2018

Factors regulating year-class strength of Silver Carp throughout the Mississippi River basin

Christopher J. Sullivan
Iowa State University

Michael J. Weber
Iowa State University, mjw@iastate.edu

Clay L. Pierce
U.S. Geological Survey, cpierce@iastate.edu

David H. Wahl
Illinois Natural History Survey

Quinton E. Phelps
West Virginia University

See next page for additional authors

Factors regulating year-class strength of Silver Carp throughout the Mississippi River basin

Abstract
Recruitment of many fish populations is inherently highly variable inter-annually. However, this variability can be synchronous at broad geographic scales due to fish dispersal and climatic conditions. Herein, we investigated recruitment synchrony of Silver Carp Hypophthalmichthys molitrix across the Mississippi River basin. Year-class strength (YCS) and synchrony of nine populations (max linear distance = 806.4 km) was indexed using catch-curve residuals correlated between sites and related to local and regional climatic conditions. Overall, Silver Carp YCS was not synchronous among populations, suggesting local environmental factors are more important determinants of YCS than large-scale environmental factors. Variation in Silver Carp YCS was influenced by river base flow and discharge variability at each site, indicating that extended periods of static local discharge benefit YCS. Further, river discharge and air temperature were correlated and synchronized among sites, but only similarities in river discharge was correlated with Silver Carp population synchrony, indicating that similarities in discharge (i.e., major flood) among sites can positively synchronize Silver Carp YCS. The positive correlation between Silver Carp YCS and river discharge synchrony suggests that regional flood regimes are an important force determining the degree of population synchrony among Mississippi River Silver Carp populations.

Keywords
spatial synchrony, Asian Carp, rivers, catch-curve, year-class strength, discharge, recruitment

Disciplines
Environmental Indicators and Impact Assessment | Natural Resources and Conservation | Natural Resources Management and Policy

Comments
This is an Accepted Manuscript of an article published by Taylor & Francis in Transactions of the American Fisheries Society on 03/13/2018, available online: http://www.tandfonline.com/10.1002/tafs.10054.

Authors
Christopher J. Sullivan, Michael J. Weber, Clay L. Pierce, David H. Wahl, Quinton E. Phelps, Carlos A. Camacho, and Robert E. Colombo

Article type : Article

Factors regulating year-class strength of Silver Carp throughout the Mississippi River basin[†]

Christopher J. Sullivan[1*], Michael J. Weber[1], Clay L. Pierce[2], David H. Wahl[3], Quinton E. Phelps[4], Carlos A. Camacho[1], and Robert E. Colombo[5]

[1]Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011, USA

[2]U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II, IA, USA

[3]Illinois Natural History Survey, Kaskaskia Biological Station, 1235 County Road 1000N, Sullivan, IL 61951, USA

[4]Division of Forestry and Natural Resources, West Virginia University, 322 Percival Hall, Morgantown, WV 26506-6125, USA

[5]Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920, USA

*Corresponding author current address: phone (219) 616 – 5594 College of Natural Resources, University of Wisconsin – Stevens Point, 800 Reserve Street, Stevens Point, WI 54481, USA

E-mail: csulliva@uwsp.edu

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/tafs.10054

[†] This draft manuscript is distributed solely for purposes of scientific review. Its content is deliberative and predecisional, so it must not be disclosed or released by reviewers. Because the manuscript has not yet been approved for publication by the U.S. Geological Survey (USGS), it does not represent any official USGS finding or policy.

Running Title: Silver Carp regional year-class strength

Key words: spatial synchrony, Asian Carp, rivers, catch-curve, year-class strength, discharge, recruitment

<A>Abstract

Recruitment of many fish populations is inherently highly variable inter-annually. However, this variability can be synchronous at broad geographic scales due to fish dispersal and climatic conditions. Herein, we investigated recruitment synchrony of Silver Carp *Hypophthalmichthys molitrix* across the Mississippi River basin. Year-class strength (YCS) and synchrony of nine populations (max linear distance = 806.4 km) was indexed using catch-curve residuals correlated between sites and related to local and regional climatic conditions. Overall, Silver Carp YCS was not synchronous among populations, suggesting local environmental factors are more important determinants of YCS than large-scale environmental factors. Variation in Silver Carp YCS was influenced by river base flow and discharge variability at each site, indicating that extended periods of static local discharge benefit YCS. Further, river discharge and air temperature were correlated and synchronized among sites, but only similarities in river discharge was correlated with Silver Carp population synchrony, indicating that similarities in discharge (i.e., major flood) among sites can positively synchronize Silver Carp YCS. The positive correlation between Silver Carp YCS and river discharge synchrony suggests that regional flood regimes are an important force determining the degree of population synchrony among Mississippi River Silver Carp populations.

Fish recruitment into the adult population can be highly variable inter-annually due to the sensitivity of early life-stages to fluctuations in environmental conditions (Hjort 1926). Drivers of recruitment variation are often numerous and vary across systems, combining the cumulative interactions between biotic and abiotic factors such as temperature (e.g., Henderson and Corps 1997), river discharge (e.g., Zorn and Nuhfer 2007), prey availability (e.g., Adams et al. 1982; Dettmers et al. 2003), and reservoir retention (e.g., Maceina 1997). Despite the high degree of variability in recruitment within and among fish populations, the occurrence of synchronously fluctuating populations is now considered a common ecological phenomenon (Ranta et al. 1998), often driven by inter-annual variation in regional climatic conditions (Phelps et al. 2008; Dembkowski et al. 2016; Honsey et al. 2016) and dispersal of individuals among populations (Lande et al. 1999; Kendall et al. 2000). The effect of correlated climatic conditions on recruitment synchrony (i.e., via the Moran effect; Moran 1953) has been largely studied in spatially distinct populations, such as Cisco *Coregonus artedi* (Rook et al. 2012; Myers et al. 2015), Yellow Perch *Perca flavescens* (Dembkowski et al. 2016; Honsey et al. 2016), and Common Carp *Cyprinus carpio* (Phelps et al. 2008; Weber et al. 2017). Alternatively, the synchronization of fish recruitment can be locally restricted but augmented through dispersal (Haydon and Steen 1997), especially with either highly migratory species or interconnected populations (Bunnell et al. 2010; Goldwyn and Hastings 2011). Hence, determining the degree and relative influence of regional climatic factors or dispersal on recruitment synchrony over broad geographic areas can add valuable insights into the nature of fish population fluctuations.

Recruitment synchrony often decreases with increasing distance between populations (Myers et al. 2015; Honsey et al. 2016), with freshwater recruitment synchrony generally limited to distances of 50 km or less (Myers et al. 1997). However, more recent examples suggest that synchronous recruitment of some lentic fishes can exceed 50 km (Rook et al.

2012; Myers et al. 2015). For instance, Yellow Perch populations synchronously recruit at scales greater than 150 km within the Laurentian Great Lakes (Honsey et al. 2016) and Prairie Pothole Region (Dembkowski et al. 2016). Similarly, Common Carp populations in the Prairie Pothole Region exhibited synchronous recruitment across a 175 km^2 area (Phelps et al. 2008) but recruitment became asynchronous at distances greater than 750 km (Weber et al. 2017). As such, synchronous recruitment at smaller spatial scales in lentic systems may be due to the stronger influence of biotic factors on early life stages (Myers et al. 1997) or lack of dispersal potential (e.g., Phelps et al. 2008; Dembkowski et al. 2016).

Among lentic systems, synchronous fluctuations in recruitment appears to be influenced by regional climatic events, such as similarities in water temperature (Bunnell et al. 2010; Honsey et al. 2016), wind patterns (Rook et al. 2012), or a combination of these variables (Rook et al. 2012; Myers et al. 2015; Bunnell et al. 2016). Additionally, recruitment in lotic systems can also be largely dependent upon hydrological variables, as these systems vary naturally in the magnitude, duration, timing, rate of change, and predictability of discharge events across systems (Naiman et al. 2008), potentially inducing synchronous fluctuations in recruitment (Cattanéo et al. 2003; Tedesco et al. 2004). However, regional synchrony in lotic systems has generally only been evaluated at small spatial scales (<200 km) and in small wadable systems (Zorn and Nuhfer 2007; but see Cattanéo et al. 2003; Chevalier et al. 2015). Thus, the extent to which abiotic factors or dispersal influence the synchronization of fish populations in larger, interconnected lotic systems at broader spatial scales remains largely unknown.

Silver Carp *Hypophthalmichthys molitrix* are an invasive species that have elicited substantial concern among ecologists and recreational users since their introduction into a Mississippi River tributary in the mid-1970s (Freeze and Henderson 1982). Silver Carp life history attributes (e.g., rapid growth, early maturation, high fecundity, broad diets; Schrank and Guy 2002; Williamson and Garvey 2005; Garvey et al. 2006) and their ability to tolerate a wide range of environmental factors (e.g., temperature, turbidity, water quality; Kolar et al. 2007) have facilitated their successful establishment and subsequent expansion into much of the Mississippi River basin. Silver Carp are a highly mobile species, moving more than 3.0 km per day (Coulter et al. 2016) and processes such as source-sink dynamics are thought to regulate populations (Hayer et al. 2014). Thus, fish dispersal from downstream to upstream habitats may synchronize recruitment at local scales (i.e., <70 km; Prechtel et al. 2018). In contrast, large-scale spatial synchrony resulting from similarities in broad scale environmental conditions could influence recruitment patterns but has yet to be evaluated for Silver Carp. Across native and invaded ranges, Silver Carp typically spawn in rapidly flowing river segments (thalweg habitats; 0.6-2.3 m/s) in conjunction with temperatures ranging from 18-30°C (Verigin et al. 1978). In addition, sudden increases in river discharge serve as a cue for Silver Carp spawning (Li et al. 2006) and year-class strength (YCS) may be weak when these hydrological conditions are not met (DeGrandchamp et al. 2007; Lohmeyer and Garvey 2009; Gibson-Reinemer et al. 2017). Thus, similar spatiotemporal variation in river conditions (i.e., long duration flood events) may synchronize Silver Carp recruitment throughout the Mississippi River basin.

