A question of scale: Weak evidence for broad regional synchrony in fish year-class strength within or among species in inland lakes

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Abstract

Spatially-correlated abiotic and biotic conditions can potentially induce synchrony in the dynamics of disparate populations or species. However, such potential synchrony among species or populations may be tempered by dynamics operating at finer temporal and spatial scales, as well as species-specific responses to environmental conditions. We examined within- and among-species synchrony in year-class strength across 130 lakes in northern Indiana over 30 years to evaluate the relative scale of potential synchrony and its possible ecological mechanisms in five recreationally important fish species: black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), redear sunfish (*L. microlophus*), and yellow perch (*Perca flavescens*). Bluegill and black crappie recruitment was significantly positively correlated when the species coexisted, and relative year-class strength of both species was positively related to mean annual wind speed. However, there were few other instances of recruitment synchrony between or within species, regardless of whether synchrony was assessed within or among lake systems. In addition, habitat similarity and regional weather patterns also played a limited and inconsistent role in shaping recruitment strength or synchrony in these small inland systems. These results suggest that fish recruitment dynamics in small, inland systems are most often a function of system-specific biotic interactions that mask limited input from broader climatological influences, and that understanding recruitment in small lakes will require examinations on appropriately fine spatial and temporal scales.

Key words: *climate; abiotic variables; e-folding scale; year-class strength; catch curve; habitat*

1. Introduction

Broad spatial correlations in environmental conditions can potentially induce synchrony in the characteristics of animal populations across wide geographic areas, a phenomenon collectively referred to as the Moran effect (Cattanéo et al., 2003; Moran, 1953; Ripa, 2003). However, the strength of these broad-scale environmental effects on populations, and therefore the level of synchrony among populations, is tempered by dynamics operating at finer temporal and spatial resolutions (Engen and Sæther, 2005; Ranta et al., 1997). Factors such as population density (Grenouillet et al., 2008), biotic interactions among coexisting species (Durant et al., 2007; Kelly et al., 2009), or local variations in ecosystem productivity (Wheeler et al., 2016) can have major effects on resulting population characteristics and dynamics, influencing potential Moran effects and limiting potential synchrony in population dynamics (Weber et al., 2017). In fact, strong local variation in environmental conditions could induce more similar population dynamics among coexisting species than in geographically disparate populations of the same species (Howeth and Leibold, 2013; Robinson et al., 2013). Understanding the relative importance of broad- and fine-scale environmental and climatic factors in synchronizing population characteristics could therefore inform relevant scales of management (Feiner et al., 2016; Hansen et al., 2015; Tonkin et al., 2017) and offer an avenue to predict the impacts of broad-scale, long-term disturbances such as climate change on populations and communities (Collingsworth et al., 2017; Hansen et al., 2017).

Fish recruitment, i.e., the survival of offspring to contribute to the adult population, has represented an enigmatic and consistent problem for biologists seeking to understand how abiotic and biotic conditions drive fluctuations in fish populations (Myers, 1998). Large fluctuations in recruitment from year to year, often seemingly disconnected to variation in adult abundance

(Feiner et al., 2015; Gilbert, 1997), give the appearance of stochastic processes strongly influenced by external forces (Koslow, 1992). Studies in large, interconnected marine or freshwater systems have documented considerable intraspecific synchrony in year-class strength (i.e., the abundance of recruits produced in a given year relative to average production levels) across large geographic distances. These observations suggest that, at least in these large systems, dispersal combined with broad climatic factors have the potential to structure the survival and production of large year classes and drive similar dynamics among populations (Cloern et al., 2010; Kelly et al., 2009; Myers et al., 1997; Ward et al., 2016).

