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Factors Regulating Year-Class Strength of Silver Carp Throughout the Mississippi River Basin

Christopher J. Sullivan*¹ and Michael J. Weber

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

Clay L. Pierce

U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, Iowa 50011, USA

David H. Wahl

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

Quinton E. Phelps

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

Carlos A. Camacho

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

Robert E. Colombo

Department of Biological Sciences, Eastern Illinois University, Charleston, Illinois 61920, USA

Abstract

Recruitment of many fish populations is inherently highly variable interannually. 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 (maximum linear distance = 806.4 km) were 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 that 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. Furthermore, river discharge and air temperature were correlated and synchronized among sites, but only similarities in river discharge were correlated with Silver Carp population synchrony, indicating that similarities in discharge (i.e., major flood) among sites can positively synchronize Silver Carp YCS. The

*Corresponding author: csulliva@uwsp.edu

¹Present address: College of Natural Resources, University of Wisconsin–Stevens Point, 800 Reserve Street, Stevens Point, Wisconsin 54481, USA.

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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 interannually 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 interannual 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 the Cisco *Coregonus artedii* (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), and freshwater recruitment synchrony is 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-km² 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 appear 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 (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.

The Silver Carp *Hypophthalmichthys molitrix* is an invasive species that has elicited substantial concern among ecologists and recreational users since its 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, and 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, and water quality; Kolar et al. 2007) have facilitated their successful establishment and subsequent expansion into much of the Mississippi River basin. Silver Carp are highly mobile, moving more than 3.0 km/d (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°C to 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 whether recruitment is synchronized among Silver Carp populations in the Missouri, Des Moines, Mississippi (middle and lower river reaches), Illinois, and Wabash rivers; (3) estimate the spatial scale for recruitment synchrony if detected; 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.

METHODS

Study area.—The Missouri, Des Moines, Illinois, and Wabash rivers are four major tributaries of the Mississippi

River basin (river-specific details are provided 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 floodwaters (Rasmussen 1979). In contrast, the Wabash River contains nearly 661 river kilometers (rkm) of free-flowing river downstream from its single main-stem 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 factors that could influence Silver Carp YCS.

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 rkm), and sites were located greater than 70 km from one another except for the three sites located on the Illinois River and two sites on the Wabash River, where within each site, Silver Carp were collected from locations between 6.1 and 43.1 rkm apart. Silver Carp home ranges are less than 70 km (Prechtel et al. 2018), and egg deposition models determined that Asian carp eggs can hatch within 6.4 km of release in pooled river sections and suggested that recruitment probabilities are not limited due to dams (Murphy et al. 2016); thus, all locations less than 70 km apart were considered a single site rather than 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 A, 100–500 V, and 60 pulses/s, with two netters) using a “standardizing by power” approach (i.e., Miranda 2009) focused on side channel, channel border, and backwater

TABLE 1. Length (river kilometers [rkm]), drainage area (km²), and mean, minimum, and maximum annual discharge values (m³/s) for the five rivers evaluated in this study.

River	Length (rkm)	Drainage area (km ²)	Discharge (m ³ /s)		
			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

