

Quantifying the spatial scale of common carp (*Cyprinus carpio*) recruitment synchrony

Michael J. Weber, Michael L. Brown, David H. Wahl, and Daniel E. Shoup

Abstract: Understanding spatial and temporal fluctuations in animal populations remains a central theme in ecology. Here, we investigated the extent of common carp (*Cyprinus carpio*) recruitment synchrony across North America in relation to a suite of climatic conditions. Common carp were collected from 21 populations up to a linear distance of 2300 km between the most southern and northern locations. Age-frequency histograms were used to estimate year-class strength, and correlation coefficients were used to evaluate synchrony among populations and environmental variables. We then evaluated relationships between common carp recruitment and winter growing degree-days (GDD), summer GDD, precipitation, wind events, and the El Niño Southern Oscillation Index (ENSO). Common carp recruitment was synchronous up to 756 km but asynchronous at larger scales. Winter and summer GDD, precipitation, and wind were also synchronous among locations up to 1640 km apart. Summer GDD appeared most influential to common carp recruitment but varied across latitudes, with negative effects identified at low latitudes and positive effects identified at higher latitudes. Our results provide new insights into the spatial scale of recruitment synchrony of a non-native freshwater fish and indicate that climatic conditions at local to regional scales likely influence recruitment patterns.

Résumé : La compréhension des fluctuations spatiales et temporelles dans les populations animales constitue un thème central en écologie. Nous examinons l'ampleur du synchronisme du recrutement de carpes communes (*Cyprinus carpio*) en Amérique du Nord par rapport à une série de conditions climatiques. Des carpes communes ont été prélevées de 21 populations séparées par des distances linéaires allant jusqu'à 2300 km. Des histogrammes de la fréquence selon l'âge ont été utilisés pour estimer la force des classes d'âge et des coefficients de corrélation ont été utilisés pour évaluer le synchronisme entre les populations et en fonction de variables environnementales. Nous avons ensuite évalué les relations entre le recrutement de carpes communes et les degrés-jours de croissance (DJC) hivernaux et estivaux, les précipitations, les épisodes venteux et l'indice El Niño oscillation australe (ENSO). Le recrutement de carpes communes est synchrone jusqu'à une distance de 756 km, mais asynchrone à plus grande échelle. Les DJC hivernaux et estivaux, les précipitations et les vents sont également synchrones entre des sites distants de jusqu'à 1640 km. Les DJC estivaux semblent exercer la plus grande influence sur le recrutement des carpes, mais varient selon la latitude, des effets négatifs ayant été notés à basse latitude et des effets positifs, à plus haute latitude. Nos résultats fournissent de nouveaux renseignements sur l'échelle spatiale du synchronisme du recrutement d'un poisson d'eau douce non indigène et indiquent que les conditions climatiques aux échelles locales à régionales influencent vraisemblablement les motifs de recrutement. [Traduit par la Rédaction]

Introduction

Understanding the mechanisms regulating variability in animal population dynamics is an important aspect of ecology. Animal populations commonly fluctuate both spatially and temporally (Glazier 1986; Pimm and Redfearn 1988), but these fluctuations can occur synchronously over large geographic ranges. For example, feral sheep (Grenfell et al. 1998), musk oxen (*Ovibos moschatus*) (Post and Forchhammer 2002), Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) (Fogarty et al. 2001) populations all display some detectable level of recruitment synchrony. Two primary forces are hypothesized to result in recruitment synchrony of animal populations: dispersal or climatic factors. Dispersal of individuals can result in synchrony on a regional scale (i.e., within a single system or among several systems in proximity with high connectivity; Cattaneo et al. 2003), whereas climatic processes are often necessary to synchronize animal pop-

ulations across larger geographic ranges (i.e., Moran effect; Moran 1953; Bjornstad et al. 1999).

Synchrony in fish stocks has been demonstrated extensively in marine fishes (Fox et al. 2000; Fogarty et al. 2001; Stige et al. 2006). Yet, comparatively less is known about the degree of large-scale synchrony in freshwater fishes (but see Cattaneo et al. 2003; Bunnell et al. 2010; Dembkowski et al. 2016). Lentic freshwater fish populations may provide an ideal situation to examine climate-induced synchrony owing to the ability of these systems to minimize dispersal potential. Although climate-driven synchrony among marine species often occurs across large spatial scales (>500 km; Koslow et al. 1987; Thompson and Page 1989; Fox et al. 2000), synchrony among freshwater fish populations typically occurs at much smaller spatial scales (<50 km; Myers et al. 1997), potentially because dispersal of these populations is limited in isolated lentic systems. However, synchrony of some freshwater fishes can occur

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M.J. Weber* and M.L. Brown. Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA.

D.H. Wahl. Illinois Natural History Survey, Kaskaskia Biological Station, University of Illinois at Urbana-Champaign, 1235 CR 1000 North, Sullivan, IL 61951, USA.