Observations of broad-scale recruitment synchrony in large lakes coupled with research showing stronger abiotic influences on recruitment in marine systems compared to stronger biotic influences in freshwater systems suggests a paradigm where the importance of climatic factors is correlated with system size. Smaller systems (i.e., inland lakes) should exhibit limited recruitment synchrony compared to their larger, interconnected counterparts due to a lack of dispersal of individuals among systems and stronger influences of local biotic interactions (Houde, 1994; Janssen et al., 2014; Myers et al., 1997). However, this paradigm is challenged by evidence for consistent responses of freshwater fish populations to broad-scale climate patterns or climatological events (Bunnell et al., 2016; Hansen et al., 2015; Schupp, 2011; Weber et al., 2017). In addition, there is some evidence that fishes inhabiting small freshwater systems can show considerable synchrony in recruitment patterns over much greater geographic distances than expected, even in the absence of high dispersal potential (Dembkowski et al., 2016; Grenouillet et al., 2008; Phelps et al., 2008; Weber et al., 2017). Therefore, under some conditions, fish recruitment (and management) could be better informed by understanding the relative importance of biotic and abiotic influences operating at multiple spatial and temporal scales, even when populations are relatively small or isolated.

Beyond within-species recruitment synchrony, examinations of the synchrony of multiple species either within or among systems are lacking (Edwards et al., 2007; Michaletz and Siepker, 2012; Rook et al., 2012), limiting potential inferences that could be made about the relative importance of fine- and broad-scale environmental conditions to recruitment of entire assemblages. Species-specific traits (e.g., spawning phenology, early life history, trophic niche) could determine which environmental factors are most important to recruitment success in fishes, on what scale such factors may act, and how environmental variation may structure recruitment synchrony across populations and species. Therefore, examining recruitment synchrony within and among several species coexisting in small lakes (thereby eliminating dispersal as a potential mechanism for synchrony) offers an avenue toward distinguishing the mechanisms by which environmental variables drive fish population dynamics on different spatial scales by addressing several hypotheses simultaneously: 1) If fine-scale, within-lake interactions are most important to fish recruitment and species respond similarly to environmental variation, there should be high synchrony among species inhabiting the same lakes; 2) If broad-scale, climatological variation is more important to recruitment success and species respond similarly to climatological influences, there should be high geographic synchrony within and among species across different lakes; and 3) If interactions between species' traits and environment are most important to determining recruitment success, synchrony may be low both within and among species at any geographic scale.

We sought to address these predictions using a temporally (~ 30 years) and spatially (130 glacial lakes covering ~200 km in geographic distance) expansive set of observations of year-class strength in five ecologically and recreationally important freshwater fish species that are prevalent in North American lakes: black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), redear sunfish (*L. microlophus*), and yellow perch (*Perca flavescens*). These species exhibit different traits and their recruitment has been linked to both abiotic and biotic environmental conditions in inland lakes (Dembkowski et al., 2017; DeVries et al., 2009; Garvey et al., 2002). Examining within- and among-species variability in recruitment in a suite of species enabled us to infer how species traits and environmental conditions interact to shape dynamics of lentic populations across geographic and temporal scales.

2. Methods

2.1. Fish data

The five focal species of this study represent different reproductive life histories and responses to environmental variation. The centrarchids (largemouth bass, black crappie, bluegill, and redear sunfish) are nesting species exhibiting parental care of eggs until hatch, whereas yellow perch exhibit no parental care. Yellow perch spawn earliest in spring at temperatures between 4 to 15 °C (Feiner and Höök, 2015), followed by largemouth bass and black crappie at temperatures between 15 and 20 °C, and bluegill and redear sunfish spawn latest at temperatures between 20 to 25 °C (Cooke and Philipp, 2009). Bluegill and redear sunfish have the capacity to produce multiple broods per year, whereas the other species typically spawn once per year. Each species produces larvae that initially inhabit pelagic areas before transitioning to demersal habitats later in summer and fall (Bryan and Scarnecchia, 1992; Faber, 1967), during which conditions promoting sufficient young-of-year growth to allow individuals to survive overwinter (e.g., warm temperatures, abundant invertebrate resources) are thought to represent an important recruitment bottleneck (Bunnell et al., 2011; Miller and Storck, 1984; Santucci Jr. and Wahl, 2011). Largemouth bass, black crappie, and yellow perch all transition from invertivory to piscivory to varying extents during their ontogeny (Mittelbach and Persson, 1998), whereas bluegill and redear sunfish rely primarily on invertebrate prey throughout life (Huckins, 1997; Werner and Hall, 1974).

