity meter. Secchi depth (cm) was also measured and used as a surrogate for water turbidity. Mean weekly discharge and gauge height were taken from USGS gauges nearest each sampling site (Table 1). Cumulative growing degree days were calculated for each tributary using a base temperature of 10°C (Coulter et al. 2016). When field measurements of water temperature were not available, I used site-specific regression equations that modeled water temperature as a function of air temperature to estimate water temperature (Table 1).

Laboratory Techniques

I identified ichthyoplankton and determined their relative densities to quantify the magnitude of bigheaded carp reproductive events. Larval fish were identified to the lowest taxonomic level possible based on morphometric and meristic features (Auer 1982; Chapman 2006). I identified most individuals to family level, except for fish in the families Cyprinidae and Centrarchidae. Cyprinid larvae were categorized as *Cyprinus carpio* (common carp), native cyprinids, *Ctenopharyngodon idella* (grass carp), and *Hypophthalmichthys* sp. (bighead carp and silver carp). Larval centrarchids were identified to genus when possible. Eggs > 3.5 mm in diameter were identified as *Hypophthalmichthys* (Parkos et al. 2021). Larval fish density was determined for each net type by standardizing number of captured bigheaded carp larvae to volume of water filtered (fish/m^3 filtered water). Densities between gear types were not combined due to differences in catch rates between these active and passive gear types. For drift nets, volume of water sampled was estimated using:

$$Water\ filtered\ (m^3) = area\ of\ drift\ net\ opening\ (m^2) \times water\ velocity\ \left(\frac{m}{s}\right) \times duration\ of\ sample\ (s)$$

The amount of water filtered using larval push nets was determined using a General Oceanics Flowmeter and the following equations:

$$Water\ filtered\ (m^3) = \left(\frac{3.14 \times net\ diameter^2}{4}\right) \times distance\ (m)$$

$$Distance\ (m) = \left(flow\ count\ \times \frac{26{,}873}{999{,}999}\right)$$

Sestonic chlorophyll *a* was analyzed by filtering 100 mL of surface water sample onto Whatman GF/C filters. Filters were immersed in 90% ethanol and placed in the dark at 4°C to extract pigments for 24 hours. The extract was clarified by syringe filtering and absorbances (665 and 750 nm) were measured with spectrophotometer before and after acidification with 2N HCl to calculate chlorophyll *a* concentrations (APHA 2017). Chlorophyll *a* concentrations were calculated using:

$$Chlorophyll\ a\ \left(\frac{\mu g}{L}\right) = 29.6 \times \big((665\ nm\ absorbance - 750\ nm\ absorbance) - (acid\ 665\ nm\ absorbance - acid\ 750\ nm\ absorbance)\big) \times ethanol\ dilution / (pathlength\ (cm) \times volume\ filtered\ (L))$$

Total phosphorus concentration was analyzed in the laboratory using a Hach DR3900 spectrophotometer and Hach TNTPlus vials that test for phosphorus with the Ascorbic Acid Method.

Statistical Techniques

The first step in my approach for identifying environmental parameters that influence invasive carp reproduction involved finding the environmental variables that account for the greatest variation among tributaries and then quantifying that variation. I narrowed down environmental parameters of interest in each set of tributaries, grouped by Illinois and Wabash Rivers, using Principal Components Analysis (PCA). The PCA included water temperature, cumulative growing degree days (CGDD), mean daily discharge, CV of mean daily discharge, drainage basin area, dissolved oxygen, and Secchi depth. Environmental variables with axis loading > |0.5| and principal components (PCs) with eigenvalue > 1 were deemed important and selected for further analyses (Kaiser 1960). Directionality of the environmental loadings (+ / -) determines what tributaries show higher or lower values of the associated environmental parameter. Next, I used Pearson's product-moment correlation analysis to see which of the parameters were most collinear, retaining only variables with low (|r| < 0.50) correlation for future analysis. I compared the remaining environmental parameters among basins and basin-nested tributaries using a multivariate analysis of variance (MANOVA) based on individual observations at all sites and times periods on each tributary. Environmental data from individual tributaries were compared using either a one-way Kruskal-Wallis test with a Dunn post-hoc test when environmental variables did not conform to the assumptions of normality and homogeneity of variances, or a one-way analysis of variance (ANOVA) with a Tukey's post-hoc test for variables that did meet these assumptions.

I compared spatiotemporal variation of bigheaded carp reproduction between tributaries and between tributaries and their associated mainstem river. To compare tributaries over time, I used a repeated measures analysis of variance (RMANOVA) using yearly peak larval densities from push net collections for each tributary. I only used push net data in this analysis due to the higher capture efficiency of larvae from push nests compared to drift nets (Roth et al. 2021) and to avoid issues associated with combining active and passive gear type effort. Comparisons consisted of tributaries and between years as the repeated factor. I used a Kruskal-Wallis test with a Dunn post-hoc test to determine individual differences between tributaries and a Mann-Whitney U two sample test to determine differences between basins. Additionally, I used a Z-test to determine if mean density of larval bigheaded carp in 2020 differed between the Wabash River and its tributaries. Mean larval densities for Wabash mainstem-tributary comparisons were calculated from push-net densities measured across all sample periods and used densities from the lower tributary locations for tributary values. Inconsistencies in sample sites and sampling frequency between mainstem and tributary locations precluded mainstem to tributary comparisons in the Illinois River basin.

To relate the environmental conditions identified in the previous analyses to bigheaded carp reproduction and determine the differences between tributaries and basins, I used multiple logistic regressions with stepwise model selection. For these logistic regressions, I used presence or absence of bigheaded carp larvae which incorporates all gear types (push and drift nets) and sample periods to maximize sample size along and allows for inclusion of all instances of reproduction. Larval presence for each site was modeled against site-specific environmental parameters. I modelled each basin individually using data from 2015 to 2020 along with separate basin-specific models that used only 2019 to 2020 data so as to assess the potential importance of chlorophyll *a* and total phosphorus. Model parameter additions/subtractions were ranked based on Akaike's information criterion (AIC), and the lowest AIC model was retained for final comparison. Regression coefficients from the multiple logistic regression models indicated the strength and direction (+ or −) of the association between environmental factors and the presence of bigheaded carp larvae in the tributaries. I determined overall model fit using the Hosmer-Lemeshow test.