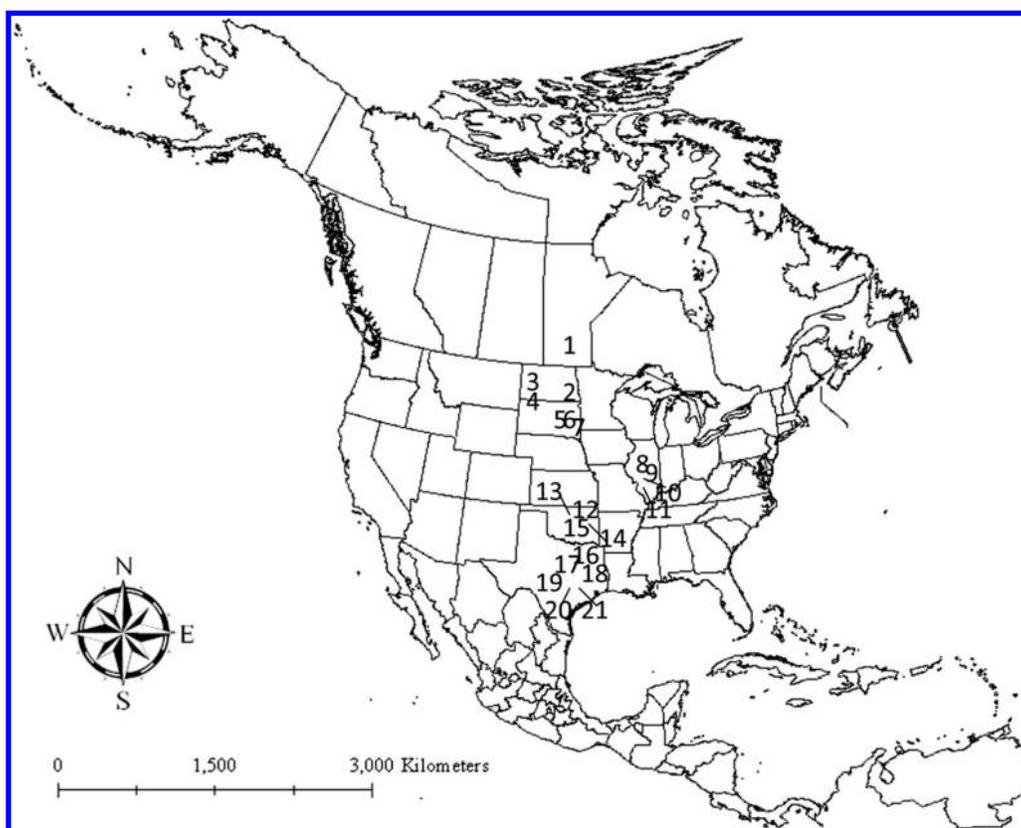
D.E. Shoup. Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agricultural Hall, Stillwater, OK 74078, USA.

Corresponding author: Michael J. Weber (email: mjw@iastate.edu).

*Present address: Department of Natural Resource Ecology and Management, Iowa State University, 339 Science Hall II, Ames, IA 50011, USA.

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Fig. 1. Locations of 21 lakes where common carp were sampled (numbers) in Manitoba, Canada ($n = 1$), North Dakota ($n = 3$), South Dakota ($n = 3$), Illinois ($n = 4$), Oklahoma ($n = 4$), and Texas ($n = 6$), USA. Numbering system and description of lakes is provided in Table 1.



over much larger distances in lotic (160–375 km; Grenouillet et al. 2001; Tedesco et al. 2004) and large lentic (150–800 km; Bunnell et al. 2010; Rook et al. 2012; Honsey et al. 2016) systems. This disparity in the scale of recruitment synchrony highlights the variability associated with the unique life-history characteristics expressed among species and the general lack of knowledge surrounding factors influencing recruitment synchronization in freshwater species.

Common carp (*Cyprinus carpio*) is one of the most widely introduced and distributed fish species worldwide. Originally introduced to many venues for aquaculture production, common carp have become highly abundant in many ecosystems (Panek 1987; Britton et al. 2007). Common carp populations exert negative effects on shallow aquatic ecosystems, inducing a regime shift from the clear- to turbid-water state (review by Weber and Brown 2009), potentially reducing native species abundance and diversity (Haas et al. 2007; Weber and Brown 2011) and altering basic ecosystem processes and services (Weber and Brown 2013a). Thus, aquatic resource managers are particularly interested in mechanisms regulating common carp populations. Common carp recruitment in the northern portion of the United States appears erratic (Wichers 1976; Mueller and Downen 2000) but highly synchronized on a local scale, regulated in part by climatic conditions (i.e., wind, temperature, water levels) during early life stages (Phelps et al. 2008a; Weber and Brown 2013b). In contrast, common carp recruitment may be more consistent at lower latitudes (Starrett and Fritz 1965), indicating that recruitment synchrony may become less pronounced at larger spatial scales and that climatic factors associated with latitude may play an important role in recruitment patterns.

Although regional common carp recruitment synchrony has been suggested for populations in the upper Midwest (Phelps et al. 2008a), the scale at which carp recruitment synchrony declines is

unknown. Populations may be synchronized by large-scale environmental conditions (i.e., El Niño) or synchrony may break down, or be less detectable, at larger spatial scales, as latitude produces stronger effects on population dynamics of fishes by exposing them to a range of environmental conditions (i.e., temperature, precipitation, etc.). Understanding the degree to which populations are synchronized and the underlying synchronizing mechanisms is important to explain the relationship between population dynamics and extrinsic environmental variation, an interaction that has important implications for biological management. The resilience of populations to manipulation, biological control, and attempts at eradication may be related to the degree of synchrony in population dynamics (Cavaliere and Kocak 1995; Myers and Rothman 1995; Bolker and Grenfell 1996). Therefore, we evaluated the degree to which common carp populations and climatic conditions were synchronized across North America and then evaluated relationships between common carp recruitment and climatic conditions. We hypothesized that common carp recruitment synchrony would occur at local scales as a function of similar local climatic conditions, but that synchrony among populations would decrease with increasing spatial separation and corresponding reduced similarity in environmental conditions.

Methods

Common carp were collected from 21 natural lakes or reservoirs in Canada, North Dakota, South Dakota, Illinois, Oklahoma, and Texas to cover the majority of their latitudinal range throughout North America (Fig. 1). The distance between our most southern and northern locations was nearly 2300 km. Common carp were collected during spring 2009 from South Dakota, North Dakota, Illinois, Oklahoma, and Texas using daytime pulsed direct-current

electrofishing at each location. The amount of effort at each location varied but continued until ~100 individuals were captured. Common carp in Canada were collected with large mesh experimental gill nets (137 m long; six panels consisting of 3.8, 5, 7.6, 8.9, 10.8, and 12.7 cm bar mesh (23 m long each)). Two sites in North Dakota (Edward Arthur Patterson and Bowman-Haley lakes) were sampled following a rotenone application. Individuals were measured to the nearest 1 mm total length, and the dorsal spine was removed at the base and used for age analysis (Weber and Brown 2011). Dorsal spines were air-dried for 2 weeks, and transverse sections (0.8 mm width) were removed from the distal to the basal groove using a low-speed Isomet saw. Annuli were counted under a dissecting microscope on separate occasions by two independent readers who were experienced with aging common carp spines. If age estimates differed between the two readers (5% of spines aged), the spine was reevaluated by both readers until a unanimous agreement was made. In total, nearly 1900 common carp were aged from 21 populations across North America.