Fish were collected from 130 lakes across northern Indiana during standardized annual surveys performed by the Indiana Department of Natural Resources from 1987 to 2009 (Table 1, Figure 1). During annual surveys, fish were collected during summer (May – October) using three possible gear types: night electrofishing (DC, 5-6 amps, 530 volts, 60 pps with two netters, in 15 minute transects in shallow nearshore habitats), overnight gill nets (76 x 1.8 m with five, 15 m panels of 1.3, 2.5, 3.8, 5.1, and 6.4 cm square mesh, fished on the bottom and set perpendicular to shore beginning < 2 m deep), and overnight trap nets (13.7 m lead, two rectangular 1.8 x 3 m frames, four 0.8 m diameter circular fames set 1.2 m apart with 1.5mm stretched mesh, fished in waters < 1 m deep with the opening toward shore). Effort was standardized to account for lake size (see Sullivan et al., 2015). Because surveys were completed in multiple years for some lakes, we selected a single sampling year from each lake to include in our analysis. Sampling years with the most available data (e.g., highest catch rates, most fish aged) for each species were selected to represent each lake in the final dataset.

For each survey all fish were measured for total length, while a subset of fish also had scales removed for age determination. Scale samples were removed from fish below the lateral line, near the pectoral fin using a pocket knife and placed in a scale envelope. Scale impressions were prepared on clear acetate slides using a hydraulic laboratory press or roller press as described by (Nielsen and Johnson, 1983). Scale impressions were magnified and viewed under microfiche readers by the IDNR district fisheries biologists that completed the survey. Scales are known to underestimate the ages of older fish depending on species and reader experience (Long and Fisher, 2001; Maceina and Sammons, 2006). However, precision and agreement of age estimates using scales for fish younger than 6 to 7 years is similar to those of age estimates using otoliths, spines, or opercular bones (e.g., Hoxmeier et al., 2001; Isermann et al., 2010; Long and Fisher, 2001; Vandergoot et al., 2008). Less than 5% of our total dataset consisted of fish older than seven years, suggesting that age estimates included in this study are likely relatively precise. In addition, we used weighted regression to reduce the importance of old, rare fish on the results of our analyses (see below). Therefore, our results should be robust to potential biases arising from the use of scales in ageing fish.

To estimate the relative abundance of age classes for each species and lake, age-length keys were developed using the aged and measured subsample from each species and lake by dividing fish into 4 mm length bins and only including lakes with at least three year classes present. Within datasets of aged fish, ages were linearly interpolated across length bins where no aged fish were captured. Unaged individuals in length bins greater than the largest aged individual were excluded from further analyses. Species- and lake-specific age-length keys were then applied to the remainder of measured fish to estimate the abundance of each age-class, which was then expressed in terms of catch per unit effort (fish hr^{-1} electrofishing, and fish net-$night^{-1}$ for gillnetting and trapnetting). Because of inherent biases in how each gear samples the fish community and different sizes of fish (Sullivan et al., 2015), catches from only one gear per species were included in further analyses based on highest available sample size (and therefore likely highest catchability of that species in that gear) and a previous study demonstrating high catchability of specific species or guilds in each gear (Sullivan et al., 2015). Specifically, bluegill and largemouth bass recruitment was indexed from night electrofishing catches, redear sunfish from trapnet catches, and black crappie and yellow perch from gillnet catches.