To easily apply significant bigheaded carp environmental parameters to uninvaded system, I used drainage area because it incorporated the environmental variables of interest from the multiple logistic regression due to their high correlation determined with Pearson's product-moment correlation. This helped identify individual parameters that incorporate variation from significant factors for bigheaded carp reproduction. Next, I used simple linear regression to model the environmental parameter identified against bigheaded carp densities giving a basis for comparison to predict reproduction in uninvaded systems. All statistical analyses for this study were performed in Program R (version 4.1.2) using packages "car", "e1071", "ResourceSelection", and "FSA".

RESULTS

Bigheaded carp ichthyoplankton were collected at a variety of sites, time periods, and environmental conditions throughout the five-year sampling period. From 1,741 drift net samples taken at upper and lower tributary sites and 774 push net samples at lower tributary sites, I found relatively high numbers of bigheaded carp larvae in the Sangamon (n = 4,485), Little Wabash (n = 2,267), and Embarras (n = 415) Rivers compared to the Spoon (n = 48), Mackinaw (n = 16), and Vermilion (n = 65) Rivers for a total of 7,296 larval bigheaded carp collected. This trend was mirrored with egg collection, with the Sangamon (n = 1,962), Little Wabash (n = 1,417), and Embarras (n = 2,070) comprising the majority of egg collections compared to the Spoon (n = 5), Mackinaw (n = 5), and Vermilion (n = 325) Rivers for a total of 5,784 bigheaded carp eggs collected. Of these collections, very few larvae (n = 0 to 153) and eggs (n = 0 to 428) were collected at upper tributary sites. Additionally, when both gear types were used, drift net catches only accounted for between 6 and 37% of total bigheaded carp catches. Across our yearly sample period (April to September), 61% of all bigheaded carp were collected in the month of July. I calculated the discharge (mean = 145.6 m^3/s, SE = 9.6), temperature (mean = 24.6 °C, SE = 0.2), dissolved oxygen (mean = 5.94 mg/L, SE = 0.2), Secchi depth (mean = 19.56 cm, SE = 0.8), chlorophyll *a* (mean = 14.2 µg/L, SE = 2.2), and total phosphorus (mean = 0.89 mg/L, SE = 0.1) among all the tributaries when bigheaded carp larvae were collected.

Tributaries within each basin showed association to different environmental variables. The Wabash tributaries PCA explained 56.6% of total variation between PC1 (30.9%) and PC2 (25.7%), while the Illinois tributaries PCA explained 60% of total variation between PC1 (38.2%) and PC2 (22.2%). PC1 for the Wabash tributaries positively loaded discharge and negatively loaded both Secchi and dissolved oxygen and PC2 negatively loaded water temperature, CGDD, and drainage area (Figure 3). PC1 for the Illinois tributaries negatively loaded discharge and positively loaded CV discharge and CGDD, while PC2 positively loaded both temperature and drainage area (Figure 3). While there was overlap in confidence intervals between some tributaries, the Sangamon and Mackinaw Rivers were different for the Illinois basin and the Little Wabash and Vermilion were different for the Wabash basin (Figure 3).

Environmental variables that were identified as important in the PCA varied between basins (MANOVA; $P < 0.0001$) and by tributary ($P < 0.0001$; Table 2). Univariate tests show the effect of tributary was significant for discharge ($P < 0.0001$), temperature ($P = 0.036$), dissolved oxygen ($P < 0.0001$), Secchi depth ($P = 0.014$), total phosphorus ($P < 0.0001$), and chlorophyll *a* ($P = 0.007$), while the effect of basin was only significant for discharge ($P = 0.0001$) and dissolved oxygen ($P = 0.013$; Table 2). Between basins, the Wabash experienced greater discharge than the Illinois (Figure 4a), whereas the Illinois experienced greater mean dissolved oxygen (Figure 4b). I found that most tributaries significantly varied by discharge, with the highest discharge in the Sangamon and the lowest in the Mackinaw and Vermilion (Figure 4a). Water temperatures were relatively homogeneous among tributaries, except for the Mackinaw which tended to be lower than the Little Wabash and Embarras (Figure 4c). Dissolved oxygen tended to be highest in the Sangamon River and lowest in the Little Wabash (Figure 4b). Secchi depth was highest in the Mackinaw and Vermilion Rivers, with similar Secchi depth between the remaining tributaries (Figure 4d). The Mackinaw and Vermilion Rivers had significantly lower total phosphorus concentrations than the other four tributaries, which had similar mean concentrations (Figure 4e). Mean chlorophyll *a* was relatively similar among tributaries with higher chlorophyll *a* in the Sangamon and Embarras Rivers compared to the Vermilion River (Figure 4f).

Tributaries differed in the amount of bigheaded carp reproduction that they supported. The repeated measures analysis of variance indicated that peak larval bigheaded carp densities varied by tributary ($P < 0.001$), year ($P < 0.001$), and a tributary × year interaction ($P < 0.001$; Table 3). By comparing individual tributaries using a Kruskal-Wallis test and a Dunn post-hoc test, I found that on average the Little Wabash, Sangamon, and Embarras Rivers had the highest mean peak densities (Figure 5). I compared the Illinois and Wabash tributaries peak larval densities using a Mann Whitney U test ($P = 0.042$) and found that the Illinois River tributaries had the highest overall peak densities (Figure 5). By comparing Wabash tributary densities to densities measured in the mainstem Wabash River, I found that the Embarras and Vermilion Rivers had lower larval bigheaded carp densities than the mainstem Wabash ($z < 0.0001$ and $z = 0.049$ respectively), whereas the density of larval bigheaded carp in the Little Wabash was greater than or equal to densities in the Wabash River ($z = 0.548$) during the 2020 field season.

Additionally, I used tributary environmental characteristics to help explain variation in bigheaded carp presence/absence and applied these characteristics to predict reproduction in uninvaded environments. Stepwise multiple logistic regressions for the Illinois tributaries retained two parameters and indicated a positive correlation and significant effect of temperature ($P = 0.002$; $\exp\beta = 1.03$) and discharge ($P = 0.02$; $\exp\beta = 1.14$), whereas the Wabash tributaries indicated a significant positive correlation with discharge ($P < 0.001$; $\exp\beta = 5.48$) and retained dissolved oxygen ($P = 0.119$; $\exp\beta = 0.81$; Table 4). After introducing measures of primary production into 2019-2020 models, I found negative association of total phosphorus ($P = 0.034$; $\exp\beta = 0.002$) for the Illinois tributaries and chlorophyll *a* ($P = 0.12$; $\exp\beta = 0.23$) for the Wabash tributaries compared to larval bigheaded carp presence (Table 4). The addition of chlorophyll *a* and total phosphorus improved the models by reducing AIC, however chlorophyll *a* was not significant in the model. All multiple logistic regression models fit the data well with Hosmer-Lemeshow $P \geq 0.25$. As drainage area for all tributaries was highly correlated ($|r| \geq 0.5$) with river discharge, temperature, and total phosphorus, I used drainage area in a further regression analysis to be able to easily predict systems that have the potential to support bigheaded carp reproduction. Simple linear regression analysis indicated that drainage area significantly correlated ($P = 0.004$, $R^2 = 0.90$) to the mean larval density in the tributaries from 2016-2020 with larger tributaries showing higher mean bigheaded carp densities (Figure 6).