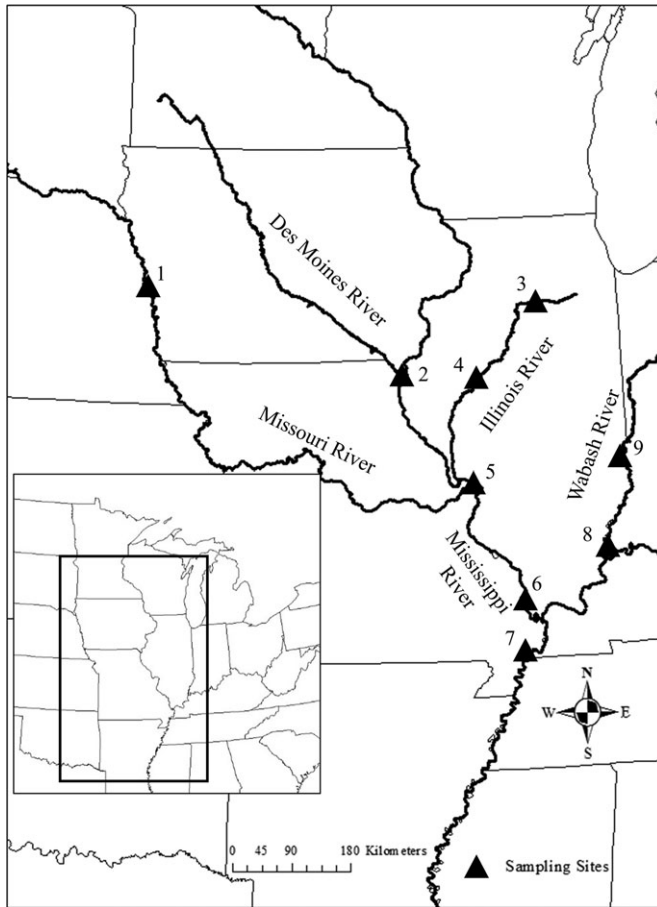


FIGURE 1. Locations of nine Mississippi River basin sampling sites used to assess synchrony of Silver Carp year-class strength (1 = Missouri River; 2 = Des Moines River confluence; 3 = upper Illinois River; 4 = middle Illinois River; 5 = Illinois River confluence; 6 = middle Mississippi River; 7 = lower Mississippi River; 8 = lower Wabash River; 9 = upper Wabash River).

habitats (e.g., Wanner and Klumb 2009; Stuck et al. 2015).

Silver Carp were measured (TL; 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 by 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, the estimated age of the other otolith, or the source river. If the readers disagreed, the otolith was assessed by both readers jointly.

Calculations of environmental variables from raw environmental data.—Air temperature and river discharge

data were obtained from U.S. Geological Survey (USGS; <https://www.usgs.gov/>) and National Oceanic and Atmospheric Administration (NOAA; <https://www.ncdc.noaa.gov/>) gauging 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 discharge [DISR]) and July–October (postreproductive season discharge [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-d minimum flow/mean flow for year) calculated from the Indicators of Hydrological Alteration (IHA) model (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 gauging 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 nonreproduction seasons would lead to an increase in Silver Carp YCS, whereas higher variability in discharge would decrease YCS 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 were hypothesized to improve larval Silver Carp growth potential during the first growing season, which 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 we hypothesized that more severe winter regimes could lead to decreased YCS due to the decreased growth rates and higher metabolic rates of age-0 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 YCS. Age-0 Silver Carp seek shallow, backwater nursery habitats during the summer months posthatch (Kolar et al. 2007), and increases in air temperatures can cause such habitats to exceed the upper temperature threshold for age-0 Silver Carp (26.9°C; Kolar et al. 2007), potentially causing high mortality rates of cohorts.

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 the National Weather Service [NWS] Climate Prediction Center, College Park, Maryland), El Niño–Southern Oscillation Index (ENSO; data obtained from the NWS Climate Prediction Center), 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 NAO can influence temperature regimes and precipitation distributions over a broad geographic range (Hurrell 1995). The ENSO causes either cool or warm phases that influence both winter precipitation and temperature regimes (Zhang et al. 1997). Last, the PHDI indicates the severity of a wet or dry period, ranging from greater than 4 (indicating extreme wetness) to less than –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 the NAO and warmer mean annual air temperature) would increase Silver Carp YCS as floods and warmer thermal regimes can positively affect Silver Carp recruitment and growth (Kolar et al. 2007).

Statistical analysis.—Age-3 and younger Silver Carp 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

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

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. Values of the RVI range 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 3 year-classes) between the Missouri River and middle Illinois River, correlations between these two 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 ($^{\circ}\text{C}$) indices for each site were correlated between each possible site combination using the methods described above. Next, to test whether correlations in individual sites' river discharge and air temperature indices among sites were related to synchrony of Silver Carp YCS, ρ values between population-specific Silver Carp YCS and environmental variables (river discharge, m^3 ; and air temperature, $^{\circ}\text{C}$) were examined using Pearson's product-moment correlation coefficient (Pearson's r).