Year-class frequency distributions (number of fish collected that were born each year based on age estimates derived from dorsal spines) were used to determine patterns of recruitment in each population, and the recruitment residual method was used to determine the relative strength or weakness of each year-class (Maceina 1997). This method assumes that positive and negative residuals derived from linear regressions of $\log(\text{abundance} + 1)$ versus age for age-3 and older fish are solely attributed to variation in year-class strength and that mortality is constant among age-classes. Weighted catch curves (Maceina 1997; Maceina and Bettoli 1998) were derived by regressing the natural log frequency of age-3 and older fish against age using the predicted values for the natural log of number at age as weighting factors when the catch curve was recalculated. The weighting factor reduces the influence of rarer, older fish on the linear regression model. Common carp are generally sexually mature by age 3 (Smith and Walker 2004; Weber and Brown 2012), sampling targeted spawning habitats, and age-frequency histograms generally indicated that carp were recruited to electrofishing and gill nets by age 3. Although it was not possible to sample all populations with electrofishing, sampling during spawning, targeting spawning locations, and including only fish \geq age 3 likely minimized any differences among sampling techniques. After year-class strength was quantified with residuals, the modified correlogram method (Koenig and Knops 1998) was used to evaluate whether common carp recruitment was spatially synchronized. Pearson correlations were calculated with residual recruitment values between each possible lake combination, and the correlation coefficient was used to index synchrony among populations. At least five year-classes (Myers et al. 1997; Honsey et al. 2016) were present for all populations except for Hi Lions, Texas, where residuals for only four year-classes could be estimated.

Two approaches were used to test for the spatial scale of synchrony. First, linear distances between lakes were measured, and the Mantel test was used to evaluate the geographical patterns in population fluctuation (Koenig and Knops 1998; Koenig 1999; Bunnell et al. 2010). A distance matrix of all possible paired locations and a correlation matrix, where the elements are the correlation coefficients of annual variation in year-class strength, were constructed for all possible pairs of study locations. The correlation coefficient was plotted against the distance between the pairs of study locations to evaluate the strength and scaling of common carp recruitment synchrony across North America. Next, lake pairs were grouped into distance categories, and mean Pearson correlation coefficients were calculated for all pairwise combinations within each distance category. Because spatial synchrony of carp populations <200 km apart has been documented (Phelps et al. 2008), our first distance category examined synchrony at a similar scale (<200 km) with increasing increments. Distance categories selected were <200, 201–500, 501–1000, 1001–1500,

and >1501 km. Owing to lack of independence among correlations, bootstrap 95% confidence intervals (CIs) were calculated for mean synchrony values within each distance category by resampling time points with replacement 1000 times (Lillegård et al. 2005). This technique overcomes lack of independence among correlations, because correlations estimated from bootstrap replications are not resampled from the observed set of correlations, with resulting CIs approximating nominal 95% intervals (Lillegård et al. 2005). If the 95% CI of a distance category overlapped with zero, we concluded that spatial synchrony did not occur at that spatial scale.

Second, an e-folding scale was calculated by fitting the model

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

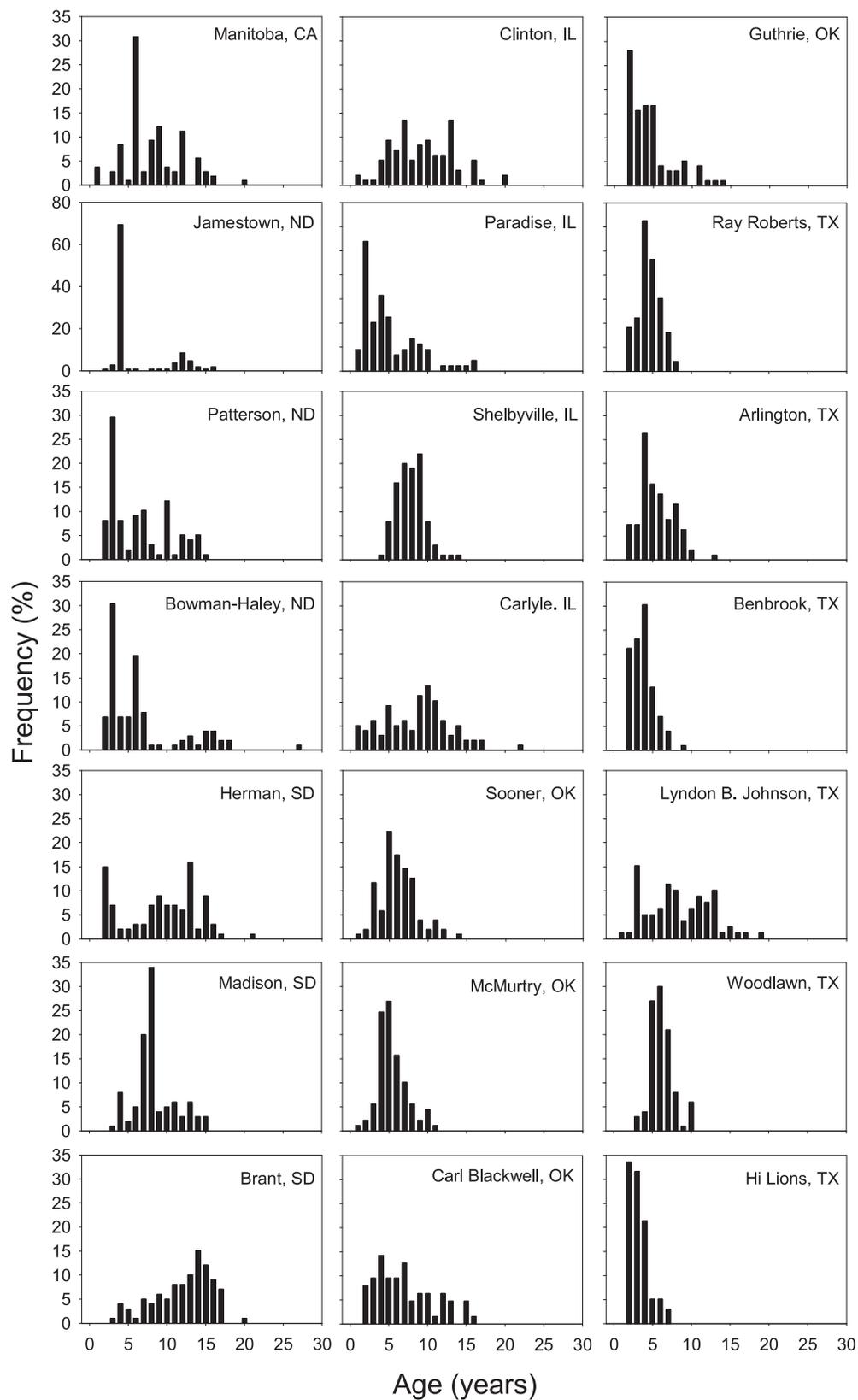
where ρ_0 is the correlation between two data sets at zero separation (constrained to have an absolute value ≤ 1), d is the great circle distance between sampling locations, and v is the e-folding scale, defined as the distance over which the pairwise correlation between recruitment time series is reduced by a factor of e^{-1} (Myers et al. 1997; Honsey et al. 2016). The model was fit with nonlinear least-squares regression weighted by the number of overlapping year-classes between the two populations used in the pairwise correlation coefficient.