Investigating the role of environmental conditions in regulating Silver Carp recruitment synchrony can aid in the understanding of population fluctuations. However, an evaluation of the underlying mechanisms regulating and potentially synchronizing YCS has not been conducted. Therefore, the objectives of this study were to (1) describe spatiotemporal patterns in Silver Carp YCS, (2) determine if recruitment among Silver Carp populations in the Missouri, Des Moines, Mississippi (middle and lower river reaches), Illinois, and Wabash rivers is synchronized, (3) if found, estimate the spatial scale for recruitment synchrony, and (4) examine the role of abiotic factors (both local and regional) in regulating Silver Carp recruitment. We hypothesized that Silver Carp recruitment would be synchronized among adjacent populations due to similarities in river discharge (e.g., high water periods) and air temperature patterns (e.g., warmer spring/summer conditions) but that synchrony would decline as distance between populations increases as a result of dissimilarities in environmental conditions.

<A>Methods

<B>*Study area.* - The Missouri, Des Moines, Illinois, and Wabash rivers are four major tributaries of the Mississippi River basin (river specific details in Table 1). Since the early 1900s, the Mississippi, Missouri, Des Moines, and Illinois rivers have undergone modifications (i.e., channelization, dam construction, and bank stabilization) that have altered their natural flow regime. As a result, these modifications have created an unnaturally pooled and regulated hydrograph upstream and a seemingly more natural hydrograph in farthest downstream portions where floodplain habitats disperse flood waters (Rasmussen 1979). In contrast, the Wabash River contains nearly 661 river km of free-flowing river downstream from its single mainstem dam near Huntington, Indiana (Skibsted 2012). In all, the selected study systems are widespread across the Mississippi River basin, encompassing a large diversity of local environmental influences that could influence Silver Carp YCS.

<B>*Field sampling and laboratory analysis.* - Silver Carp were captured from June through September 2015 at nine locations from four major Mississippi River tributaries (Des Moines, Illinois, Missouri, and Wabash rivers) as well as the lower and middle reaches of the Mississippi River (Figure 1). At each location, Silver Carp were collected within a small area (<5.0 river kilometers [rkm]) and sites were located greater than 70km from one another except for the three sites located on the Illinois River and two sites on the Wabash River where, within each site, Carp were collected from locations between 6.1 and 43.1 rkm apart. Because Silver Carp home ranges are <70 km (Prechtel et al. 2018) and egg deposition

models determined that Asian Carp eggs can hatch within 6.4 km of release within pooled river sections and suggests that recruitment probabilities are not limited due to dams (Murphy et al. 2016), all locations located less than 70 km apart were considered a single site rather that grouping sites by river characteristics (i.e., pooled versus free-flowing). At each site, Silver Carp were captured using daytime boat electroshocking (Smith-Root [Des Moines and Missouri river sites only] or MBS-1D Wisconsin style control box; DC; 4-13 amps, 100-500 V, 60 pulses per second with two netters) using a “standardizing by power” approach (i.e., Miranda 2009) focused on side channel, channel border, and backwater habitats (e.g., Wanner and Klumb 2009; Stuck et al. 2015).

Silver Carp were measured (total length; 1 mm) and lapillar otoliths were removed and processed for age analysis. A 1-mm thick cross section was cut at the nucleus of the otolith using a Buehler Isomet low-speed saw. Wetted 2,000-grit sandpaper was used to polish each side of the cross section. The section was then placed in immersion oil to improve clarity and annuli were counted under a dissecting microscope with transmitted light (Seibert and Phelps 2013). Lapillar otoliths were independently aged by two experienced readers with no knowledge of fish length, estimated age of the other otolith, or source river. If the readers disagreed, the otolith was assessed by both readers jointly.

<B>*Calculations of environmental variables from raw environmental data.*- Air temperature and river discharge data were obtained from United States Geological Survey (USGS; https://www.usgs.gov/) and National Oceanic and Atmospheric Administration (NOAA; https://www.ncdc.noaa.gov/) gaging stations within the Mississippi, Des Moines, Wabash, Ohio, Illinois, and Missouri river basins from 2002 to 2010. From these data, we calculated a number of variables. First, we calculated cumulative seasonal river discharge (m^3/s) during May and June [Silver Carp reproductive season (DISR)] and July through October [post-reproductive season (DISNR)] as well as the cumulative coefficient of

variation of the mean daily discharge (COVR) during the reproductive season separately for each site and year. We also evaluated river base flow (BASE.FLOW; 7-day minimum flow/mean flow for year) calculated from the indicators of hydrological alteration model (IHA; Richter et al. 1996; Nature Conservancy 2007). Data input for the IHA models were raw, site-specific mean daily discharge (m^3/s) values obtained from USGS gaging stations. As Silver Carp are generally believed to spawn during periods of sustained, elevated discharge (Kocovsky et al. 2012) and elevated discharges can allow access to larval refuge habitats (e.g., Huet 1970), we hypothesized that higher river discharges during the reproductive and non-reproduction seasons will lead to an increase in Silver Carp year-class strength whereas higher variability in discharge will decrease year-class strength due to inadequate spawning conditions (Verigin et al. 1978) and restricted access to rearing habitats.

Second, we calculated site-specific cumulative growing degree days (GDD), winter severity (WS), and summer severity (SS) metrics using air temperature data derived from NOAA monitoring stations to evaluate the effects of temperature on Silver Carp YCS. Air temperatures are highly correlated with water temperatures across systems (Chezik et al. 2014) while time lags between air and water temperature are generally short depending on river depth (Stefan and Preud'homme 1993). Therefore, air temperature data were used as a surrogate for river thermal environments. Growing degree days were calculated as the annual (January – December) cumulative air degree days above 17°C and was hypothesized to improve larval Silver Carp growth potential during the first growing season that may result in larger year-classes through 'bigger is better' mechanisms where the largest individuals are more likely to survive due to reduced starvation and susceptibility to predation (Miller et al. 1988). Winter severity was calculated as cumulative air degree days below 0°C after the first growing season (Phelps et al. 2008) and hypothesize that more severe winter regimes could lead to decreased year-class strength due to the decreased growth rates and higher metabolic rates of YOY Silver Carp (Kolar et al. 2007). Additionally, SS was calculated as the cumulative air degree days over 27°C during the first growing season. Increases in SS were hypothesized to suppress year-class strength. YOY Silver Carp seek shallow, backwater, nursery habitats during the summer months post-hatch (Kolar et al. 2007), and increases in air temperatures can cause such habitats to exceed the upper temperature threshold for YOY Carp (26.9 °C; Kolar et al. 2007), potentially causing high mortality rates of cohorts.

In order to assess the influence of broad-scale climatic variables on Silver Carp YCS across the Mississippi River basin, additional regional-level variables were considered: North Atlantic Oscillation Index (NAO; data obtained from National Weather Service Climate Prediction Center, College Park, MD, USA), El Niño Southern Oscillation Index (ENSO; data obtained from National Weather Service Climate Prediction Center, College Park, MD, USA), the Palmer Hydrological Drought Index (PHDI; data obtained from NOAA), and the mean annual air temperature greater than 17°C (distinguishing the beginning of the reproductive season) across all sites (data obtained from NOAA). The North Atlantic Oscillation can influence temperature regimes and precipitation distributions over a broad geographic range (Hurrell 1995). The El Niño Southern Oscillation causes either cool or warm phases that influences both winter precipitation and temperature regimes (Zhang et al. 1997). Last, PHDI indicates the severity of a wet or dry period, ranging from greater than 4 (indicating extreme wetness) to less than negative 4 (indicating extreme drought; Heim 2002). We hypothesized that wetter environmental conditions (i.e., positive values of PHDI) and warmer spring/summer conditions (i.e., positive phases of NOA, and warmer mean annual air temperature) will increase Silver Carp year-class strength as floods and warmer thermal regimes can positively affect Carp recruitment and growth (Kolar et al. 2007).

<B>*Statistical Analysis.-* Silver Carp ≤3 years old were excluded from the analysis because they were not fully vulnerable to the gear resulting in infrequent captures (e.g.,

Wanner and Klumb 2009). Site-specific Silver Carp age-frequency distributions were constructed and weighted catch-curve regressions were used to quantify YCS using studentized residuals to account for differences in variances among sampling locations (i.e., the residual method; Maceina 1997). To diminish the influence of older, rarer fish on the linear regression model, a weighting factor was used (i.e., the age term in the regression was proportionally weighted to the sample size at each age). Residuals (observed minus predicted number of fish per age class) estimated relative YCS for Silver Carp populations captured at each site: positive residuals indicated relatively strong year-classes whereas negative residuals represented weaker year-classes.