The spatial scale of population synchrony for both great-circle distance (km; hereafter, “linear distance”) and river distance (rkm) was estimated using an exponential decay function (hereafter, “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 ($^{\circ}\text{C}$) values at zero separation, and d is linear distance.

Generalized linear mixed-effects models using all possible model combinations were used to explore the

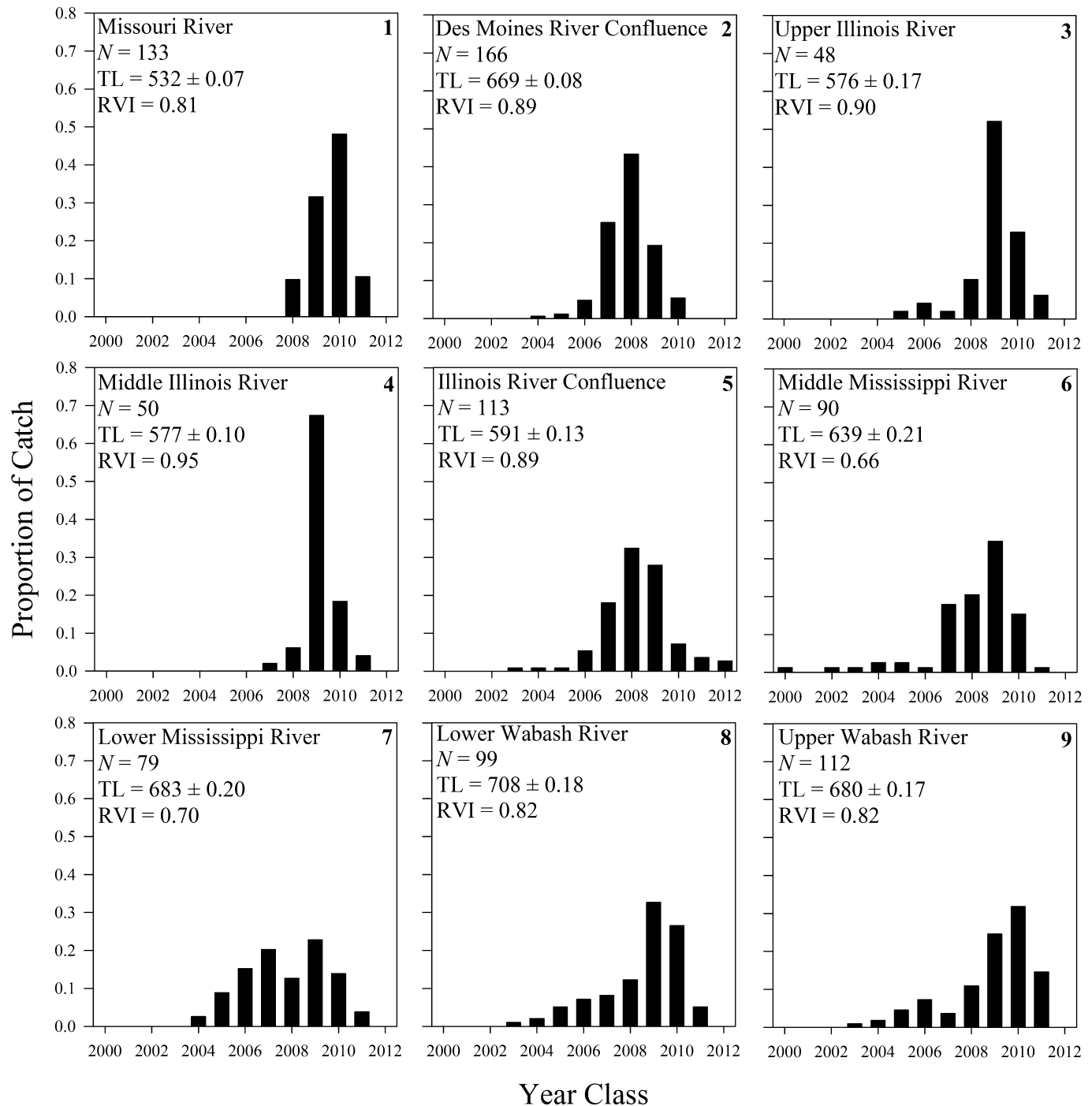


FIGURE 2. Silver Carp year-class histograms and associated sample sizes (N), mean TLs (mm; \pm SE), and recruitment variability index (RVI) scores for nine locations across the Mississippi River basin (see Figure 1) used to assess the regional synchrony of Silver Carp year-class strength.

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: DISR, DISNR, COVR, GDD, WS, SS, and BASE.FLOW. Variables were log-transformed to meet the assumptions of

normality and homogeneity of variance as needed. To distinguish the most parsimonious model, Akaike's information criterion corrected for small sample size (AIC_c) 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 less than 2.0 or