2.2. Determination of year-class strength and environmental conditions

Once the relative abundance of age classes was determined for each lake and species, year-class strength was determined using catch curve analysis (Maceina, 2004; Tetzlaff et al., 2011). For each species and lake where at least three age classes were present, weighted linear regression using the natural log CPUE of each age class as the response variable and age as the predictor variable was used to develop a catch curve and predicted relative abundances for each age class (Quinn and Deriso, 1999). To ensure that only age classes that were fully recruited to the gear in each lake were used in the catch curve, we started each catch curve at the age of peak abundance for each species and lake. The influence of rare, old age classes on the results of each catch curve was limited by weighting observations by the natural log of the predicted number of fish comprising each age class (Honsey et al., 2016). Quality of fit was further ensured via visual inspection and assessment of catch curve explanatory power. The residuals of each catch curve regression were then retained as relative indicators of year-class strength, where positive residuals indicate that an age-class was more abundant than expected, suggesting a good year class, and negative residuals indicate an age-class was less abundant than expected, suggesting a poor year class. Catch curve residuals were then assigned to the year of birth for that age class by subtracting the age of the fish from the year sampling occurred.

The abundance and age structure of species varied considerably across lakes, and catch curve residuals were generally negatively skewed, complicating use of linear or parametric models in assessing variability in recruitment. Furthermore, high recruitment variability observed in many species may render the exact magnitudes of year-class strength less important to managers than an assessment of whether recruitment was generally “good” or “poor” over time or in response to environmental conditions (Hansen et al., 2015). Therefore, we transformed catch curve residuals into a binary index of relative year-class strength by assigning year classes with positive residuals (i.e., abundance was higher than expected – a “good” year class) a value of one, and year classes with negative residuals (i.e., abundance was lower than expected – a “poor” year class) a value of zero (following Honsey et al., 2016) to standardize estimates of relative year-class strength across lakes.

In addition to understanding the extent of recruitment synchrony within and among species in Indiana lakes, we were also interested in elucidating potential environmental drivers of any observed synchrony. We obtained measures of lake habitat, including lake area (km^2), maximum depth (m), the ratio of maximum to mean depth (a measure of littoral habitat availability), and lake shoreline development index (a measure of lake circularity) from the USGS National Hydrography dataset and Indiana Department of Natural Resources publications (IDNR, 1993, 1966; Perry, 2011; USGS, 2004). As indicators of water quality, resource availability, and oxythermal habitat quality (Downing et al., 1990; Magnuson et al., 1979; Missaghi et al., 2017; Persson et al., 1991), Secchi depth (m), total phosphorus ($\mu g\ L^{-1}$), dissolved oxygen at 1.5 m ($mg\ L^{-1}$), and water temperature at 1.5 m (°C), were obtained from the Indiana Clean Lakes Program (ICLP; http://www.indiana.edu/~clp/indianalakeinfo.php). These metrics had been previously identified as potentially important and non-collinear variables influence fish assemblage structure in Indiana lakes (Feiner et al., 2016). We characterized regional weather patterns by obtaining daily wind speed ($km\ h^{-1}$) and air temperature (°C) data from four land-based NOAA weather stations and precipitation data (2.54-mm increments) from six NOAA weather stations around northern Indiana from 1983 to 2010. From these sources, we estimated annual mean daily wind speed, annual mean daily temperature, mean daily spring (April – June) temperature, the number of winter days (mean daily temperature < 0 °C), and cumulative annual and spring (April – June) precipitation for each year by averaging measures across weather stations (see Supplement 1 and Feiner et al., 2016 for detailed information on environmental and climatic variables). We scaled and centered each climatic variable to a mean of 0 and standard deviation of 1 by subtracting the mean from each value and dividing by the standard deviation (resulting in coefficients with units of change in response per one standard deviation change in predictor) to standardize interpretations of environmental effects on recruitment.

Moran effects are assumed to operate via synchronous climatic conditions across space driving synchrony in population dynamics (Engen and Sæther, 2005). We tested for spatial correlations in our climatic variables by correlating annual measures of climatic (wind, temperature, and precipitation) variables between all pairwise combinations of weather stations. Correlations were highly significant across all wind (mean $\rho = 0.83$, $P \leq 0.001$) and temperature variables (mean $\rho = 0.67$, $P \leq 0.016$; Table S2) and most precipitation correlations (mean $\rho = 0.48$, $P < 0.05$ in all but 4 out of 30 correlations; Table S3). Thus, climatic variables were consistently spatially synchronous in northern Indiana during the study, supporting this key assumption for the Moran effect.