DISCUSSION

This study demonstrates the effects of spatiotemporal environmental variability in relation to bigheaded carp reproduction. There were differences present between tributaries for many environmental factors, while basin-level differences in environmental conditions were only apparent for river discharge and dissolved oxygen. Mean peak larval densities were highest among Illinois tributaries compared to the Wabash, while the tributaries with the highest mean peak densities were the Sangamon, Little Wabash, and Embarras Rivers. Additionally, when relating larval production of Wabash tributaries compared to the mainstem river, I found that the Little Wabash has the potential to produce similar invasive carp densities compared to the mainstem Wabash. By relating the environmental data to the presence of bigheaded carp, I was able to find patterns in reproduction between tributaries and basins. Overall, discharge was the most consistent predictor of bigheaded carp larval presence at the basin level, while temperature was more important for Illinois tributaries, and measures of primary production show some association with invasive carp presence between basins. By representing these environmental parameters by a catchment scale variable such as drainage area, I provided a basis for comparison of reproductive potential to currently uninvaded systems such as Lake Michigan.

Quantifying environmental variation between basin and tributaries was my first step in explaining reproductive variation among systems. My findings show that between the Illinois and Wabash River tributaries there were relatively few variables that differed at the basin level. As expected, discharge was significantly greater in tributaries of the Wabash River than the heavily impounded Illinois River. The Illinois River tributaries retained some amount of flow variation consistent with more unaltered rivers (Poff et al. 1997); however, most of this variation was reduced in magnitude mirroring hydrological trends in heavily altered rivers (Magilligan and Nislow 2005; Zhang et al. 2010; Lian et al. 2012). The only other environmental variable that differed between basins was dissolved oxygen which was higher overall in Illinois tributaries. Other studies have found that dissolved oxygen is dependent on factors such as primary production and temperature which may indicate increased primary production on Illinois tributaries (Morgan et al. 2006). Among tributaries, lower Secchi depth experienced in the Mackinaw and Vermilion compared to other tributaries could be due to their relatively low average discharge which reduces suspended solids (Hintz et al. 2017). While also typically related to discharge (Banner et al. 2009), Royer et al. 2008 found that increased sestonic chlorophyll *a* in rivers of Illinois were more dependent on increased drainage area due to reduced canopy cover which was consistent with our larger tributaries having the highest mean chlorophyll *a*. The variability in total phosphorus concentrations among tributaries is consistent with other research in rivers of Illinois and is often attributed to discharge, but varies with point and non-point source pollution (Morgan et al. 2006; Royer et al. 2008). Overall, this shows that there was more variation in environmental conditions at a local, tributary scale than a regional, basin scale. This local variation will be important in determining bigheaded carp reproduction as other studies have found that despite the importance of one environmental condition, bigheaded carp reproduction is often determined by many factors (Garcia et al. 2015).

Spatiotemporal variability of bigheaded carp reproduction was present between basins and individual tributaries during this sample period. By examining peak larval densities among basins, I found the Illinois River tributaries to have the highest mean reproduction which contradicts my prediction of the Wabash River tributaries having higher reproduction due to increased hydrological variation. This difference, however, can mostly be attributed to two instances of exceptionally high reproduction on the Sangamon River in 2018. This temporal variability in the magnitude of reproduction was present among all the tributaries and is often attributed to differences in hydrologic conditions (Gibson-Reinemer et al. 2017; Sullivan et al. 2018; Camacho et al. 2020). Despite high temporal variation in reproduction, the Sangamon and Little Wabash Rivers showed consistently higher reproduction than the other tributaries. My comparison of densities between Wabash tributaries and the mainstem river show that under the right conditions, some high-density tributaries (i.e., the Little Wabash River) have the capacity to support reproduction on the same scale as the mainstem river demonstrating the importance of tributaries to population expansion. Although the capacity of tributary reproduction to influence mainstem river populations has not been extensively studied for bigheaded carp (Camacho et al. 2020), other studies have found positive impacts of tributary reproduction on mainstem populations of native species due to the availability of ideal hydrologic conditions and spawning habitats within tributaries (Pracheil et al. 2009; Vasconcelos et al. 2021).

The dynamics of thermal and hydrologic variation in rivers are conventionally viewed as the central catalysts for bigheaded carp reproduction (Schrank et al. 2001; Kolar et al. 2007; Lohmeyer and Garvey 2009). Regardless of the basin, I found that river discharge is the strongest and most consistent predictors of larval bigheaded carp presence during this sampling period with higher river discharge values showing increased evidence of larval invasive carp reproduction. I hypothesized that the Wabash River, which is less hydrologically restricted than the Illinois River, would have invasive carp reproduction mostly influenced by hydrological variables. My findings generally support this prediction, however the magnitude of reproduction based on discharge in each basin is variable. Although the Wabash tributaries had the highest mean discharge, the Illinois tributaries had the highest mean peak densities. This could be partially due to a larger population of adult bigheaded carp in the Illinois River (Stuck et al. 2015; Shields et al. 2021) or due to the Sangamon River having the highest discharge out of all the study tributaries, with peak densities for 2018 being considerably higher than any other tributary peak density. Despite the necessity of 17 to 30°C water temperatures to trigger the release of bigheaded carp gametes (DeGrandchamp et al. 2007; Kolar et al. 2007), our findings show that temperature was a less consistent predictor of reproduction than discharge. Among Illinois tributaries, temperature showed a strong positive association with bigheaded carp reproduction, whereas no model for the Wabash tributaries retained temperature. Fluctuations in water temperature stability have been shown to negatively influence silver carp reproduction (Majdoubi et al. 2022) and the greater hydrologic variability of the Wabash tributaries compared to the Illinois could also lead to greater temperature variability (Sinokrot and Gulliver 2000; van Vliet et al. 2011), causing reduced reproductive success. Sullivan et al. (2018) measured similar discharge and temperature dynamics in the Wabash River tributaries, where discharge primarily influenced year class strength of bigheaded carp and temperature showed no association. Due in part to close geographic proximity of my study tributaries, mean temperature variation between tributaries and basins were minimal. Additionally, most larval bigheaded carp were collected well within the thresholds of reproduction, with the mean temperature of collection (24.6 °C) falling within the bounds of peak reproduction (22-26 °C; Schrank et al. 2001). Because of this, when temperatures are within known reproductive boundaries, discharge is likely the dominant environmental predictor of reproduction.