w_i values greater than 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 in which a year-class (2003–2010) from a minimum of two populations was present. Mean residual values were then regressed and correlated (using Pearson's r) 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 in each year, winter ENSO averaged for the November–February period in 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.

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). The RVI scores varied among sites (0.66–0.90) but were all greater than 0.65, indicating consistent recruitment across all sites (Figure 2). Although highly variable, studentized residuals of Silver Carp YCS were

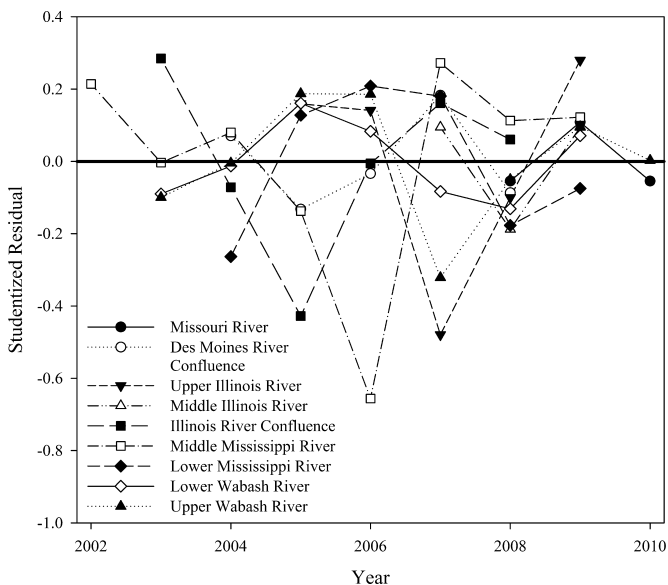


FIGURE 3. Spatiotemporal trends in year-class strength (studentized residual values) of Silver Carp collected from nine sites located throughout the Mississippi River basin. Residual values are indicative of relative year-class strength: positive values denote strong year-classes, and negative values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

generally highest (>50% of residuals across sites greater than zero in a year) during 2005–2007 and 2009, whereas they were lower during 2003–2004 and 2008 (Figure 3).

Spearman's ρ 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%) of the ρ values 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