To index annual Silver Carp recruitment variability, the recruitment variability index (RVI; Guy and Willis 1995) was calculated for each population as

$$RVI = [S_N/(N_M + N_P)] - (N_M/N_P) \quad (1)$$

where S_N is the sum of the cumulative relative frequencies across year-classes in the sample, N_M is the number of missing year-classes from the sample (year-classes beyond the oldest year-class in the sample are excluded), and N_P is the total number of year-classes present in the sample. Recruitment variability index values rage from -1 to 1, with values closer to 1 indicating more consistent recruitment.

As a measure of spatial recruitment synchrony, we computed Spearman's rank correlation coefficient (ρ) between all site pairs of studentized residuals (e.g., Honsey et al. 2016) and correlation coefficients were used to index synchrony among populations. Due to the lack of overlap in year-classes present (less than three year-classes) between the Missouri and middle Illinois rivers, correlations between these sites were not possible, resulting in a total of 21 site comparisons. A one-tailed, one sample *t*-test using Bonferroni corrections was conducted to test whether mean correlation values among all pairs was greater than zero, which would indicate synchronous population fluctuations (e.g., Honsey et al. 2016). In addition, river discharge (m^3) and regional air temperature (°C) indices for each site were correlated between each possible site combination using methods described above. Next, to test if correlations in individual sites' river discharge and air temperature indices among sites was related to synchrony of Silver Carp YCS, correlation coefficients (ρ) between population-specific Silver Carp YCS and environmental variables (river discharge [m^3] and air temperature [°C]) were correlated using Pearson's correlation coefficient (*r*).

The spatial scale of population synchrony for both great-circle distance (km; hereafter referred to as linear distance) and river distance (rkm) was estimated using an exponential decay function (hereafter referred to as the e-folding scale; Myers et al. 1997) calculated as

$$\rho(d) = \rho_0 e^{-\frac{d}{v}} \quad (2)$$

where ρ_0 is the correlation between two site-specific residual values at zero separation (i.e., ρ between all site pairs of studentized residuals), *d* is either linear distance or river distance (depending on analysis) between two sites, and *v* is the e-folding scale (Myers et al. 1997). As the degree of recruitment synchrony in fishes can be dependent upon environmental synchrony (i.e., Weber et al. 2017), the spatial scale of synchrony of both river discharge and air temperature values was evaluated as previously described; however, ρ_0 here is the correlation between two site-specific river discharge (m^3) or regional air temperature (°C) values at zero separation and *d* is linear distance.

Generalized linear mixed effects models using all possible model combinations were used to explore the relationship between Silver Carp YCS (studentized residuals) and local environmental variables. Models were built using site as a random effect and combinations of the following environmental variables as fixed effects: cumulative reproductive season discharge (DISR), cumulative post-reproductive season discharge (DISNR), coefficient of variation in river discharge during the reproductive season (COVR), growing degree days (GDD), winter severity (WS), summer severity (SS), and base flow (BASE.FLOW).

Variables were log-transformed to meet the assumptions of normality and homogeneity of variance as needed. In order to distinguish the most parsimonious model, Akaike's Information Criterion (AIC_c; AIC corrected for small sample size) and associated delta AIC_c (Δ_i) and Akaike weights (W_i) were calculated to rank models based on their relative support for the data. Only models with Δ_i values <2.0 or W_i values >0.1 were used for interpretation (Burnham and Anderson 2003).

To explore the effects of broad climatic conditions on Silver Carp YCS across the Mississippi River basin, the mean annual year-class studentized residual across all sites was calculated for each year where a year-class (2003 – 2010) from a minimum of two populations was present. Mean residual values were then regressed and correlated (using Pearson's correlation coefficient) against four large-scale environmental variables that could influence Silver Carp YCS across a large geographic area: winter NAO averaged for the November – February period for each year, winter ENSO averaged for the November – February period for each year, the mean annual PHDI for all states within the Mississippi River basin (excluding Louisiana and Mississippi), and the mean annual air temperature greater than 17°C across all sites. All statistical analyses were conducted in R Version 3.2.0 (R Development Core Team 2016) with a significance level of 0.05.

<A>Results

In all, 871 Silver Carp were captured from nine Mississippi River basin sites. Based upon age-frequency distributions by site, varying recruitment patterns were evident (Figure 2). Recruitment variability index (RVI) scores varied among sites (0.66 – 0.90); yet, scores were all greater than 0.65, indicating consistent recruitment across all sites (Figure 2). Although highly variable, studentized residuals of Silver Carp YCS were generally highest (>50% of residuals across sites >0 in a year) during 2005-2007 and 2009 while lower during 2003-2004 and 2008 (Figure 3).

Spearman's rank correlation coefficients among all pairwise combinations of YCS between populations ranged from -1.0 to 0.85 (mean = -0.08; P <0.05 for three pairwise combinations). Of the three (14.2%) relationships that were significant, each included at least one Silver Carp population in the Wabash River. Ten (47.6%) correlation coefficients were greater than zero, indicating synchrony in Silver Carp YCS between some sites. In contrast, a greater proportion of correlations (11 site pairs; 52.4%) were negative, indicating more negatively synchronous recruitment. Among pairwise combinations, Silver Carp populations in the Des Moines, Illinois, and Wabash rivers consisted of either highly negative ($\rho < -0.70$) or positive ($\rho > 0.70$) correlations with other Silver Carp populations while populations in the middle and lower Mississippi River sites were moderately correlated or not correlated with other populations throughout the basin (mean $\rho = 0.02 \pm 0.12$ SE; all $P > 0.05$). Despite synchrony observed between some locations, Silver Carp YCS was not synchronous across the Mississippi River basin ($t_{20} = -0.60$, $P = 0.72$). In contrast to Silver Carp YCS, environmental variables were positively correlated across sites as both river discharge (mean $\rho = 0.68$) and regional air temperature (mean $\rho = 0.81$) mean ρ were significantly greater than zero ($t_{20} = 19.19$, $P = <0.001$ and $t_{20} = 37.42$, $P = <0.001$, respectively). Further, river discharge correlation coefficients were positively correlated ($r = 0.59$, $P = 0.005$) with Silver Carp YCS correlation coefficients whereas regional temperature synchrony was not ($r = -0.03$, $P = 0.89$; Figure 4).

Silver Carp recruitment synchrony was not related to linear or river distances between site pairs (Figure 5), as the estimated e-folding scale estimates for Silver Carp populations overlapped with zero (distances equaled 983.7 km ± 15,808.3 SE and 118 km ± 454.0 SE, respectively). In addition, environmental synchrony of both river discharge and regional air temperature was related to linear distance between site pairs (distances equaled 581.3 km ± 132.7 SE and 2,972.0 km ± 916.5 SE, respectively; Figure 6).

Predictive models including metrics of river discharge (BASE.FLOW or COVR) received more support for explaining spatiotemporal variation in Silver Carp recruitment than models including other river discharge or temperature (GDD, SS, and WS) metrics (Table 2). The most supported model included the base flow variation (BASE.FLOW; AIC_c = -68.41, W_i = 0.57) followed by the cumulative coefficient of variation of the mean daily discharge for the reproductive season (COVR; Δ_i = 2.54, W_i = 0.14; Table 2). All other models received substantially less support (Δ_i > 2.0 and W_i > 0.1). The general linear mixed effects model coefficient for the base flow variation was not different from zero (-0.099, 95% CI = -0.28 to 0.08) while all other variable coefficient values were < 0.001.

Mean residual values averaged across all sites indicated that a stronger Silver Carp year-class throughout the Mississippi River basin was present during 2009 (mean = 0.10), a weaker year-class was present during 2008 (mean = -0.07), whereas mean residuals of the remaining year-classes (2003-2007, 2010) were less than Δ 0.03. However, NAO (r = -0.03, P = 0.95), ENSO (r = -0.14, P = 0.75), PHDI (r = 0.12, P = 0.78), and the mean annual regional air temperatures above 17°C (r = -0.09, P = 0.84) indices were not related to Silver Carp YCS (Figure 7).

<A>Discussion

Contrary to our hypothesis, YCS of Silver Carp populations inhabiting the Mississippi River basin was not synchronous across study sites, which differs from several fish populations inhabiting both lotic (Grenouillet et al. 2001; Cattanéo et al. 2003) and lentic (Phelps et al. 2008; Dembkowski et al. 2016; Honsey et al. 2016) systems. Moreover, the influence of the Moran effect has been exhibited for a variety of species, including Common Carp (Phelps et al. 2008; Weber et al. 2017), Yellow Perch (Dembkowski et al. 2016; Honsey et al. 2016), Brown Trout *Salmo trutta* (Cattanéo et al. 2003), Walleye *Sander vitreus* (Koonce et al. 1977; Schupp 2002), Roach *Rutilus rutilus* (Grenouillet et al. 2001), and planktivorous fishes in Lake Michigan (Bunnell et al. 2016). Within the current study, regional climatic variables were not related to YCS of Silver Carp populations, suggesting a lack of the Moran effect across populations. Instead, Silver Carp YCS was influenced more by local indices of river discharge and YCS tended to be more synchronized between sites as river discharge synchronized between sites.