Surrogates for primary productivity and food resources show potential as secondary factors in determining reproductive variability of tributaries. Bigheaded carp presence was negatively associated with total phosphorus concentrations, however the two tributaries with the lowest mean total phosphorus (Mackinaw and Vermilion Rivers) also showed some of the lowest peak densities. Total phosphorus alone may be a difficult parameter to use to quantify reproductive variability as these concentrations are highly dependent on point and non-point source pollution that vary with land use and drainage area (Lohman and Jones 1999) and discharge (Banner et al. 2009). While not significant, chlorophyll *a* helped improve Wabash regression models and may be improved with additional years of sampling. Total phosphorus and chlorophyll *a* together have been found to relate to discharge during extreme flooding events (Banner et al. 2009) and although they didn't highly correlate here it is likely a product of sampling during a wide range of hydrological conditions. Although not examined in this study, zooplankton diversity and abundance may be a more direct measurement of food resources as it relates to fish reproduction due to impacts of bigheaded carp on zooplankton communities (Sass et al. 2014; DeBoer et al. 2018; Tillotson et al. 2022), but even direct measurements of food availability such as these are often subject to environmental variation from factors such as water level (Bonecker et al. 2013). Therefore, determining reproductive viability of rivers may be aided by a more simplistic approach of using variables such as discharge or drainage area that encompass the variation of many factors.

The environmental predictors of bigheaded carp reproduction identified in this study can be applied to predicting tributaries susceptible to reproduction in uninvaded environments, such as Lake Michigan. Using a catchment scale variable such as drainage area due to its correlation with significant parameters found in my analyses (e.g. discharge and total phosphorus; Lohman and Jones 1999; Knighton 2014) could be beneficial to account for additional variation in reproduction. By comparing drainage area of all major tributaries of Lake Michigan, I found that the Menominee (6,550 km^2), Oconto (3,888 km^2), Fox-Wolf (10,139 km^2), Kalamazoo (3,251 km^2), Grand (6,116 km^2), and St. Joseph (7,540 km^2) rivers are the only rivers of comparable or greater drainage area to the Illinois and Wabash River tributaries that showed high reproduction.

The rivers on the Wisconsin side (Menomonee, Oconto, and Fox-Wolf) along with the Kalamazoo in Michigan all have dams or barriers < 40km from Lake Michigan to allow for eggs to remain in suspension, based on findings from Garcia et al. 2015. The Grand and St. Joseph Rivers are either undammed or dammed in a way that allows fish passage. These two rivers also have the most comparable sized (>6,000 km^2) drainage areas to the Sangamon and Little Wabash Rivers which have the highest mean larval bigheaded carp densities of our study tributaries. Prior research has also identified that the St. Joseph River (Murphy and Jackson 2013) has the capability to support bigheaded carp reproduction based on factors such as unimpounded river kilometers and discharge. These rivers are not currently connected to bodies of water with known bigheaded carp populations, but they do correspond with areas of Lake Michigan predicted to have suitable habitat to promote growth of bigheaded carp under various conditions and time periods due to the influx of nutrients they provide (Alsip et al. 2018). Additionally, as both the Grand and St. Joseph Rivers are in the southern portion of Lake Michigan, they are more likely to have water temperatures that fall within the reproductive threshold during higher discharge events in the spring. By applying drainage area in this manner, I do not mean to disregard potential reproduction in smaller tributaries that experience high discharge fluctuations and proper spawning temperatures, but rather identify the tributaries that could contribute the most reproduction based on our findings in the Illinois and Wabash tributaries.

These findings illustrate the importance of accounting for hydrologic, thermal, and other environmental variation (e.g., primary production and food availability) in determining reproductive suitability of tributary rivers along with the overall importance of tributaries to bigheaded carp reproduction. Overall reproductive output in tributaries of the unimpounded Wabash River was primarily influenced by hydrologic conditions, whereas Illinois River tributaries were influenced by a combination of thermal and hydrological variation. Additionally, some tributaries show potential to contribute similar reproduction to the mainstem river, likely a product of increased hydrologic variation. Future research should include expanding the sample size for measures of primary productivity (currently limited to 2019-2020) along with adding mainstem Illinois River sites upstream and downstream of the confluences to help quantify the contribution of bigheaded carp from each tributary. Continued and expanded monitoring of these tributary systems is needed due to their potential to serves as sources of recruitment to basin-wide bigheaded carp populations and their comparability in size to Great Lakes tributaries. Expanding on the approach of predicting tributaries susceptible to bigheaded carp reproduction can provide a method of risk assessment along invasion fronts and help direct monitoring efforts.

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TABLES

TABLE 1. Location and identification number of United States Geological Survey (USGS) gauging stations on the tributaries of Illinois and Wabash River used to obtain mean daily river discharge. Simple linear regressions between air and water temperature measurements were based on water temperatures recorded in the field and air temperature recorded at nearest airport air temperature gauges. Regression equations were used to estimate water temperature when field measurements were not taken. N refers to temperature sample sizes used to formulate regressions.