Winter, spring, and summer temperatures, precipitation, and wind events have been hypothesized as important environmental factors regulating common carp recruitment at localized scales by influencing the amount of spawning habitat and survival of early life stages (Phelps et al. 2008; Weber and Brown 2013b). Additionally, temperature appears to be an underlying mechanism synchronizing fish populations (e.g., Fox et al. 2000; Grenouillet et al. 2001). However, large-scale climatic indices often better explain ecological variables than local processes, because they simplify complex temporal and spatial interactions (Stenseth and Mysterud 2005). To an extent, large-scale factors would seemingly influence all these systems more similarly, whereas local factors would have a more pronounced effect and induce more variability among populations as scale increases (hierarchical influence). There is also a temporal aspect, in that large-scale factors tend to be persistent for extended periods, whereas local factors tend to be more short-term episodic events. Thus, using correlation analysis, variability in year-class strength of each population was related to localized weather conditions (winter GDD, summer GDD, wind, precipitation) and broad regional climate (El Niño Southern Oscillation Index; mild winters in northern North America and wet conditions in southern North America) occurring during the year in which the fish spawned. Climate data were obtained from an online database (<https://www.ncdc.noaa.gov>) using the weather station closest to each lake. GDD was calculated to index summer (May through August of the first year) and winter (October through March of the first year) thermal conditions as

$$\text{GDD} = \sum \frac{T_{\text{Max}} + T_{\text{Min}}}{2} - T_0$$

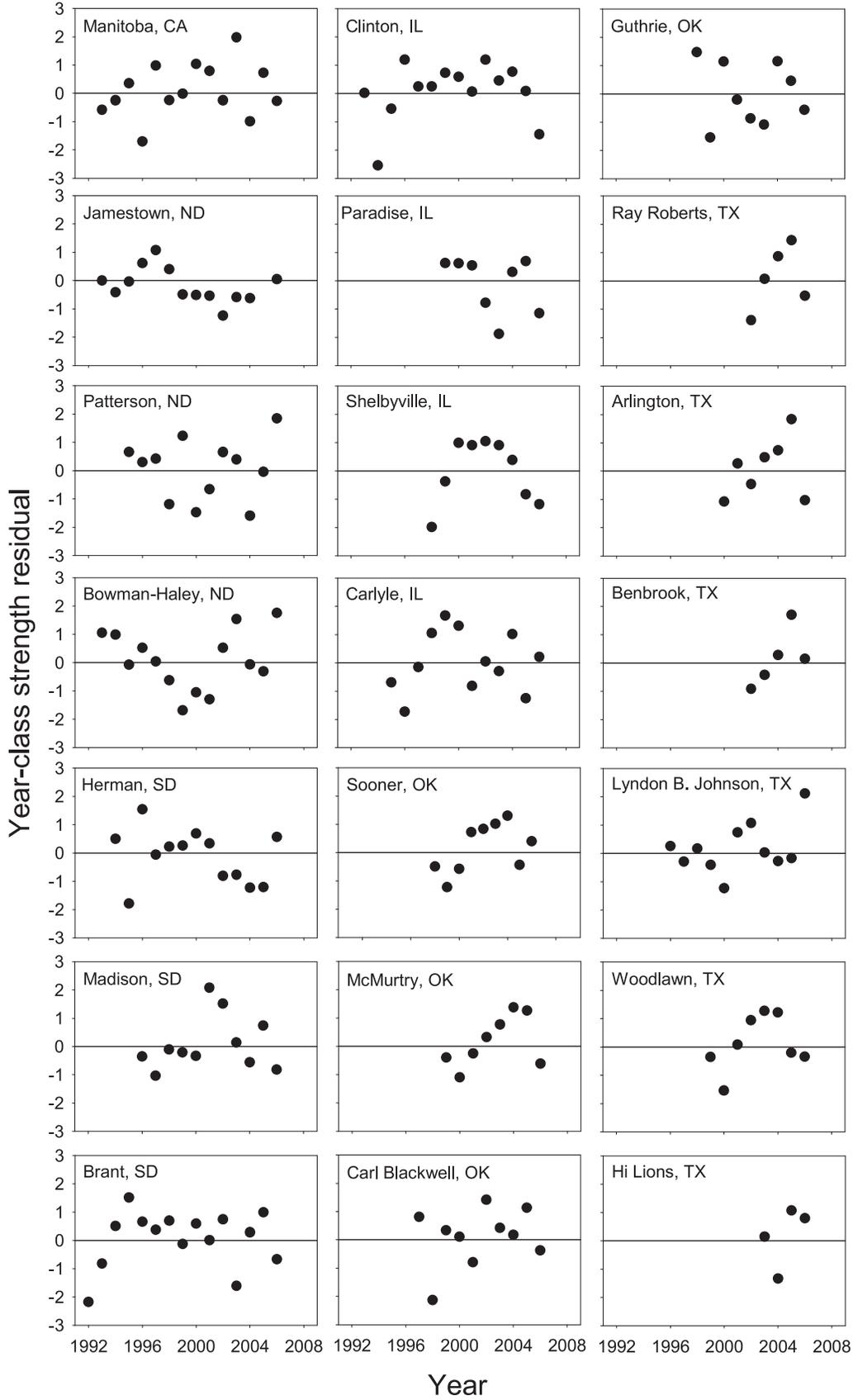
where T_{Max} and T_{Min} are the maximum and minimum daily ambient temperatures, respectively, and T_0 is the temperature below which growth and development is effectively zero, which was set at 10 °C (Chezik et al. 2014). Additionally, precipitation was calculated as the cumulative precipitation from 1 January through 31 August, and wind was calculated as the cumulative wind speed from 1 May through 31 August (Phelps et al. 2008a; Weber and Brown 2013b). Environmental variables were first \log_{10} -transformed to normalize the residuals and then evaluated for autocorrelation, but were found to be unrelated to one another ($r = 0.00\text{--}0.60$, $P > 0.10$). The degree of annual synchrony in environmental