2.3 Data analysis

2.3.1. Within-lake synchrony between species

As an initial comparison of the variability in relative year-class strength among species, we calculated the coefficient of variation (CV; standard deviation/mean × 100) of the absolute value of catch curve residuals for each lake and species, then averaged CV across lakes for each species. This index of recruitment variation was then compared across species using ANOVA with type III sums of squares to account for unbalanced number of observations among species.

To evaluate within-lake recruitment synchrony between species, we identified all instances where pairs of species had overlapping year classes in the same lake. Using this subset of paired observations, we determined proportion agreement of relative year-class strength, where each instance where both species produced either good year classes (i.e., both species binary residuals equaled 1) or poor year classes (both species residuals equaled zero) were counted as agreements (1) and cases where one species recorded a good year class and the other a poor year class were recorded as disagreements (0) (Honsey et al., 2016; Zischke et al., 2017). From this, the proportion agreement within each lake was determined as the number of year classes with agreement divided by the total number of overlapping year classes in that lake. For each species pair, we then calculated the weighted mean proportion agreement across all lakes where both species were observed, weighting each observation by the number of years the species pair overlapped in each lake; i.e., the proportion of "successes" (agreements) was weighted by the number of trials (overlapping year classes).

We used two methods to statistically evaluate pairwise species recruitment synchrony. First, we used a one-way weighted t-test (each observation was weighted by the number of years of overlap) to determine whether mean weighted proportion agreement was greater than 0.5 (expected if recruitment in each species was random). Second, we used the raw residuals (i.e., before transformation to binary values) to perform repeated-measures Spearman-rank correlations on paired recruitment observations ranked and nested within lakes (R package 'rmcorr'; Bakdash and Marusich, 2017). Each analysis was repeated for each species pair.

There was considerable variation among lakes in recruitment agreement. We further sought to evaluate how in-lake habitat and water quality may have influenced variability in recruitment synchrony between species using the suite of within-lake habitat and water quality variables developed above. We used multiple logistic regression with mean percent agreement in relative year class strength as the response and each environmental measure (Secchi depth, total phosphorus, dissolved oxygen at 1.5 m, water temperature at 1.5 m, lake area, maximum depth, maximum:mean depth, and shoreline development index) as additive explanatory variables. To limit model overfitting and identify a most-parsimonious model, we then used forward and backward stepwise model selection using AIC as a selection criterion. Model fit was assessed using McFadden's $R^2 = 1 - (loglikelihood(null)/loglikelihood(model))$, and the Hosmer-Lemeshow test, which tests whether observations with similar predicted probabilities have similar observed probabilities with a χ^2 test (where small χ^2 and large p-values indicate good model fit).

2.3.2. Among-lake synchrony within species

We sought to evaluate spatial and environmental synchrony in recruitment within each focal species using two methods. First, we examined the spatial scale of synchrony in recruitment using the *e*-folding scale method (Honsey et al., 2016; Myers et al., 1997), which determines the distance between populations required to decrease the agreement in recruitment by a factor of e^1. This analysis is normally performed on the correlation of year-class strengths between pairs of lakes; however, due to the random sampling of lakes in our study, few lake pairs had sufficient data overlaps to perform meaningful correlations. Instead, we identified all instances where pairs of lakes had overlapping observations of year-class strength for a single species and scored the agreement of recruitment strength as either 1 (both lakes had positive or negative residuals) or -1 (one lake had a positive residual while the other had a negative residual). We then averaged the agreement of each lake pair across all years where overlapping year classes were observed to develop an index of recruitment agreement ranging from 1 (all year classes agreed) to -1 (no year classes agreed). To determine the spatial extent of recruitment synchrony, we then fit this index of agreement to the exponential decay equation:

$$\rho(d) = \rho_o e^{-\left(\frac{d}{v}\right)},$$

where $\rho(d)$ is the agreement between a lake pair, ρ_0 is the agreement between lakes with no geographic separation, d is the great circle distance between lakes (km), and v is the e-folding scale parameter. We constrained ρ_0 to have values less than 1 (Myers et al., 1997) and weighted each observation by the number of overlapping year classes observed (Honsey et al., 2016).