	Site	Gauging Station	Location	Air Temperature Location	Water Temperature Equation	R^2	n
Illinois	Sangamon (SA)	USGS 5583000	Oakford, IL	Quincy Regional Airport	y = 0.9214x + 0.1273	0.76	72
	Spoon (SP)	USGS 5570000	Seville, IL	Peoria Internation Airport	y = 0.9342x - 0.3034	0.85	75
	Mackinaw (MA)	USGS 5568000	Green Valley, IL	Peoria Internation Airport	y = 1.0397x - 0.7702	0.81	66
Wabash	Little Wabash (LW)	USGS 3381500	Carmi, IL	Evansville Regional Airport	y = 0.7538x + 4.7624	0.71	51
	Embarras (EM)	USGS 3346500	Lawrenceville, IL	Lawrenceville–Vincennes Airport	y = 0.7843x + 4.1229	0.72	49
	Vermilion (VE)	USGS 3339000	Danville, IL	Willard Airport	y = 0.9194x + 0.4626	0.67	57

TABLE 2. Multivariate Analysis of Variance (MANOVA) for environmental data comparing the Sangamon, Spoon, Mackinaw, Little Wabash, Embarras, and Vermilion tributaries in addition to between Illinois and Wabash tributaries for 2016-2020 for every parameter except total phosphorus and chlorophyll *a* which include only 2019-2020.

	df	MS/Pillai's Trace	F	P
Multivariate test				
Mainstem	6, 84	0.27761	5.38	<0.0001
Tributary	24, 348	1.433	8.092	<0.0001
Univariate tests				
Discharge				
Mainstem	1	0.66532	16.56	0.0001
Tributary	4	1.535	38.197	<0.0001
Error	89	0.040		
Temperature				
Mainstem	1	1.8499	0.3208	0.57257
Tributary	4	15.510	2.689	0.03615
Error	89	5.767		
Dissolved Oxygen				
Mainstem	1	16.010	6.481	0.01262
Tributary	4	21.089	8.537	<0.0001
Error	89	2.470		
Secchi				
Mainstem	1	0.0002	0.003	0.95914
Tributary	4	0.233	3.337	0.01355
Error	89	0.070		
Total Phosphorus				
Mainstem	1	0.004	0.072	0.7886
Tributary	4	0.496	8.811	<0.0001
Error	89	0.056		
Chlorophyll *a*				
Mainstem	1	0.053	0.321	0.572683
Tributary	4	0.613	3.736	0.007398
Error	89	0.164		

TABLE 3. Repeated measures analysis comparing peak larval density of larval push samples at lower tributary sites by tributary and year for 2016-2020. Factors including year or tributary × year have F-tests reported using Pillai's Trace.

Source of variation	DF	F	p
Tributary	5, 12	25.82397	<0.001
Year	4, 9	19.1885	<0.001
Tributary x Year	20, 48	3.11716	<0.001

TABLE 4. Multiple logistic regression with stepwise model selection incorporating environmental variables and invasive carp presence absence. Models incorporate data from 2016-2020 and separate models were created for 2019-2020 to incorporate chlorophyll *a* and total phosphorus. Directionality of variable relationship to bigheaded carp presence is represented by the model coefficient. Variables greater than 1 were positive and less than one 1 were negative. Overall model fit was tested using a Hosmer-Lemeshow test.

	Tributary System	**Model Parameters**	**Model Coefficient (expβ)**	**p-value**	**Hosmer-Lemeshow p-value**
2016-2020	Illinois	Temperature	1.030	0.002	0.827
		Log Discharge	1.140	0.024	
	Wabash	Log Discharge	5.480	<0.001	0.2626
		Dissolved Oxygen	0.810	0.119	
2019-2020	Illinois	Log Discharge	37.960	0.024	0.9823
		Log Phosphorus	0.002	0.034	
		Temperature	1.450	0.084	
	Wabash	Log Discharge	4.570	0.027	0.253
		Log Chlorophyll *a*	0.230	0.123	

FIGURES

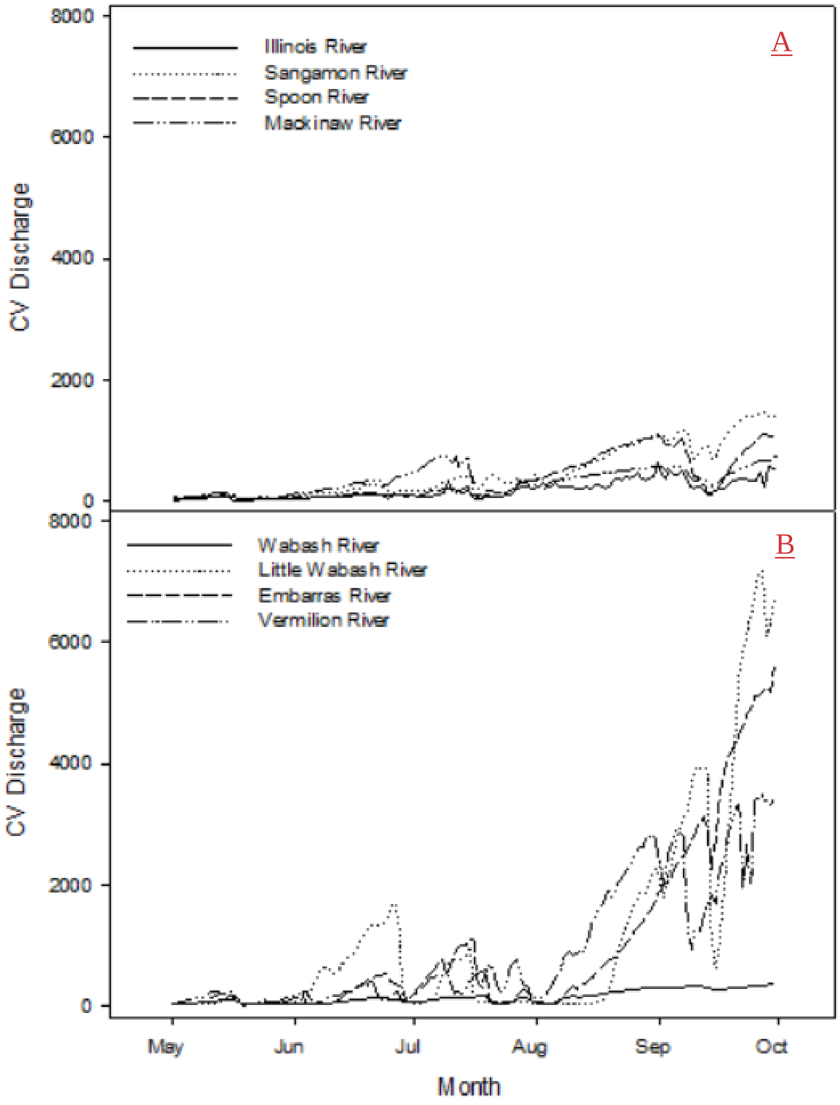

FIGURE 1. Coefficient of variation of mean daily discharge for tributaries and associated mainstem rivers of the A) Illinois River and B) Wabash River basins from May-September 2020.