Fig. 2. Age-frequency distribution of common carp populations collected from 21 populations across North America. Note the y-axis scale is the same for all populations except the one in Jamestown, North Dakota.



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Fig. 3. Common carp year-class strength residuals collected from 21 populations across North America.



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variables was compared for all possible sampling site locations using correlation coefficients and e-folding scale analysis as described above for evaluating common carp synchrony. Next, correlation coefficients (r) between population-specific year-class strength and climate data were calculated. Finally, correlation coefficients between population-specific year-class strength and environmental variables were related to latitude to evaluate how the influence of climatic variables influences populations differently across a latitudinal gradient.

Results

Common carp age structure varied considerably among populations (Fig. 2). Populations in the north comprised up to 17 year-classes with individuals >20 years old, whereas those in the south comprised as few as six year-classes up to 7 years old. Populations in the north also tended to have more erratic recruitment (i.e., no fish present in a year-class) compared with populations in the south. Subsequently, substantial variation in the timing of strong and weak year-class existed among systems (Fig. 3).

High correlation coefficients ($r > 0.50$) were detected between lake pairs that were up to 2000 km apart, but negative correlation coefficients were also detected for lakes in proximity to one another (Fig. 4). Mean correlation coefficients between sampling sites were high at sites that were close (<200 km: mean = 0.24; 201–500 km: mean = 0.29), lower at intermediate distance (501–1000 km: mean = 0.06; 1001–1500 km: mean = -0.03), and high again at sites >1500 km apart (mean = 0.24). The modified correlogram indicated that common carp recruitment exhibited significant spatial autocorrelation among sites separated by up to 500 km and at sites >1500 km apart (i.e., 95% CI did not encompass $r = 0.0$) but not at sites 500–1500 km apart (Fig. 4). The Mantel test did not detect an effect of distance on spatial autocorrelation of common carp recruitment ($r = -0.08$, $P = 0.23$), whereas the e-folding scale estimated synchrony at 756 km (95% CI: 92–1420 km; $t = 2.23$; $P = 0.03$; Fig. 4).

Environmental variables were also synchronous across North America (Fig. 5). Winter GDD was synchronous at the largest spatial scale (1640 km, 1330–1950 km 95% CI; $t = 10.36$, $P < 0.01$), followed by summer GDD (1515 km, 1158–1872 km 95% CI; $t = 8.31$, $P < 0.01$), precipitation (623 km, 419–823 km 95% CI; $t = 5.94$, $P < 0.01$), and wind (430 km, 273–587 km 95% CI; $t = 5.34$, $P < 0.01$). The spatial scale of synchrony of common carp populations and environmental variables were similar based on overlapping 95% CIs.

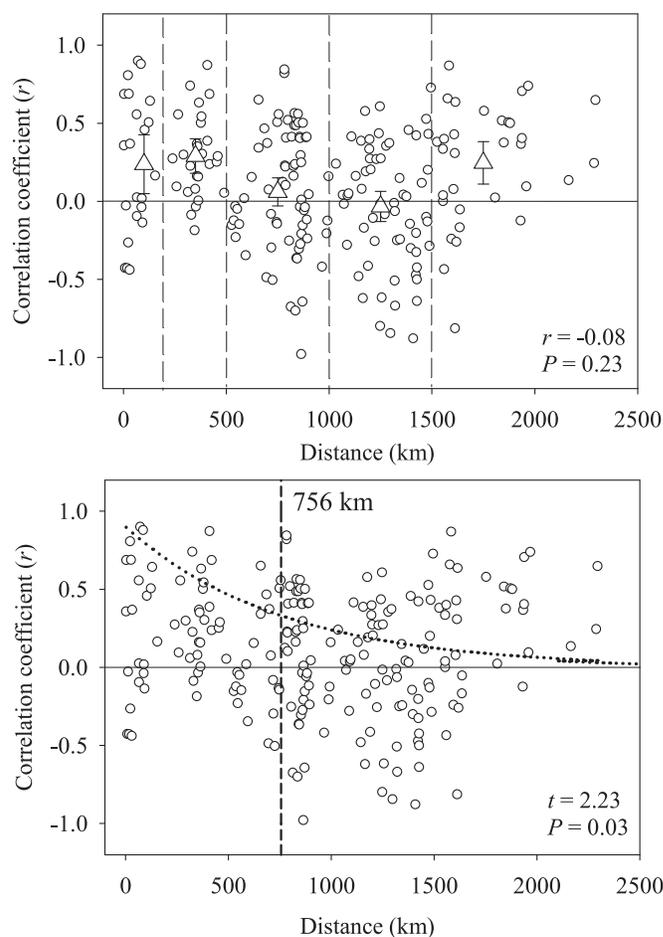
Few significant relationships were detected between environmental variables and year-class strength ($P < 0.10$; five of 105 instances). Year-class strength was positively related to summer GDD at three of the higher-latitude populations and negatively related to summer GDD at two low-latitude populations (Table 1). No other significant correlations between common carp year-class strength and environmental variables were identified. Despite the lack of strong relationships between environmental variables and year-class strength, correlation coefficients of year-class strength and summer GDD were positively correlated with latitude (Fig. 6). Common carp year-class strength at lower latitudes was negatively related to temperature, but year-class strength at higher latitudes was positively related to temperature. Similar latitudinal patterns with winter severity, precipitation, wind, and ENSO were not detected.