Despite our hypothesis that fluctuations in Silver Carp YCS would vary annually, Silver Carp recruitment was fairly consistent (indicated by RVI scores ≥0.66) throughout the Mississippi River basin. Silver Carp populations often have erratic recruitment, as large-scale floods may result in large year-classes. For example, age structure of Silver Carp in three Missouri River tributaries was dominated by the 2010 year-class that coincided with a large flood event (Hayer et al. 2014). Similarly, Asian Carp populations captured in the middle Mississippi River and the Illinois River confluence were composed mainly of the 2000 year-class that also coincided with large-scale flooding (Garvey et al. 2006). Within the current study, Silver Carp recruitment was generally consistent across sites while inter-annual river discharge values varied drastically. Yet, increases in river discharge promoted stronger year-classes of Silver Carp across the study sites. For example, during 2009 a strong year-class of Silver Carp identified herein and in other studies within the Illinois River (Morgeson 2015; Stuck et al. 2015) coincided with high river discharges. However, large year-classes of Silver Carp in the middle Illinois River were also reported in 2008 (Gibson-Reinemer et al. 2017) but not observed in this study, suggesting that Carp are not recruited into the adult population as YOY or mortality via commercial fishery harvest is effective at removing larger, older Carp from the population (i.e., Roth et al 2012), precluding their capture throughout this study. Thus, although increases in discharge can promote stronger year-classes, Silver Carp recruitment can be successful under a wide range of environmental conditions.

Although synchronous recruitment of freshwater fishes can extend to spatial scales greater than 50 km (e.g., Myers et al. 2015; Honsey et al. 2016; Weber et al. 2017), our results indicate that Silver Carp recruitment does not exhibit synchronous fluctuations at the spatial scale evaluated though environmental conditions were synchronous. Two explanations could help elucidate the lack of synchrony among populations. First, the spatial extent of synchrony generally occurs at distances less than 50 km for a suite of freshwater fish species, and even at distances less than 15 km in some instances (e.g., Northern Pike *Esox lucius*; Myers et al. 1997). In the current study, the shortest linear distance between sites was 75.4 km (lower and middle Mississippi River sites) and most sites are separated by more than 200 km linearly. Second, Prechtel et al. (2018) found that most Silver Carp in the Wabash River exhibited home ranges <70 km over a three year period; however, our study sites were separated by more than 177.6 rkm. Therefore, due to the lack of sites located closer in proximity where home ranges of Silver Carp would overlap, our analysis indicates that Silver Carp populations separated by >75km experience asynchronous recruitment due to differences in localized environmental conditions.

Although their influence was highly variable, periods of high, sustained discharge typically led to stronger Silver Carp year-classes while more variable discharge during the reproductive season typically resulted in weaker year-classes. For example, Silver Carp populations captured from both the Illinois (Stuck et al. 2015) and Wabash (Morgeson 2015) river sites produced stronger year-classes during 2009 where high, sustained discharge events were present for greater than three months (USGS 2016). In other studies, similar patterns have been qualitatively discussed (Hayer et al. 2014) as well as the combination of high discharges and temperatures above 17°C in the Upper Mississippi River promoting strong year-classes (Garvey et al. 2006; DeGrandchamp et al. 2007; Lohmeyer and Garvey 2009). Similar to studies in lentic systems, high water levels can also result in strong year-classes

(Phelps et al. 2008; Dembkowski et al. 2016), potentially augmenting productivity, inundating larval fish nursery habitat, providing spawning substrate, and predator refuge habitat (Nunn et al. 2012). Given the stochastic nature of lotic systems, the availability of nursery habitat becomes crucial to young-of-year fish survival (e.g., Cattanéo et al. 2003). Spawning during high flow can facilitate larval dispersal into floodplain, creek, or low-flow habitats that serve as nursey areas, increasing larval survival (Huet 1970). Alternatively, low flow conditions have the ability to disconnect mainstem habitats from nursery habitats, potentially leading to weak YCS. Collectively, elevated, sustained river discharge during the first year of life seems to be influential in regulating YCS of Silver Carp at local scales across the Mississippi River basin.

As the Moran effect predicts that biological and environmental synchrony will be roughly equal (Lundberg et al. 2000), we propose that in lotic systems, dynamic environmental variables that can synchronize over a broad area in response to extreme climatic conditions (i.e., discharge) can synchronize Silver Carp recruitment while recruitment can become asynchronous when environmental conditions are asynchronous and operate independently. During years where regional floods occur, our results suggest that stronger year-classes of Silver Carp will be produced across a more broad geographic range and compose a large proportion of local Silver Carp populations (e.g., Garvey et al. 2006).

As large-scale recruitment in freshwater fishes is often synchronous across broad geographic areas in response to similarities in temperature regimes (i.e., Grenouillet et al. 2001), we hypothesized that warmer spring/summer temperature regimes would promote stronger year-class strength of Silver Carp. Contrary to our hypothesis, models incorporating temperature metrics received no support. Although thermal regimes are important for larval Silver Carp development (Chapman and George 2011; George and Chapman 2013), warmer thermal regimes during the growing season did not promote year-class strength, indicating that either Silver Carp recruitment is more regulated by river discharge patterns or that our study design did not incorporate study sites where thermal regimes vary drastically. For example, the coefficient of variation (CV) for the annual degree days over 17°C across the study sites was low (CV = 0.35). Furthermore, summer temperatures rarely exceeding an upper thermal tolerances across the study sites. As such, future research should be directed at evaluating the effects of a wide range of thermal regimes on Silver Carp recruitment.

The information provided here will lead to an improved understanding of Silver Carp recruitment dynamics throughout North America and represents a step towards understanding the underlying mechanisms influencing recruitment. The degree of correlation among river discharge patterns between sites appears to be an important mechanism regulating the degree of recruitment synchrony among Mississippi River Silver Carp populations. In addition to Silver Carp, the Mississippi River currently has reproducing populations of Bighead (Schrank et al 2001), Grass (Raibley et al. 1995), and Black (Nico and Jelks 2011) carp, all posing a severe threat to native biodiversity throughout the basin. As their range expansion within the basin continues, the results presented could aid in the understanding of abiotic factors influencing population recruitment dynamics of these additional species populations across multiple spatial scales.

<A>Acknowledgements

We thank the numerous technicians who were involved with data collection, particularly, Matt Diana (INHS). Special thanks to Timothy Parks for comments on a draft of the manuscript. This study was funded through the Fish and Wildlife Trust Fund to the Iowa Department of Natural Resources. This study was performed under the auspices of Iowa State University Institutional Animal Care and Use Committee (IACUC) protocol permit 7-

13-7599-I, and animals were collected under state permit SC1037. Use of trade, product, or firm names is descriptive and does not imply endorsement by the U.S. Government.

<A>References

Adams, S. M., R. B. McLean, and M. M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Canadian Journal of Fisheries and Aquatic Sciences 39:1175-1184.

Bunnell, D. B., J. V. Adams, O. T. Gorman, C. P. Madenjian, S. C. Riley, E. F. Roseman, and J. S. Shaeffer. 2010. Population synchrony of a native fish across three Laurentian Great Lakes: evaluating the effects of dispersal and climate. Oecologia 162:641-651.

Bunnell, D. B., T. O. Höök, C. D. Troy, W. Liu, C. P. Madenjian, and J. V. Adams. 2016. Testing for synchrony in recruitment among four Lake Michigan fish species. Canadian Journal of Fisheries and Aquatic Sciences 74:306-315.

Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Cattanéo, F., B. Hugueny, and N. Lamouroux. 2003. Synchrony in Brown Trout, *Salmo trutta*, population dynamics: a 'Moran effect' on early-life stages. OIKOS 100:43-54.

Chapman, D. C., and A. E. George. 2011. Developmental rate and behavior of early life stages of Bighead Carp and Silver Carp. U.S. Geological Survey Scientific Investigations Report 2011-5076, 11p.

Chevalier, M., P. Laffaille, J. B. Ferdy, and G. Grenouillet. 2015. Measurements of spatial population synchrony: influence of time series transformations. Oecologia 179:15-28.

Chezik, K. A., N. P. Lester, and P. A. Venturelli. 2014. Fish growth and degree-days I: selecting a base temperature for a within population study. Canadian Journal of Fisheries and Aquatic Sciences 71:47-55.

Coulter, A. A., E. J. Bailey, D. Keller, and R. R. Goforth. 2016. Invasive Silver Carp movement patterns in the predominantly free-flowing Wabash River (Indiana, USA). Biological Invasions 18:471-485.

DeGrandchamp, K. L., J. E. Garvey, and L. A. Csoboth. 2007. Linking adult reproduction and larval density of invasive Carp in a large river. Transactions of the American Fisheries Society 136:1327-1334.

Dembkowski, D. J., D. W. Willis, and M. R. Wuellner. 2016. Synchrony in larval Yellow Perch abundance: the influence of the Moran Effect during early life history. Canadian Journal of Fisheries and Aquatic Sciences 73:1567-1574.

Dettmers, J. M., M. J. Raffenberg, and A. K. Weis. 2003. Exploring zooplankton changes in southern Lake Michigan: implications for Yellow Perch recruitment. Journal of Great Lakes Research 29:355-364.

Freeze, M., and S. Henderson. 1982. Distribution and status of the Bighead Carp and Silver Carp in Arkansas. North American Journal of Fisheries Management 2:197-200.