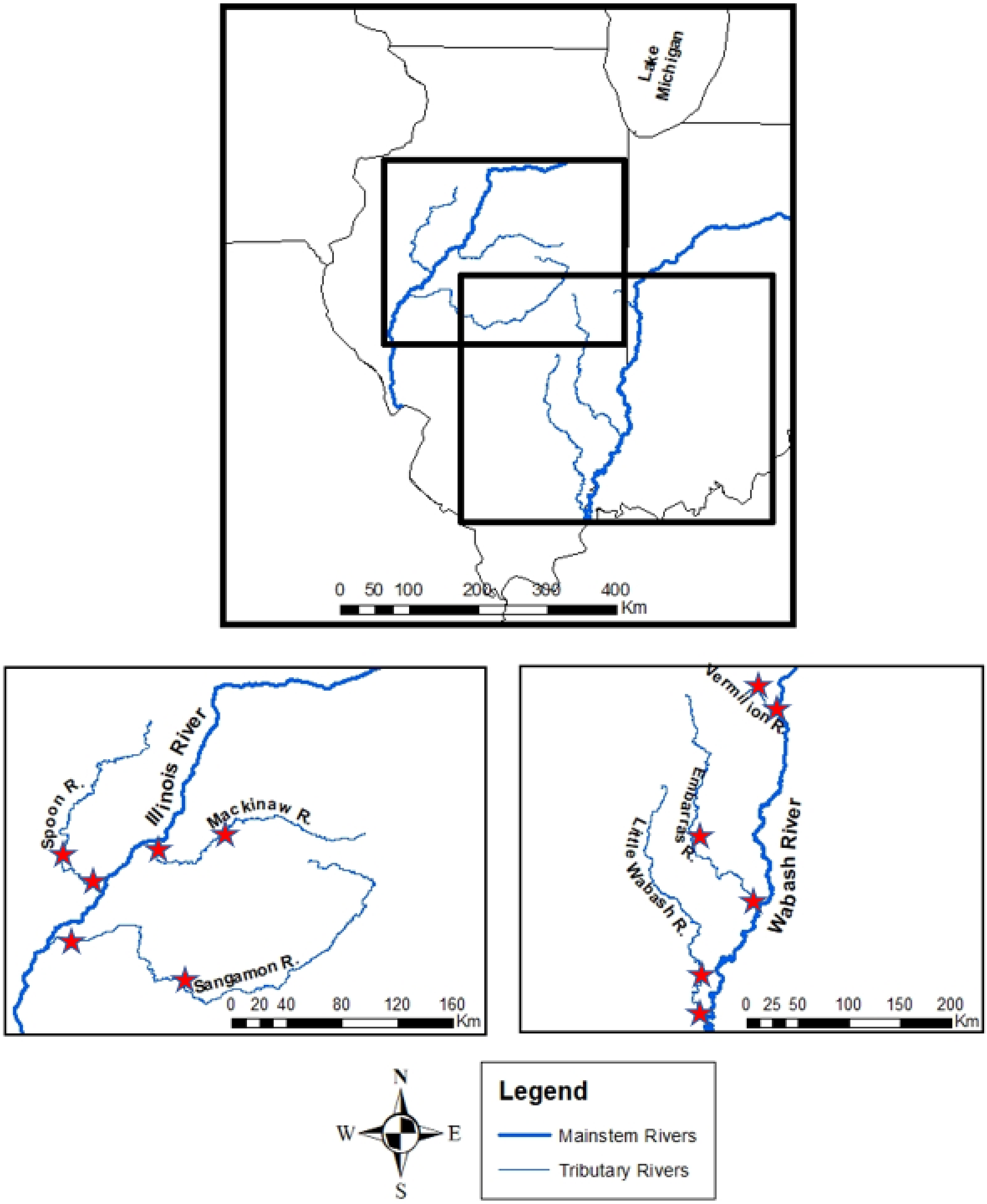

FIGURE 2. Map of six Illinois and Wabash River tributaries sampled from 2016-2020, and the downstream and upstream sampling sites on each tributary.