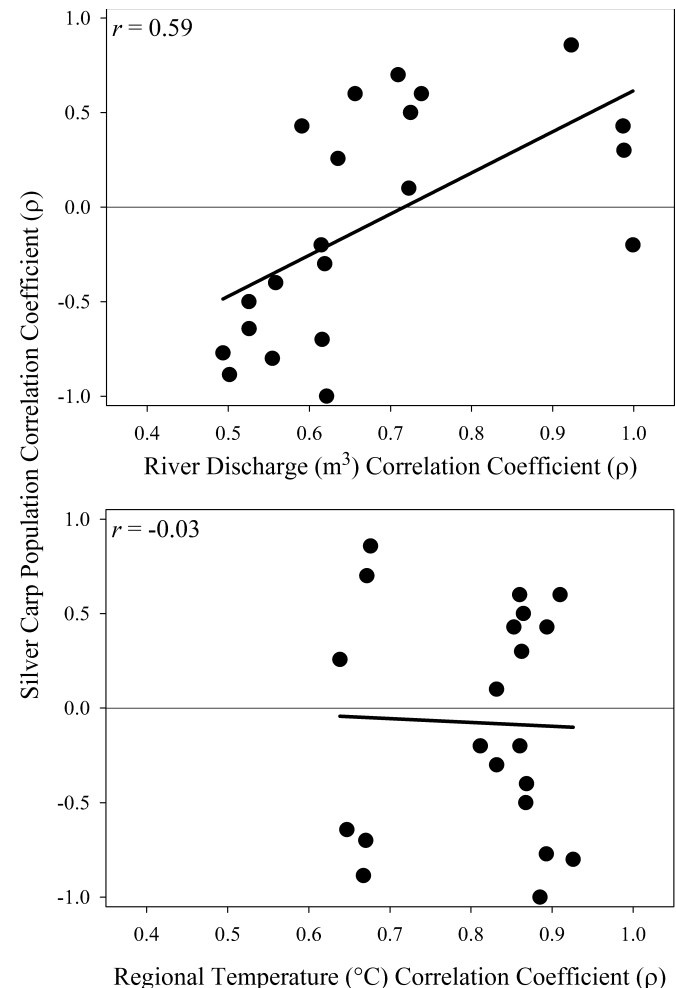


FIGURE 4. Spearman's rank correlation coefficients (ρ) for river discharge (m^3 ; top) and regional temperature ($^{\circ}\text{C}$; bottom) versus ρ values for Silver Carp relative year-class strength (y -axis) between populations in the Mississippi River basin (r = Pearson's product-moment correlation coefficient).

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 $\rho \pm SE = 0.02 \pm 0.12$; 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 mean ρ values for both river discharge (mean $\rho = 0.68$) and regional air temperature (mean $\rho = 0.81$) were significantly greater than zero (discharge: $t_{20} = 19.19$, $P < 0.001$; air temperature: $t_{20} = 37.42$, $P < 0.001$). Further, river discharge ρ values were positively correlated (Pearson's $r = 0.59$, $P = 0.005$) with Silver Carp YCS ρ values, whereas regional temperature synchrony ρ values were not (Pearson's $r = -0.03$, $P = 0.89$; Figure 4).