Garvey, J. E., K. L. DeGrandchamp, and C. J. Williamson. 2006. Life history attributes of Asian Carps in the upper Mississippi River system. Reports. Paper 3. http://opensiuc.lib.siu.edu/fiaq_reports/3

Garvey, J. E., G. G. Sass, J. Trushenski, D. Glover, M. K. Brey, P. M. Charlebois, J. Levengood, B. Roth, G. Whitledge, S. Secchi, W. Bouska, R. MacNamara, B. C. Small, S. J. Tripp, A. F. Casper, J. Lames, S. Varble, R. M. Pendleton, C. J. Hinz, J. A. DeBoer, and M. W. Fritts. 2015. Fishing down the Bighead and Silver Carps: reducing the risk for invasion to the Great Lakes. Research Summary, 193p.

George, A. E., and D. C. Chapman. 2013. Aspects of embryonic and larval development in Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *Hypophthalmichthys molitrix*. PLoS ONE 8:e73829. DOI:10.1371/journal.pone.0073829.

Gibson-Reinemer, D. K., L. E. Solomon, R. M. Pendleton, J. H. Chick, and A. F. Casper. 2017. Hydrology controls recruitment of two invasive cyprinids: Bigheaded Carp reproduction in a navigable large river. PeerJ 5:e3641; DOI 10.7717/peerj.3641.

Goldwyn, E. E., and A. Hastings. 2011. The roles of the Moran effect and dispersal in synchronizing oscillating populations. Journal of Theoretical Biology 289:237-246.

Grenouillet, G., B. Hugueny, G. A. Carrel, J. M. Olivier, and D. Pont. 2001. Large-scale synchrony and inter-annual variability in Roach recruitment in the Rhone River: the relative role of climate factors and density-dependent processes. Freshwater Biology 46:11-26.

Guy, C. S., and D. W. Willis. 1995. Population characteristics of Black Crappie in South Dakota waters: a case for ecosystem-specific management. North American Journal of Fisheries Management 15:754-765.

Haydon, D., and H. Steen. 1997. The effects of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis. Proceedings of the Royal Society B 264:1375-1381.

Hayer, C. A., J. J. Breeggemann, R. A. Klumb, B. D. Graeb, and K. N. Bertrand. 2014. Population characteristics of Bighead and Silver Carp on the northwestern front of their North American invasion. Aquatic Invasions 9:289-303.

Heim, R. R. 2002. A review of twentieth-century drought indices used in the United States. Bulletin of the American Meteorological Society 83:1149-1165.

Henderson, P. A., and M. Corps. 1997. The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. Journal of Fish Biology 50:280-295.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. ICES Journal of Marine Science 1:5-38.

Honsey, A. E., D. B. Bunnell, C. D. Troy, D. G. Fielder, M. V. Thomas, C. T. Knight, S. C. Chong, and T. O. Höök. 2016. Recruitment synchrony of Yellow Perch (*Perca flavescens,* Percidae) in the Great Lakes regions, 1966-2008. Fisheries Research 181:214-221.

Huet, M. 1970. Textbook of fish culture: breeding and cultivation of fish. Fishing News Ltd., Surrey and London.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic oscillation regional temperatures and precipitation. Science 269:676-679.

Irons, K. S., G. G. Sass, M. A. McClelland, and J. D. Stafford. 2007. Reduced condition factor of two native fish species coincident with invasion of nonnative Asian Carps in the Illinois River, U.S.A. Is this evidence for competition and reduced fitness? Journal of Fish Biology 71:258-273.

Kendall, B. E., O. N. Bjørnstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. The American Naturalist 155: 628-636.

Kocovsky, P. M., D. C. Chapman, and J. E. McKenna. 2012. Thermal and hydrological suitability of Lake Erie and its major tributaries for spawning of Asian Carps. Journal of Great Lakes Research 38:159-166.

Kolar, C. S., D. C. Chapman, W. R. Courtenay, C. M. Housel, J. D. Williams, and D. P. Jennings. 2007. Bigheaded Carps: a biological synopsis and environmental risk assessment. Special Publication 33. American Fisheries Society, Bethesda, Maryland.

Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Nagięć. 1977. Factors influencing year-class strength of percids: a summary and model of temperature effects. Journal of Fisheries Research Board of Canada 34:1900-1909.

Lande, R., S. Engen, and B. E. Sæther. 1999. Spatial scale of population synchrony: Environmental correlation versus dispersal and density regulation. The American Naturalist 154:271-279.

Li, C., J. Peng, and W. Liao. 2006. Study on the eco-hydrological factors and flow regime requirements on spawning of four major Chinese Carps in the middle reaches of the Yangtze River. Journal of China Institute of Water Resources and Hydropower Research 14:170-176.

Lohmeyer, A. M., and J. E. Garvey. 2009. Placing the North American invasion of Asian Carp in a spatially explicit context. Biological Invasions 11:905-916.

Lundberg, P., E. Ranta, J. Ripa, and V. Kaitala. 2000. Population variability in space and time. Trends in Ecology and Evolution 15:460-464.

Maceina, M. J. 1997. Simple application of using residuals from catch-curve regressions to assess year-class strength in fish. Fisheries Research 32:115-121.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670.

Miranda, L. E. S. 2009. Standardizing electrofishing power for boat electrofishing. In: Standard methods for sampling North American freshwater fishes. Eds. S. Bonar, W. A. Hubert, and D. Willis. American Fisheries Society, Bethesda, Maryland.

Moran, P. A. 1953. The statistical analysis of the Canadian Lynx cycle, II. Synchronization and Meteorology. Australian Journal of Zoology 1:291-298.

Morgeson, C. W. 2015. Asian Carp population status and reproductive potential in Illinois River tributaries. Master's thesis. Eastern Illinois University, Charleston, Illinois.

Murphy, E. A., T. Garcia, P. R. Jackson, and J. J. Duncker. 2016. Simulation of hypothetical Asian carp egg and larvae transport in the Lockport, Brandon Road, Dresden Island, and Marseilles pools of the Illinois waterway by use of the fluvial egg drift simulator (FluEgg) model. U.S. Geological Survey Scientific Investigations Report 2016-1011, 31p.

Myers, R. A., G. Mertz, and J. Bridson. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 54:1400-1407.

Myers, J. T., D. L. Yule, M. L. Jones, T. D. Ahrenstorff, T. R. Hrabik, R. M. Claramunt, M. P. Ebener, and E. K. Berglund. 2015. Spatial synchrony in Cisco recruitment. Fisheries Research 165:11-21.

Naiman, R. J., J. J. Latterell, N. E. Pettit, and J. D. Olden. 2008. Flow variability and the biophysical vitality of river systems. Comptes Rendys Geoscience 340:629-643.

Nature Conservancy. 2007. Indicators of hydrological alteration. Version 7. User's manual. http://www.nature.org/initiatives/freshwater/files/ihav7.pdf

Nico, L., and H. L. Jelks. 2011. The Black Carp in North America: an update. In: Invasive Asian Carps in North America. Eds. D. C. Chapman and M. H. Hoff. American Fisheries Society, Maryland. 89-104pp.

Nunn, A. D., L. H. Tewson, and I. G. Cowx. 2012. The foraging ecology of larval and juvenile fishes. Reviews in Fish Biology and Fisheries 22:377-408.

Phelps, Q. E., B. D. Graeb, and D. W. Willis. 2008. Influence of the Moran Effect on spatiotemporal synchrony in Common Carp recruitment. Transactions of the American Fisheries Society 137:1701-1708.

Prechtel, A. R., A. A. Coulter, L. Etchison, P. R. Jackson, and R. R. Goforth. 2018. Range estimates and habitat use of invasive Silver Carp (*Hypophthalmichthys molitrix*): evidence of sedentary and mobile individuals. Hydrobiologia 805:203-218.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org. (August 2016).

Raibley, P. T., D. Blodgett, and R. E. Sparks. 1995. Evidence of Grass Carp (*Ctenopharyngodon idella*) reproduction in the Illinois and Upper Mississippi Rivers. Journal of Freshwater Ecology 10:65-74.

Ranta, E., V. Kaitala, and J. Lindström. 1998. Spatial dynamics of populations: In: Modeling Spatiotemporal Dynamics in Ecology. Eds. J Bascompte and R. V. Solé, Springer, Berlin. 47-62pp.

Rasmussen, J. L. 1979. A compendium of fishery information on the upper Mississippi River, 2nd ed. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10:1163-1174.

Rook, B. J., M. J. Hansen, and O. T. Gorman. 2012. The spatial scale for Cisco recruitment dynamics in Lake Superior during 1978-2007. North American Journal of Fisheries Management 32:499-514.

Schrank, S. J., P. J. Braaten, and C. S. Guy. 2001. Spatiotemporal variation in density of larval Bighead Carp in the lower Missouri River. Transactions of the American Fisheries Society 130:809-814.

Schrank, S. J., and C. S. Guy. 2002. Age, growth, and gonadal characteristics of adult Bighead Carp, *Hypophthalmichthys nobilis*, in the lower Missouri River. Environmental Biology of Fishes 64:443-450.

Schupp, D. H. 2002. What does Mt. Pinatubo have to do with Walleyes? North American Journal of Fisheries Management 22:1014-1020.

Seibert, J. R., and Q. E. Phelps. 2013. Evaluation of Aging Structures for Silver Carp from Midwestern U.S. Rivers. North American Journal of Fisheries Management 33:839-844.

Skibsted, R. 2012. Wabash River strategic plan. National Great Lakes Research and Education Center, Alton, Illinois, USA.

Stefan, H. G., and E. B. Preud'homme. 1993. Stream temperature estimation from air temperature. Journal of the American Water Resources Association 29: 27-45.