Discussion

Our results indicate that common carp recruitment was synchronized among populations up to nearly 800 km apart, but that broader scale synchrony was less prevalent. The most general pattern of synchrony is that it tends to decrease with increasing spatial separation among populations (Koenig 1999; Honsey et al. 2016). Additionally, synchrony of freshwater fish populations tends to occur on much smaller spatial scales (<50 km; but see Dembkowski

et al. 2016; Honsey et al. 2016) compared with marine fish populations, which tend to be synchronized over much larger spatial scales (~500 km; Myers et al. 1997). Thus, recruitment synchrony of common carp observed here represents one of the largest scales of synchrony in freshwater fish recruitment among different systems documented to date.

Dispersal is often responsible for synchronizing populations in lotic or highly interconnected systems (Koenig 1999). However, the populations sampled in this study were closed and dispersal was not possible. Instead, synchrony in climatic conditions has been suggested as the primary mechanism underlying synchrony of spatially discrete populations (Moran 1953; Grenouillet et al. 2001; Bunnell et al. 2010). For example, roach (*Rutilus rutilus*) (Grenouillet et al. 2001), largemouth bass (*Micropterus salmoides*) (Maceina and Bettoli 1998), crappie (*Pomoxis* spp.) (Michaletz and Siepker 2013), bloater (*Coregonus hoyi*) (Bunnell et al. 2010), cisco (*Coregonus* spp.) (Rook et al. 2012), yellow perch (*Perca flavescens*) (Dembkowski et al. 2016; Honsey et al. 2016), and common carp (Phelps et al. 2008) synchrony have been explained by synchro-



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Fig. 5. E-folding scale of distance versus correlation coefficient for winter growing degree-days (GDD), summer GDD, precipitation, and wind. Included in each panel are the model prediction (dotted line), asynchronous recruitment (below solid horizontal line), and scale of recruitment synchrony (v , vertical dashed line with associated value).

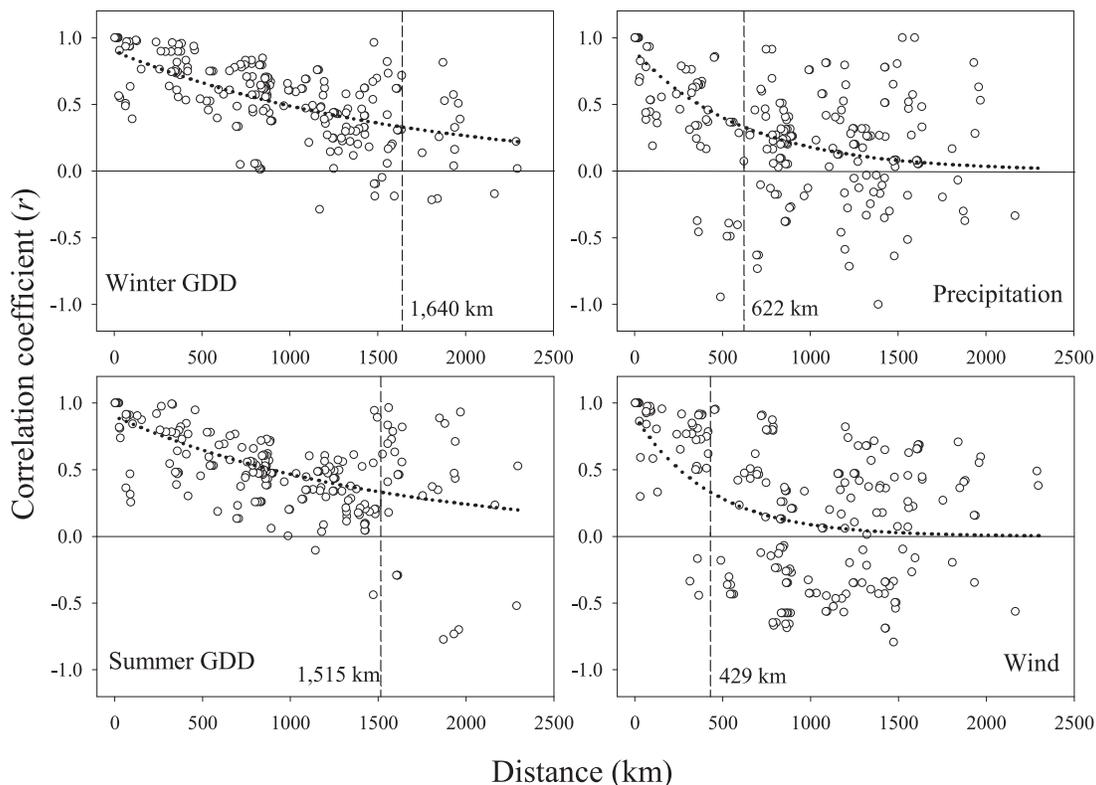


Table 1. Correlation coefficients (r) between summer growing degree-days (GDD) and common carp year-class strength from 21 populations collected across North America.