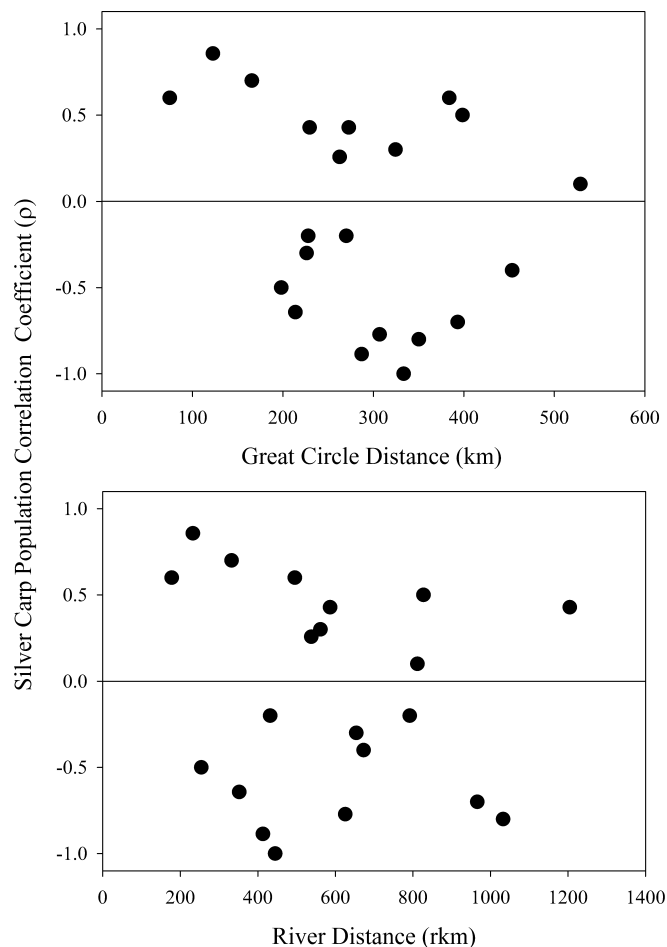


FIGURE 5. E-folding scale of distance (great circle distance, km [top]; river distance, rkm [bottom]) versus pairwise Spearman's rank correlation coefficients (ρ) of relative year-class strength between Mississippi River basin Silver Carp populations. The spatial scale of synchrony overlapped with zero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

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 (mean $\pm SE = 983.7 \pm 15,808.3$ km for linear distance; 118.0 ± 454.0 km for river distance). In addition, environmental synchrony of both river discharge and regional air temperature was related to linear distance between site pairs (mean $\pm SE = 581.3 \pm 132.7$ km for river discharge; $2,972.0 \pm 916.5$ km for air temperature; 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 BASE.FLOW ($AIC_c = -68.41$, $w_i = 0.57$) followed by COVR ($\Delta_i = 2.54$, $w_i = 0.14$; Table 2). All other models received substantially less support ($\Delta_i > 2.0$, $w_i > 0.1$). The general linear mixed-effects model coefficient for BASE.FLOW was not different from

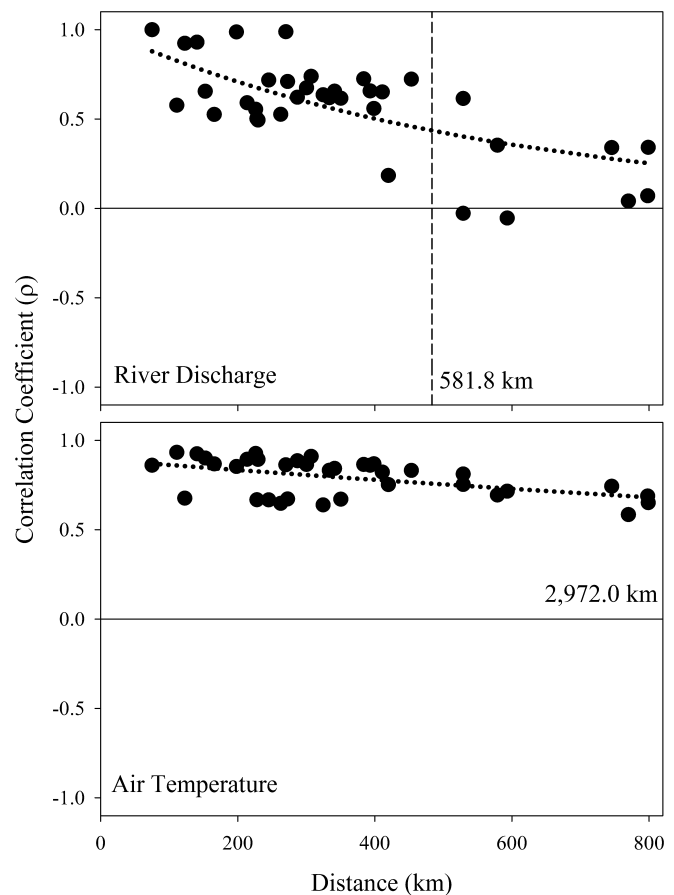


FIGURE 6. E-folding scale of distance (great circle distance, km) versus pairwise Spearman's rank correlation coefficients (ρ) of both river discharge (m^3 ; top) and regional air temperature ($^{\circ}C$; bottom) among Mississippi River basin Silver Carp populations.