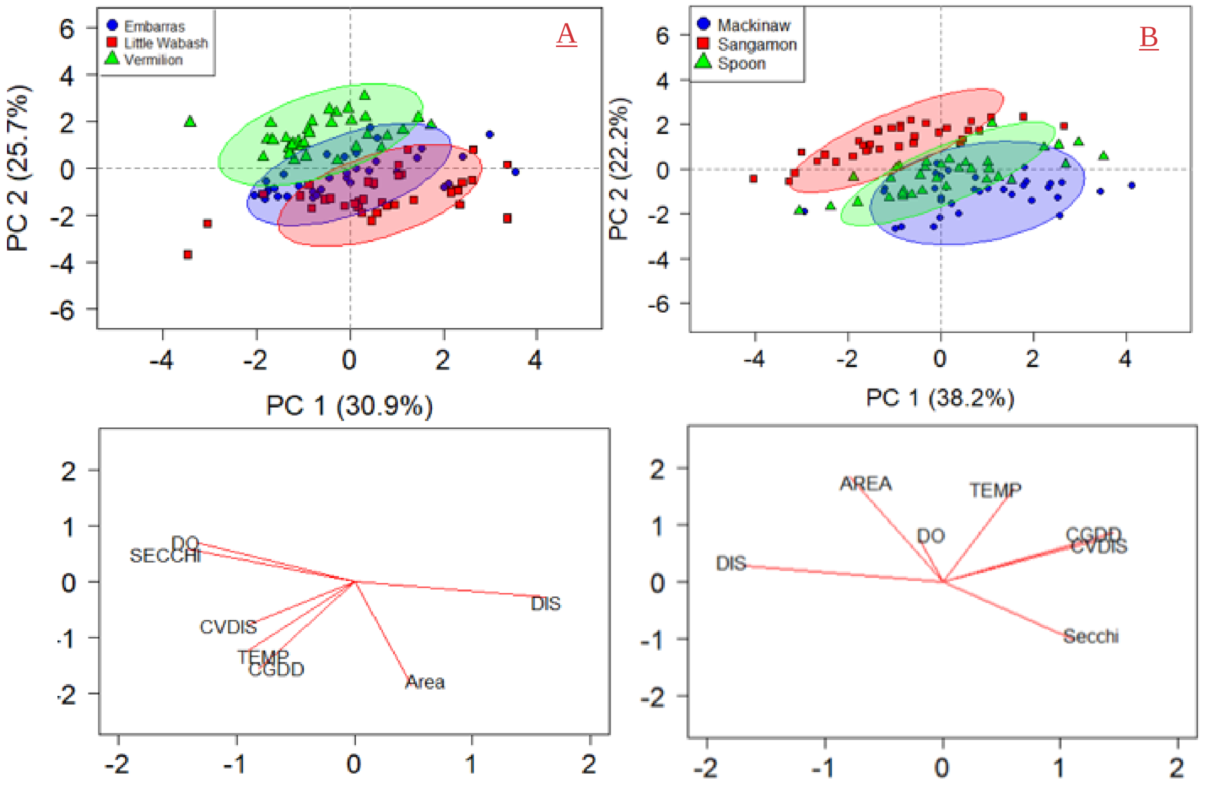

FIGURE 3. Principal component analysis (PCA) of environmental data including dissolved oxygen (DO), Secchi depth, mean daily discharge (DIS), CV discharge, temperature, cumulative growing degree days (CGDD), and drainage area (Area) for tributaries of the A) Wabash and B) Illinois River. Ellipses indicate 95% confidence intervals for each tributary.

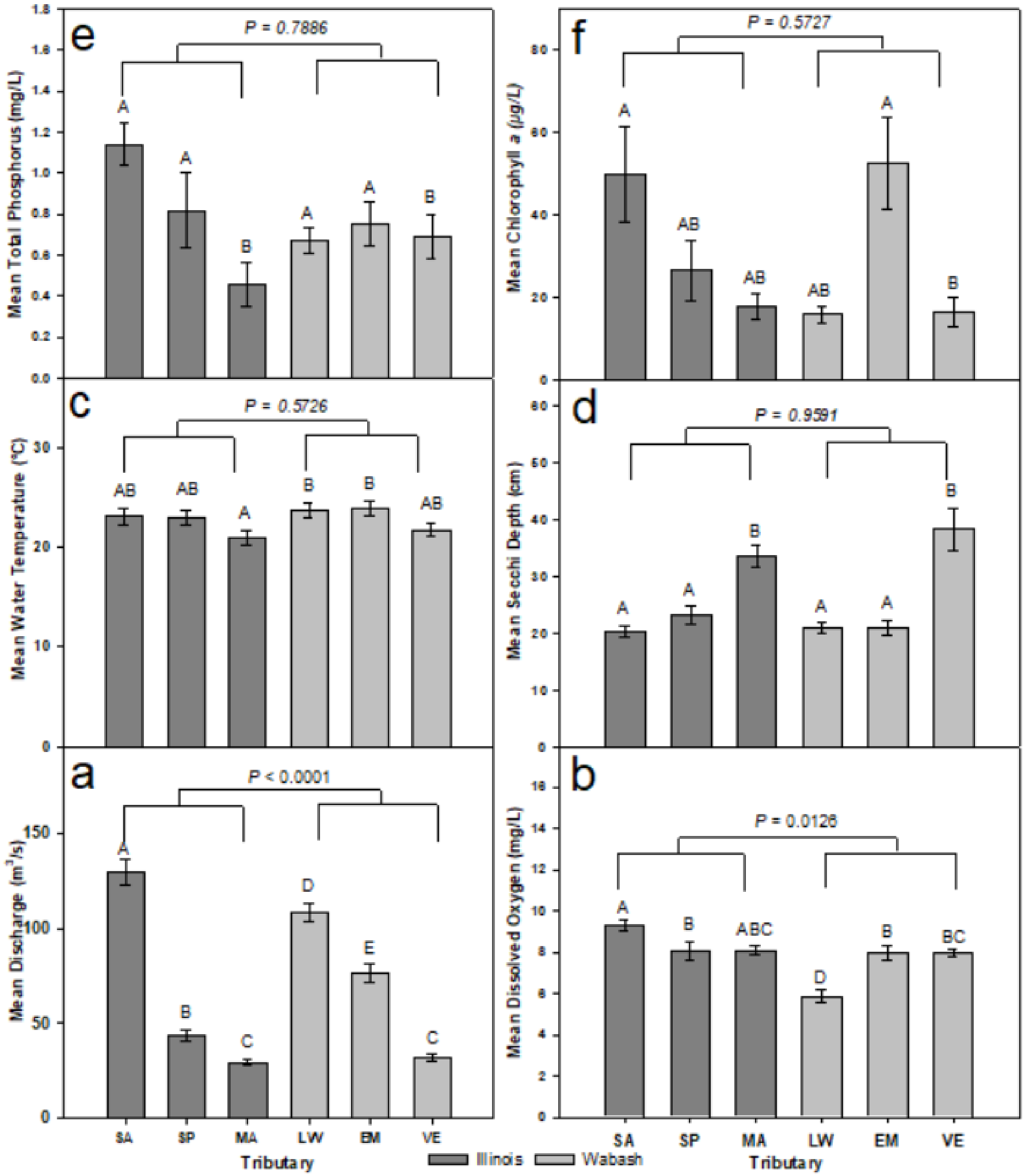

FIGURE 4. Graphs of mean environmental data ± SE among tributaries incorporating field data from 2016-2020. Tributaries were compared using either Kruskal-Wallis tests with a Dunn post-hoc test or an ANOVA with a Tukey's post-hoc test depending on normality and homogeneity of variances. Tributaries that were statistically different from each other were represented by unique letters. Mainstem grouped tributaries were compared with univariate MANOVA *P* values. Significance was determined using α = 0.05. Refer to Table 1 for tributary abbreviation key.