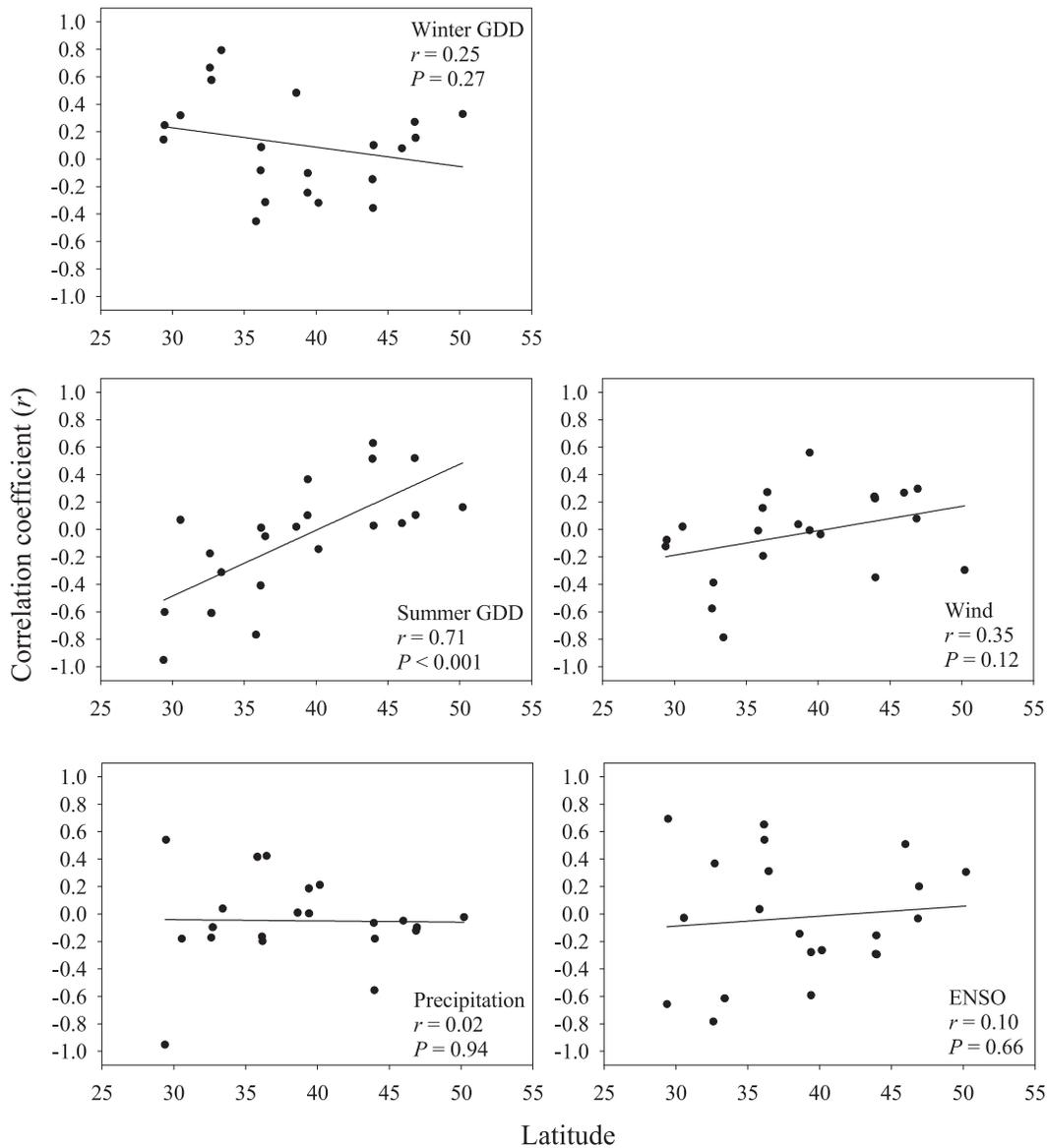
Population No.	Lake	Location	Lat. (°N)	N	Summer GDD	
					r	P
1	Manitoba	Manitoba, Canada	50.199	14	0.16	0.61
2	Jamestown	North Dakota, USA	46.931	13	0.11	0.72
3	Edward Arthur Patterson	North Dakota, USA	46.858	12	0.52	0.08
4	Bowman-Haley	North Dakota, USA	45.976	14	0.05	0.88
5	Herman	South Dakota, USA	43.991	13	0.03	0.93
6	Madison	South Dakota, USA	43.958	11	0.63	0.04
7	Brant	South Dakota, USA	43.921	15	0.52	0.05
8	Clinton	Illinois, USA	40.160	14	-0.14	0.63
9	Paradise	Illinois, USA	39.410	8	0.37	0.42
10	Shelbyville	Illinois, USA	39.408	9	0.10	0.81
11	Carlyle	Illinois, USA	38.614	12	0.02	0.95
12	Sooner	Oklahoma, USA	36.164	9	0.01	0.97
13	McMurtry	Oklahoma, USA	36.135	8	-0.41	0.31
14	Carl Blackwell	Oklahoma, USA	35.819	10	-0.77	0.01
15	Guthrie	Oklahoma, USA	36.458	9	-0.05	0.90
16	Ray Roberts	Texas, USA	33.405	5	-0.31	0.61
17	Arlington	Texas, USA	32.709	7	-0.61	0.15
18	Benbrook	Texas, USA	32.606	5	-0.17	0.78
19	Lyndon B. Johnson	Texas, USA	30.556	11	0.07	0.85
20	Woodlawn	Texas, USA	29.452	8	-0.60	0.11
21	Hi Lions	Texas, USA	29.385	4	-0.95	0.05

Note: N, number of year-classes used in analyses.

nous environmental conditions across regional areas. All four climatic indices evaluated here were synchronized on broad spatial scales (up to 1640 km). Of the environmental variables evaluated in this study, summer GDD likely had the strongest influence on common carp recruitment variation based on correlation coeffi-

icients. Temperature is the primary mechanism cited as responsible for animal population synchrony (Grenouillet et al. 2001; Phelps et al. 2008), can be synchronized among systems separated by >1500 km (this study), and has been identified as an important factor influencing localized carp recruitment patterns (Weber and

Fig. 6. Relationships between latitude and correlation coefficients (r) of winter growing degree-days (GDD), summer GDD, precipitation, wind, and the El Niño Southern Oscillation Index (ENSO) with common carp year-class strength for 21 populations across North America.