Stuck, J. G., A. P. Porreca, D. H. Wahl, and R. E. Colombo. 2015. Contrasting population demographics of Invasive Silver Carp between an impounded and free-flowing river. North American Journal of Fisheries Management 35:114-122.

Tedesco, P. A., B. Huegeny, D. Paugy, and Y. Fermon. 2004. Spatial synchrony in population dynamics of West African fishes: a demonstration of an intraspecific and interspecific Moran effect. Journal of Animal Ecology 73:693-705.

U.S. Geological Survey. 2016. October. USGS water resources of the United States. http://nwis.waterdata.usgs.gov/usa/nwis/uv/?cb_00055=onandcb_00060=onandcb_00065=onandformat=gif_statsandsite_no=05568500andperiod=andbegin_date=2009-01-01andend_date=2009-12-31

Verigin, B. V., A. P. Makeyeva, and M. I. Zaki Mokhamed. 1978. Natural spawning of the Silver Carp (*Hypophthalmichthys nobilis*), the Bighead Carp (*Aristichthys nobilis*), and the Grass Carp (*Ctenopharyngodon idella*) in the Syr-Dar'ya River. Journal of Ichthyology 18:143-146.

Wanner, G. A., and R. A. Klumb. 2009. Asian Carp in the Missouri River: Analysis from multiple Missouri River habitat and fisheries programs. National Invasive Species Council materials. Paper 10 National Invasive Species Council materials. Paper 10.

Weber, M. J., M. L. Brown, D. H. Wahl, and D. E. Shoup. 2017. Quantifying the spatial scale of Common Carp *Cyprinus carpio* recruitment synchrony. Canadian Journal of Fisheries and Aquatic Sciences, DOI: 10.1139/cjfas-2016-0254

Williamson, C. J., and J. E. Garvey. 2005. Growth, fecundity, and diets of newly established Silver Carp in the middle Mississippi River. Transactions of the American Fisheries Society 134:1423-1430.

Zhang, Y., J. M. Wallace, and D. S. Battisti. 1997. ENSI-like interdecadal variability: 1900-93. Journal of Climate 10:1004-1020.

Zorn, T. G., and A. J. Nuhfer. 2007. Regional synchrony of Brown Trout and Brook Trout population dynamics among Michigan rivers. Transactions of the American Fisheries Society 136:706-717.

Table 1. Length in river kilometers (rkm), drainage area (km^2), and mean, minimum, and maximum annual discharge values (m^3/sec) for the five rivers evaluated in this study.

River	Length (rkm)	Drainage Area (km^2)	Discharge (m^3/sec)		
			Mean	Minimum	Maximum
Des Moines	845	40,940	416	17	1,088
Illinois	439	72,701	659	38	3,483
Mississippi	3,732	2,981,076	18,400	4,502	86,791
Missouri	3,767	1,371,010	2,478	17	21,238
Wabash	810	103,600	232	41	1,051

Table 2. Model selection results, including model covariates, number of parameters estimated (K), AIC_c score, difference between the AIC value of the most parsimonious model and model *i* (Δ_i), and the relative support for model *i* (W_i), for candidate models evaluating Silver Carp year-class strength in the Mississippi River basin. Variables included log-transformed cumulative coefficient of variation in river discharge (m^3/s) during the reproductive season (May-June; COVR), log-transformed cumulative river discharge (m^3/s) during the reproductive season (DISR), log-transformed cumulative river discharge (m^3/s) during the post-reproductive season (June-October; DISNR), growing degree days (GDD), cumulative annual degree days over 27°C (summer severity; SS), cumulative annual degree days under 0°C (winter severity; WS), and base flow (BASE.FLOW). All possible additive model combinations were evaluated but only the top 10 models are shown.

Model	K	AIC_c	Δ_i	W_i
BASE.FLOW	3	-68.41	0.00	0.57
COVR	3	-65.86	2.54	0.16
DISNR	3	-64.65	3.76	0.09
DISR	3	-64.59	3.82	0.08
DISR + COVR	4	-63.28	5.13	0.04
SS	3	-61.80	6.61	0.02
BASE.FLOW + COVR	4	-60.79	7.62	0.01
BASE.FLOW + DISNR	4	-60.77	7.64	0.01
BASE.FLOW + DISR	4	-59.79	8.62	0.01
DISNR + DISR	4	-59.16	9.24	0.01

Figure captions.

Figure 1. Location of nine Mississippi River basin sampling sites used to assess synchrony of Silver Carp year-class strength. 1: Missouri River, 2: Des Moines River confluence, 3: Upper Illinois River, 4: Middle Illinois River, 5: Illinois River Confluence, 6: Middle Mississippi River, 7: Lower Mississippi River, 8: Lower Wabash River, 9: Upper Wabash River.

Figure 2. Silver Carp year-class histogram and associated sample size (N), mean total length (TL; mm ± SE), and RVI scores from nine locations across the Mississippi River basin used to assess regional synchrony of Silver Carp year-class strength.

Figure 3. Spatiotemporal trends in Silver Carp year-class strength (residual values) collected from nine sites located throughout the Mississippi River basin. Residual values are indicative of relative year-class strength as positive values denote strong year-classes and negative values denote weak year-classes.

Figure 4. River discharge (m^3; top) and regional temperature (°C; bottom) correlation coefficients (ρ) versus correlation coefficients of Silver Carp relative year-class strength (ρ; Y-axis) between populations in Mississippi River basin.

Figure 5. E-folding scale of distance (great circle distance [km; top] and river distance [rkm; bottom]) versus pairwise Spearman's correlation coefficients (ρ) of relative year-class strength among Mississippi River Silver Carp populations. The spatial scale of synchrony overlapped with zero and thus, was not significant or plotted.

Figure 6. E-folding scale of distance (great circle distance [km]) versus pairwise Spearman's correlation coefficients (ρ) of both river discharge (m^3; top) and regional air temperature (°C; bottom) among Mississippi River Silver Carp populations.

Figure 7. Relationships between Annual North Atlantic Oscillation Index (NAO), El Niño Southern Oscillation Index (ENSO), Palmer Hydrological Drought Index (PHDI), and mean

annual regional temperature (°C) indices with mean Silver Carp year-class strength (Y-axis) among the nine sampling sites in the Mississippi River basin.

Figure 1.

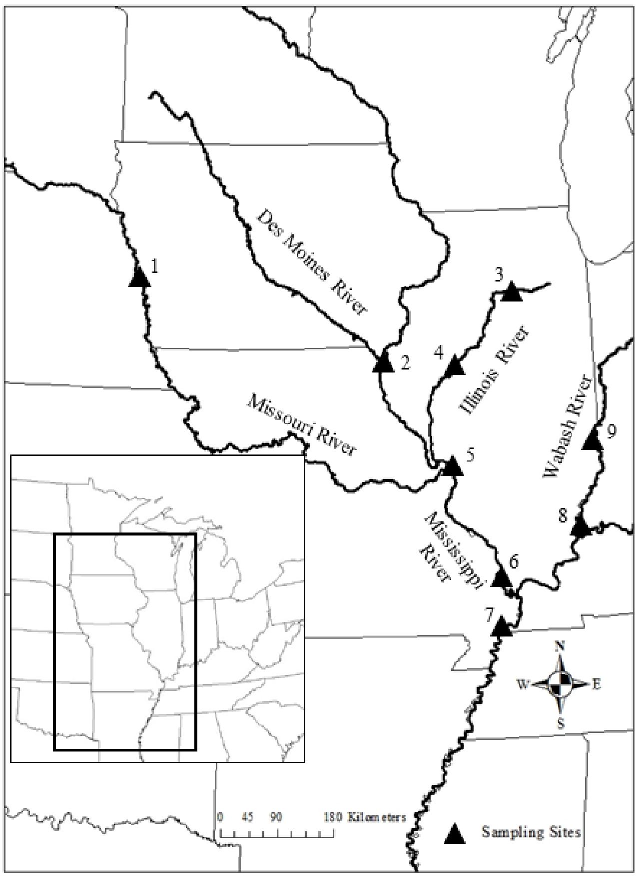


Figure 2.