TABLE 2. Model selection results, including model covariates, number of parameters estimated (K), Akaike's information criterion corrected for small sample size (AIC_c), difference between the AIC_c value of the most parsimonious model and model i (Δ_i), and the relative support for model i (Akaike weight [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 postreproductive season (June–October; DISNR), growing degree-days (GDD), cumulative annual degree-days over $27^\circ C$ (summer severity [SS]), cumulative annual degree-days under $0^\circ C$ (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

zero (−0.099; 95% confidence interval = −0.28 to 0.08), while coefficient values for all other variables were less than 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), and mean residuals of the remaining year-classes (2003–2007, 2010) were less than 0.03. However, the NAO (Pearson's $r = -0.03$, $P = 0.95$), ENSO (Pearson's $r = -0.14$, $P = 0.75$), PHDI (Pearson's $r = 0.12$, $P = 0.78$), and the mean annual regional air temperature above $17^\circ C$ (Pearson's $r = -0.09$, $P = 0.84$) were not related to Silver Carp YCS (Figure 7).

DISCUSSION

Contrary to our hypothesis, the YCS of Silver Carp populations inhabiting the Mississippi River basin was not synchronous across study sites, which differs from results reported for several fish populations inhabiting both lotic (Grenouillet et al. 2001; Cattaneo 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 the Common Carp (Phelps et al. 2008; Weber et al. 2017), Yellow Perch (Dembkowski et al. 2016; Honsey et al. 2016), Brown Trout *Salmo trutta* (Cattaneo 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 sampled from the middle Mississippi River and the Illinois River confluence were composed mainly of the 2000 year-class, which also coincided with large-scale flooding (Garvey et al. 2006). Within the current study, Silver Carp recruitment was generally consistent across sites, while interannual river discharge values varied drastically. However, 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 during 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 either that Silver Carp are not recruited into the adult population as age-0 fish or that mortality via commercial fishery harvest is effective at removing larger, older individuals from the population (i.e., Garvey 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.

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), but our results indicate that Silver Carp recruitment does not exhibit synchronous fluctuations at the spatial scale evaluated, even though environmental conditions were synchronous. Two explanations could help to 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