Brown 2013b). However, the relative influence of environmental characteristics, such as temperature, on recruitment can vary tremendously across latitudes (Conover and Present 1990; Garvey et al. 2002), as populations at different latitudes may adopt different life-history strategies (Weber et al. 2015). At low latitudes, warm spring–summer temperatures had a negative effect on common carp year-class strength, while at higher latitudes they had a positive effect. Spatially separated populations may adapt differently to similar environmental conditions, resulting in different population-level responses. Climate models predict that common carp will advance northward and inhabit much of Canada by the year 2100 (Minns and Moore 1995). Indeed, common carp have increased their northern range in recent years (Badiou and Goldsborough 2006), and our results indicate that strong year-classes of common carp populations at high latitudes are related to warm spring–summer temperatures. Thus, great potential exists for climate change to have a pronounced effect on common carp populations and range expansion as a result of warming temperatures.

Overwinter survival of small-sized age-0 fish may decrease with increasing latitude owing to increased winter duration and likelihood of starvation (Gutreuter and Anderson 1985; Conover and Present 1990; Lyons 1997). Additionally, size-specific overwinter mortality of age-0 common carp has been documented in South Dakota (Phelps et al. 2008b). Thus, we hypothesized that winter severity would have a negative effect on year-class strength of populations at high latitudes but not low latitudes. However, significant negative correlations between winter severity and year-class strength were not detected, even at high latitudes. Overwinter mortality depends upon first-year growth (Post and Evans 1989; Garvey et al. 1998), which is influenced by temperature (Weber et al. 2013b). Thus, the influence of spring–summer temperatures may have masked the effects of winter severity on year-class strength. Alternatively, increased winter temperatures can add to a fish's metabolic demand during this time, when food resources are scarce, leading to increased mortality during warmer winters (Shoup and Wahl 2011). Additionally, fish populations exhibit adaptations to local conditions to maximize survival (Conover and

Present 1990), a phenomenon that may explain why the influence of winter severity on recruitment did not fluctuate with latitude. Density-dependent mechanisms occurring throughout the first year may also influence size of age-0 common carp entering winter (Weber and Brown 2013b), where large year-classes may experience slow growth and low overwinter survival. For example, winter severity was not related to recruitment synchrony of roach, potentially owing to density-dependent interactions during the first year of life (Grenouillet et al. 2001). Predation risk can also alter overwinter survival of juvenile fish (Shoup and Wahl 2008), which may have masked winter severity effects in our study if predation risk varied among systems. Finally, winter temperatures may not have been cold enough during this period to have an effect on common carp recruitment.

Despite evidence that temperatures may be partially responsible for synchronizing common carp populations on a local scale, a substantial amount of variation in year-class strength was unexplained by climatic factors, suggesting that local, biotic factors may be more important. Similarly, many freshwater fishes — walleye (*Sander vitreus*), sauger (*Sander canadensis*), northern pike (*Esox lucius*), brook trout (*Salvelinus fontinalis*), and yellow perch — exhibit little recruitment synchrony (Myers et al. 1997; but see Dembkowski et al. 2016; Honsey et al. 2016). For populations sharing a common density-dependent structure, the Moran effect predicts that biological and environmental synchrony will tend to be equal (Lundberg et al. 2000). However, lower degrees of environmental synchrony are reported more often (Grenfell et al. 1998; Benton et al. 2001). Additionally, the demographic structure of populations also affects the equality between the degrees of biological and environmental synchrony. Thus, synchrony may not only depend on environmental synchrony but also depend on the synchrony of at least one other age-class. Common carp recruitment does appear to be regulated in part by lake-specific and density-dependent factors (Bajer et al. 2012; Weber and Brown 2013b) that are likely responsible in part for the low degree of recruitment synchrony observed among populations. Correcting for density dependence may reveal increased recruitment synchrony (Myers et al. 1997), but reliable and standardized indices of common carp spawner abundance were not available for these systems during all years. Recruitment of freshwater fishes tends to be regulated by biotic factors more than that of marine species (Houde 1994), and the small spatial scale of synchrony in freshwater populations may be attributed largely to biotic processes (Myers et al. 1997). Additionally, the relative importance of various climatic variables that result in synchrony can change from year to year (Grenouillet et al. 2001), making it difficult to pinpoint the underlying mechanism(s) of synchrony. Regional variation in population dynamics further weakens spatial synchrony relative to correlations in environmental factors (Peltonen et al. 2002), and common carp populations do vary across the latitudinal gradient evaluated here (Weber et al. 2015). Differences in carp population characteristics also exist among local, adjacent populations (Weber et al. 2010; Weber and Brown 2011; Bajer et al. 2012), potentially explaining the lack of synchrony among some neighboring populations (<200 km).

Although recruitment synchrony of common carp was detected on a large spatial scale compared with that of other freshwater fish populations, many populations exhibited little synchronization with each other, indicating that local processes may have been more important than local or regional climate patterns in driving synchrony in some instances. Other local biotic and abiotic factors not evaluated here likely have an influence on recruitment dynamics of common carp, and the relative importance of these variables may fluctuate among systems. Recruitment patterns of common carp populations may act independently of one another and may be driven by lake-specific biotic conditions. For instance, predator abundance appears to be an important variable affecting common carp recruitment in Minnesota (Bajer et al.

2012) but not in other regions (Weber and Brown 2012; Bajer et al. 2015). In some instances, broad-scale environmental conditions may synchronize reproductive output, but local processes may regulate survival to later life stages (Grenouillet et al. 2001). Thus, complex interactions occurring among environmental variables and multiple early life stages of common carp likely regulate year-class strength.

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