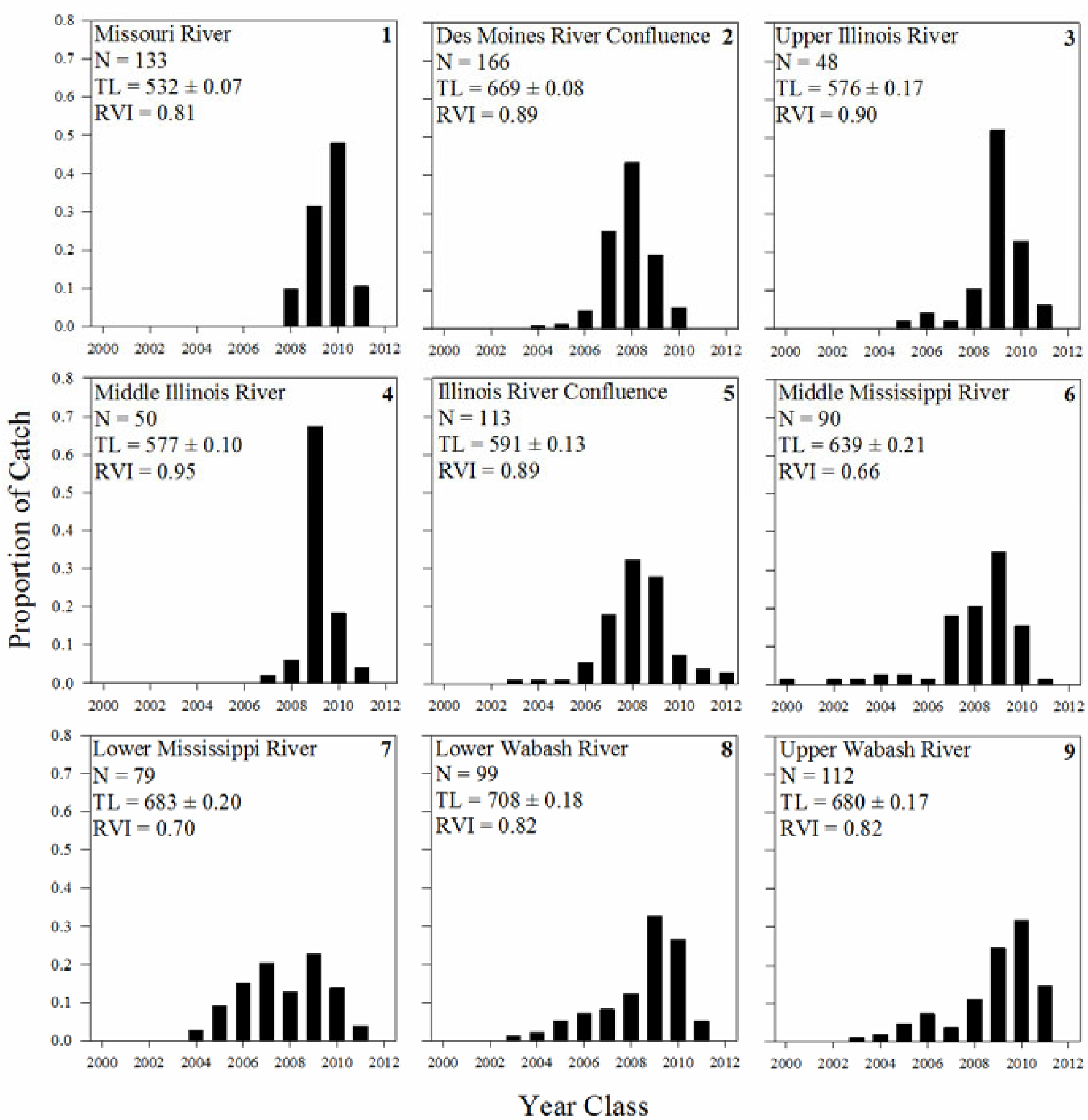
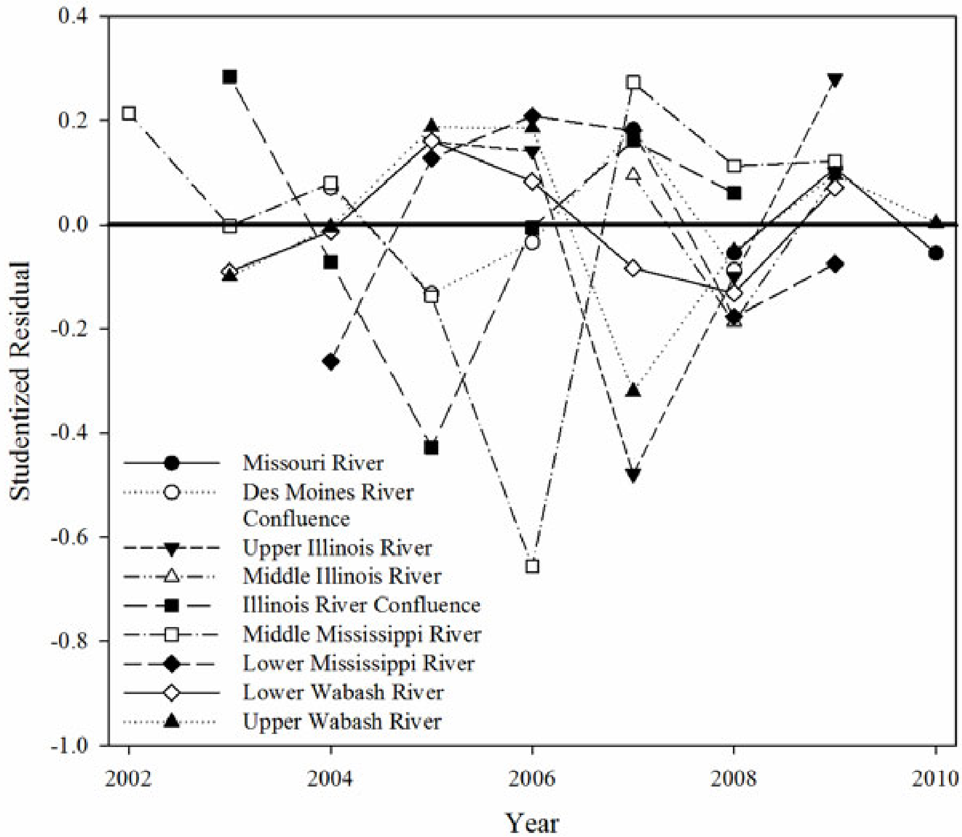
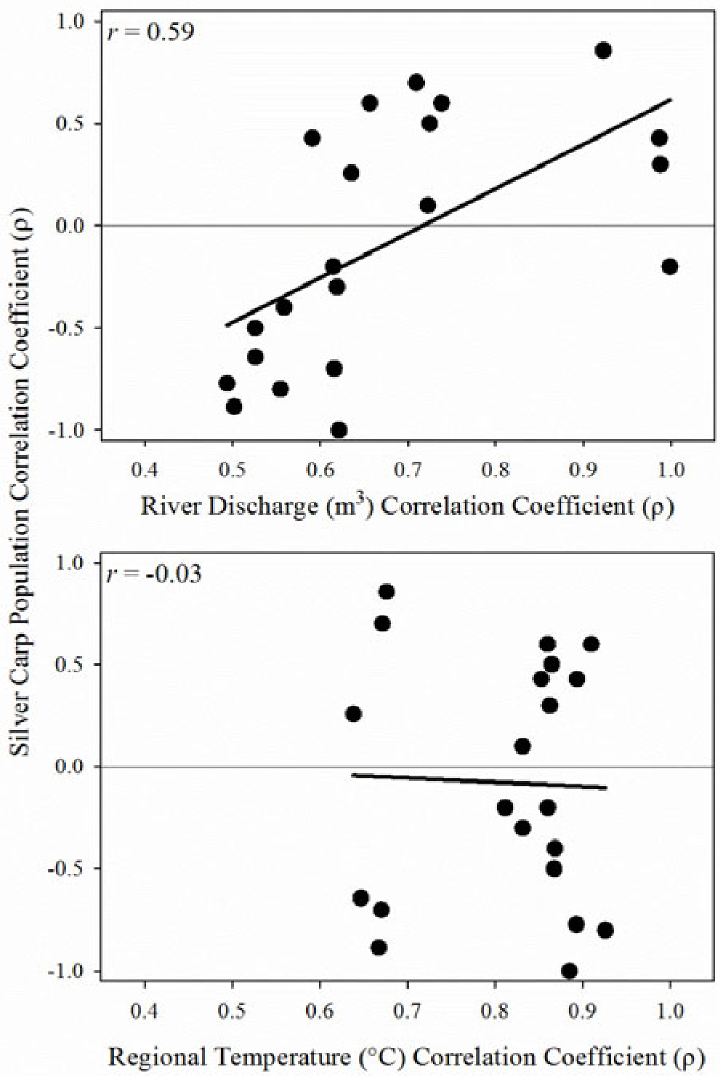

Missouri River 1
N = 133
TL = 532 ± 0.07
RVI = 0.81
Des Moines River Confluence 2
N = 166
TL = 669 ± 0.08
RVI = 0.89
Upper Illinois River 3
N = 48
TL = 576 ± 0.17
RVI = 0.90
Middle Illinois River 4
N = 50
TL = 577 ± 0.10
RVI = 0.95
Illinois River Confluence 5
N = 113
TL = 591 ± 0.13
RVI = 0.89
Middle Mississippi River 6
N = 90
TL = 639 ± 0.21
RVI = 0.66
Lower Mississippi River 7
N = 79
TL = 683 ± 0.20
RVI = 0.70
Lower Wabash River 8
N = 99
TL = 708 ± 0.18
RVI = 0.82
Upper Wabash River 9
N = 112
TL = 680 ± 0.17
RVI = 0.82
Proportion of Catch
Year Class

Figure 3.



Studentized Residual
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
2002
2004
2006
2008
2010
Year
Missouri River
Des Moines River Confluence
Upper Illinois River
Middle Illinois River
Illinois River Confluence
Middle Mississippi River
Lower Mississippi River
Lower Wabash River
Upper Wabash River

Figure 4.



r = 0.59
r = -0.03
1.0
0.5
0.0
-0.5
-1.0
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Silver Carp Population Correlation Coefficient (ρ)
River Discharge (m³) Correlation Coefficient (ρ)
Regional Temperature (°C) Correlation Coefficient (ρ)

Figure 5.