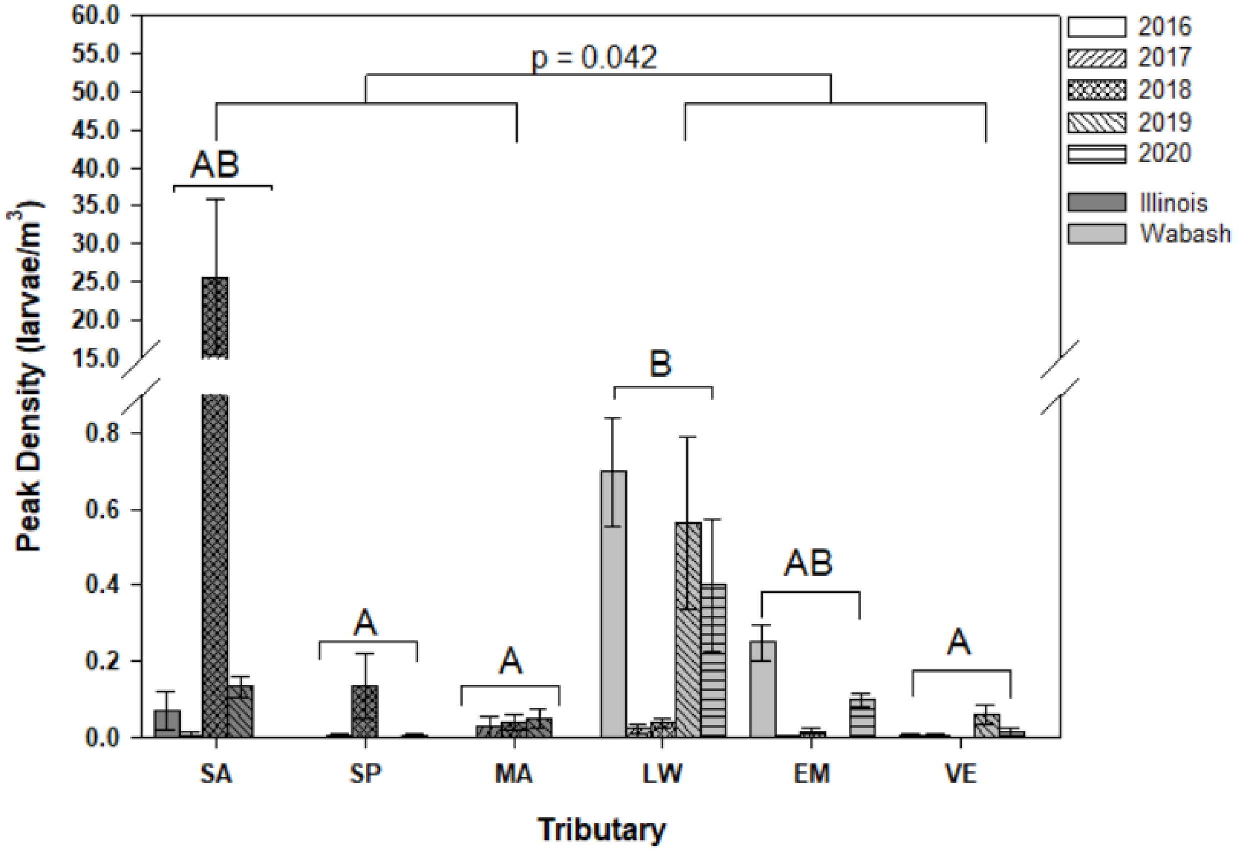

FIGURE 5. Lower tributary site peak larval density for larval push nets ± SE from 2016-2020 compared by tributary with a Kruskal-Wallis test and Dunn post-hoc test. Illinois tributaries were compared to Wabash tributaries using a Mann Whitney U two-sample test. Significant differences were indicated by unique lettering and significance was determined using α = 0.05. Refer to Table 1 for tributary abbreviation key.

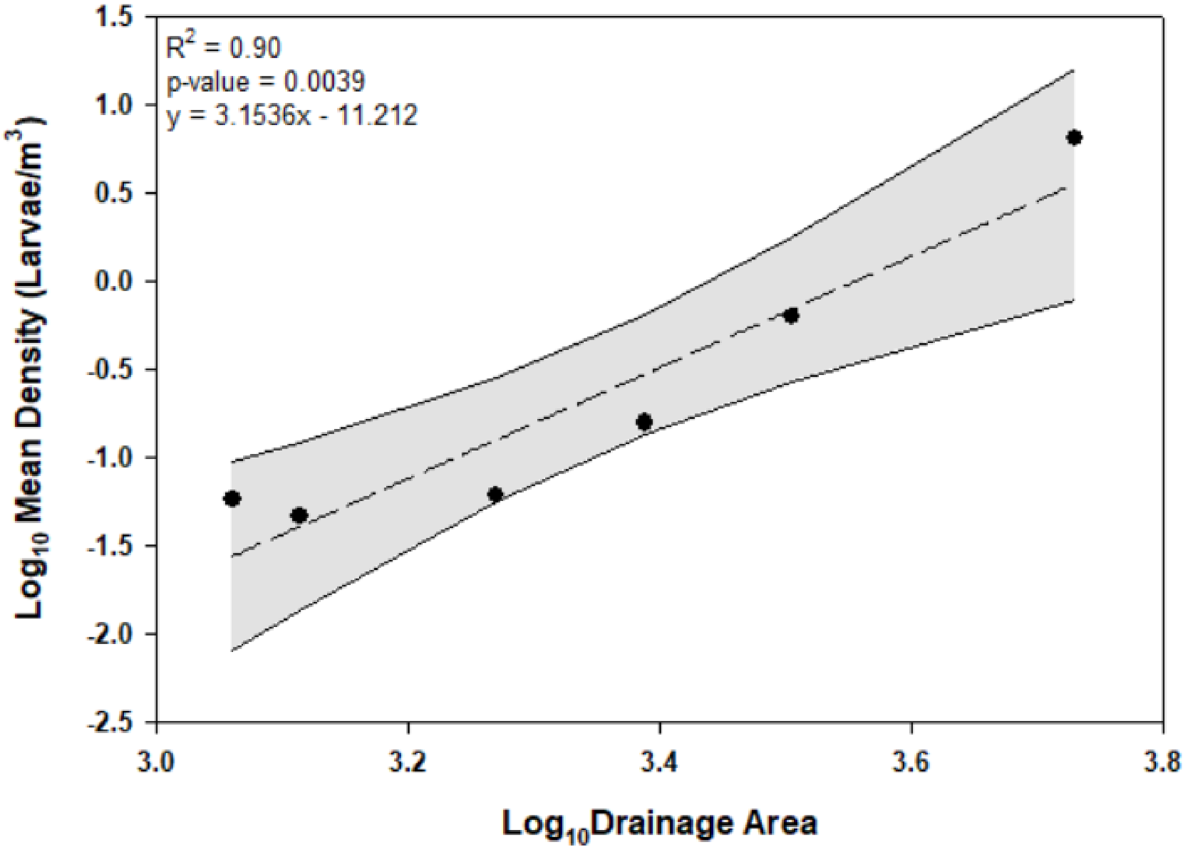

FIGURE 6. Simple linear regression with 95% confidence intervals comparing drainage area to mean invasive carp density using larval push nets for the Illinois and Wabash River tributaries from 2016-2020