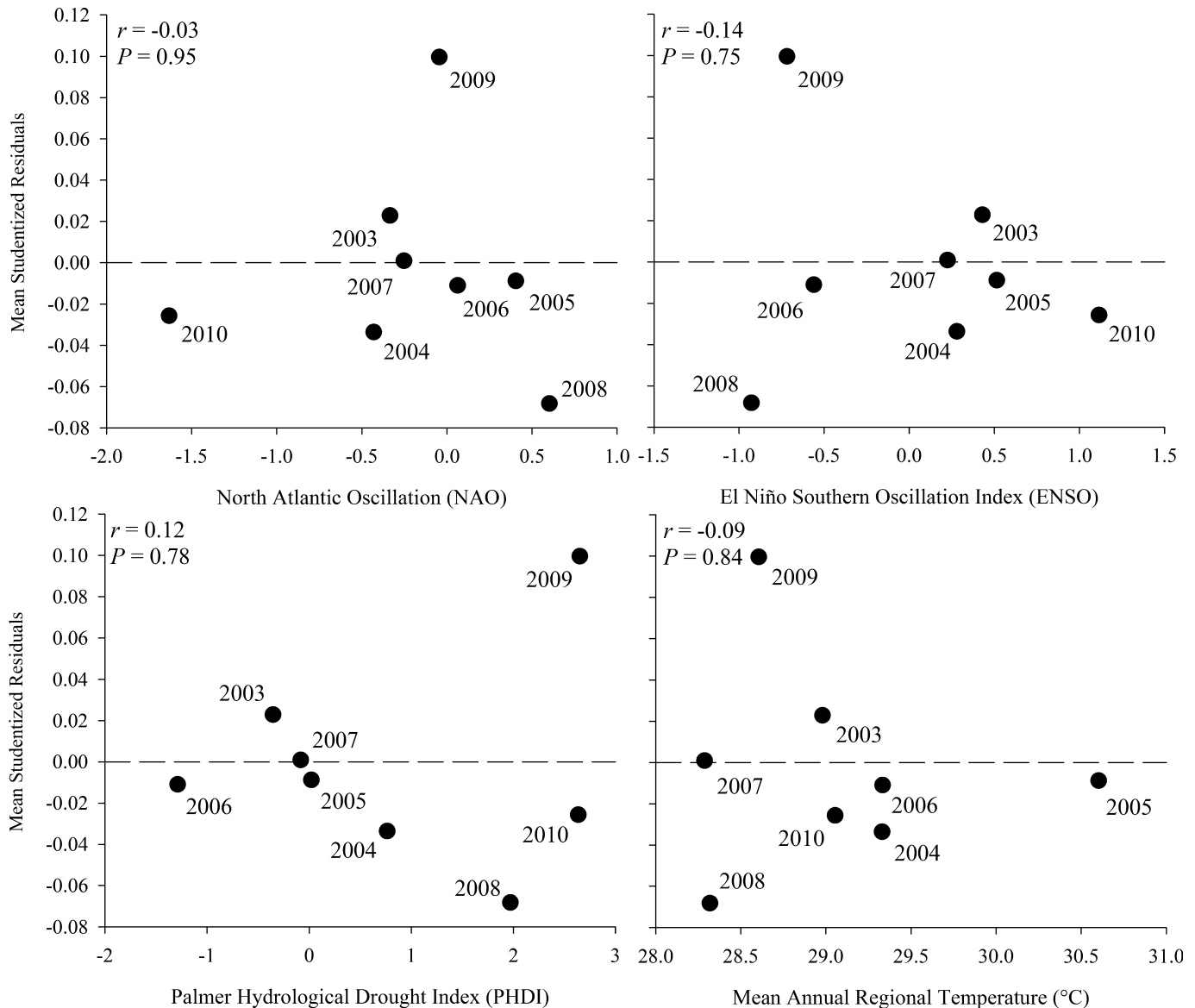


FIGURE 7. Relationships between the annual North Atlantic Oscillation Index (NAO), El Niño–Southern Oscillation Index (ENSO), Palmer Hydrological Drought Index (PHDI), or mean annual regional temperature (°C) and mean Silver Carp year-class strength (y -axis) among the nine sampling sites in the Mississippi River basin (r = Pearson's product-moment correlation coefficient).

study, the shortest linear distance between sites was 75.4 km (lower and middle Mississippi River sites), and most sites were separated by more than 200 km linearly. Second, Prechtel et al. (2018) found that most Silver Carp in the Wabash River exhibited home ranges less than 70 km over a 3-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 such that the home ranges of Silver Carp would overlap, our analysis indicates that Silver Carp populations separated by over 75 km 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 from Illinois River (Stuck et al. 2015) and Wabash River (Morgeson 2015) sites produced stronger year-classes during 2009, when high, sustained discharge events were present for greater than 3 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, and 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-the-year fish survival (e.g., Cattaneo et al. 2003). Spawning during high flow can facilitate larval dispersal into floodplain, creek, or low-flow habitats, which serve as nursery areas, increasing larval survival (Huet 1970). Alternatively, low-flow conditions have the ability to disconnect main-stem 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 the YCS of Silver Carp at local scales across the Mississippi River basin.

The Moran effect predicts that biological and environmental synchrony will be roughly equal (Lundberg et al. 2000); thus, we propose that in lotic systems, dynamic environmental variables synchronizing 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. Our results suggest that during years in which regional floods occur, stronger year-classes of Silver Carp will be produced across a broader geographic range and will 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 greater YCS 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 YCS, 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 for the annual degree-days over 17°C across the study sites was low (coefficient of variation = 0.35). Furthermore, summer temperatures rarely exceeded 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 toward 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 Carp *H. nobilis* (Schrank et al. 2001), Grass Carp *Ctenopharyngodon idella* (Raibley et al. 1995), and Black Carp *Mylopharyngodon piceus* (Nico and Jelks 2011), all of which pose a severe threat to native biodiversity throughout the basin. As the range expansion of Asian carp within the basin continues, the results presented here could aid in the understanding of abiotic factors influencing population recruitment dynamics of these additional species' populations across multiple spatial scales.

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