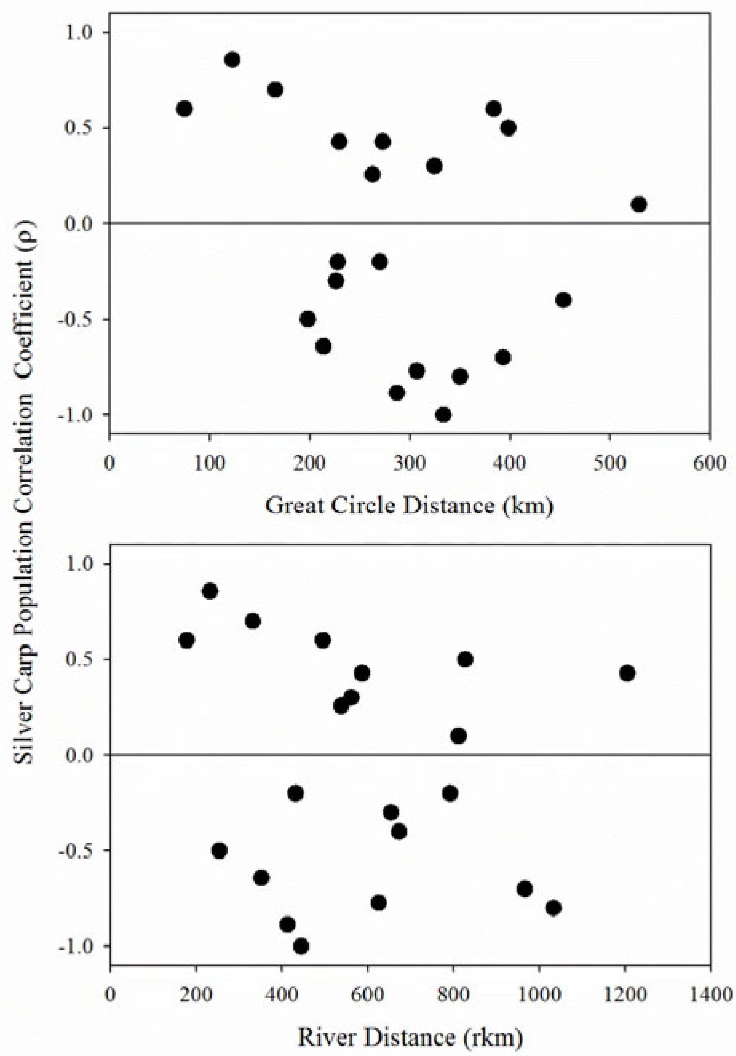

Silver Carp Population Correlation Coefficient (ρ)
1.0
0.5
0.0
-0.5
-1.0
0
100
200
300
400
500
600
Great Circle Distance (km)
1.0
0.5
0.0
-0.5
-1.0
0
200
400
600
800
1000
1200
1400
River Distance (rkm)

Figure 6.

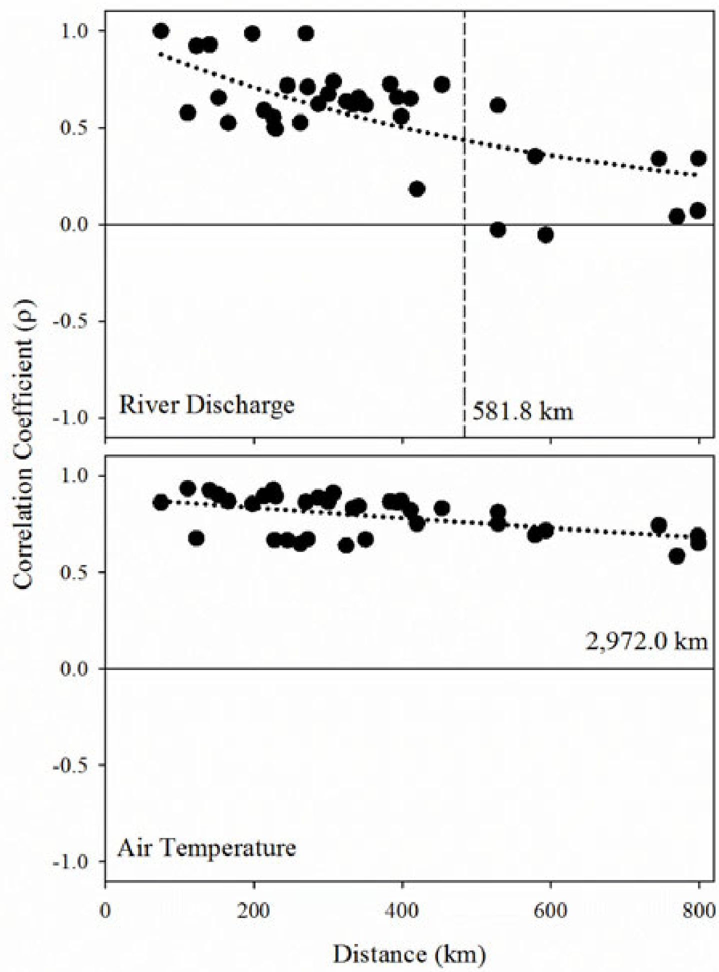
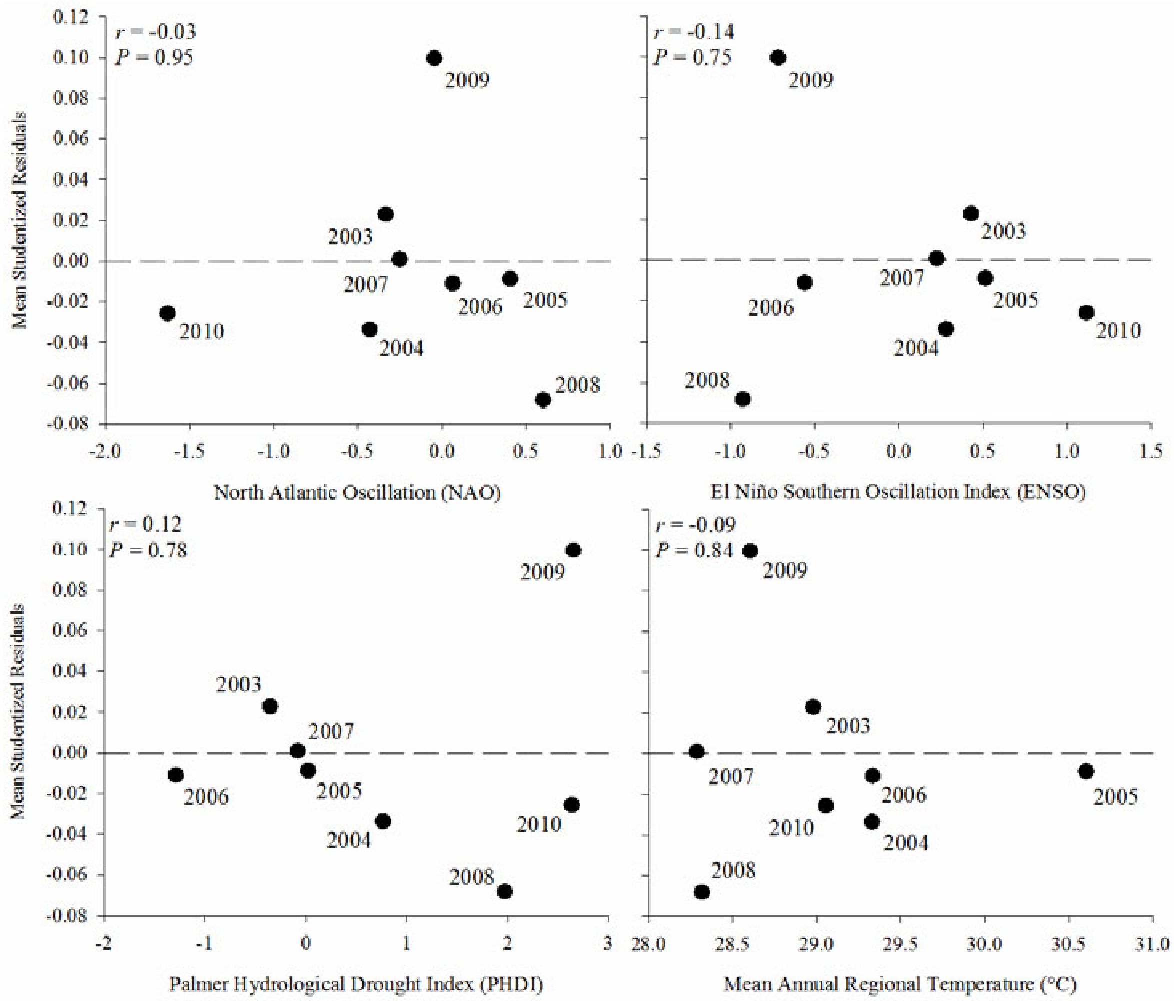

1.0
0.5
0.0
-0.5
-1.0
River Discharge
581.8 km
1.0
0.5
0.0
-0.5
-1.0
2,972.0 km
Air Temperature
Correlation Coefficient (ρ)
0
200
400
600
800
Distance (km)

Figure 7.


r = -0.03
P = 0.95
Mean Studentized Residuals
North Atlantic Oscillation (NAO)
r = -0.14
P = 0.75
El Niño Southern Oscillation Index (ENSO)
r = 0.12
P = 0.78
Palmer Hydrological Drought Index (PHDI)
r = -0.09
P = 0.84
Mean Annual Regional Temperature (°C)
2003
2004
2005
2006
2007
2008
2009
2010