We further sought to evaluate whether environmental similarity of lakes, rather than their spatial proximity, was a stronger driver of recruitment synchrony in these populations. To do so, we calculated the univariate Euclidean distance of each environmental variable (Secchi depth, total phosphorus, dissolved oxygen at 1.5 m, water temperature at 1.5 m, lake area, maximum depth, maximum to mean depth ratio, and lake shoreline development index) between each potential pair of lakes. We then used logistic regression with mean binomial (0 or 1, as in section 2.3.1) proportion agreement in relative year-class strength as the response variable and similarity in each environmental variable as the predictor variables. Each observation was weighted by the number of year-class overlaps. In this analysis, we expected that lakes similar in environmental variables (i.e., small Euclidean distances) should have higher agreement in recruitment, leading to negative relationships between environmental dissimilarity and mean proportion agreement in relative year-class strength. Forward and backward stepwise model selection using AIC was used to select the most parsimonious model explaining recruitment synchrony. Model fit was assessed using McFadden's R^2 and the Hosmer-Lemeshow test.

2.3.3. Among-lake synchrony between species

Our next question of interest was whether year-class strength exhibited synchrony between species at a regional (among-lake) level, which allowed us to expand our scope of inference to the entire time series of data, rather than being limited to specific cases where year classes from two species were sampled in the same lake. To evaluate this question, we sought to correlate mean relative year-class strengths between species across time. Specifically, we first averaged binary relative year-class strengths across lakes for each species to develop an annual measure of whether recruitment was generally good or poor each year for each species, thereby creating a continuous, normally distributed variable ranging from 0 to 1 (where 0 indicates poor recruitment across lakes that year, and 1 indicates good recruitment across lakes that year). We then used Spearman rank correlation to evaluate the correlation of mean relative year-class strengths between each potential species pair, weighting each observation by the fewest number of lakes for which relative year-class strength was determined for either species that year.

2.3.4. Climatic drivers of year-class strength

We used generalized multiple logistic regression modeling to determine the effect of climatic variables (wind, temperature, winter days, and precipitation) on mean annual recruitment for each species. Binary relative year-class strength (as developed above) was the response, the six climatic variables were additive predictors, and we included random intercepts for lake identity. Model fit was assessed by the area under the ROC curve (AUC, a measure of classification performance which ranges from 0.5 – 1.0, with values > 0.8 considered good fitting models) and the Hosmer-Lemeshow test. Significance of climatic variables was determined using t-statistics and p-values using Satterthwaite's type III degrees of freedom (R package 'lmerTest'; Kuznetsova et al., 2016).

3. **Results**

3.1. Within-lake synchrony between species

In total, recruitment from at least one species was indexed in 130 glacial lakes located across northern Indiana. Bluegill and largemouth bass were ubiquitous across the region (~100 lakes and ~500 year-class observations), whereas yellow perch, redear sunfish, and black crappie were observed less often (< 25 lakes and < 100 total year classes; Table 1, Fig. 1). Coefficients of variation in catch curve residuals were variable among lakes and species, ranging from 72 to 191%. After natural log-transforming CV to meet normality assumptions, there was evidence that within-lake variation in relative year-class strength significantly differed among species (ANOVA: $F_{4,260} = 5.50$, $p < 0.001$). Specifically, largemouth bass recruitment exhibited significantly lower mean CV of catch curve residuals across lakes than bluegill (*post hoc* Tukey's test, $p < 0.001$), indicating reduced recruitment variability in largemouth bass compared to bluegill. However, this difference was small in magnitude (16%) and no other species differed in CV (post hoc Tukey's test, $p > 0.15$). Generally, the standard deviation of catch curve residuals was slightly less than their average magnitudes (range in mean CV: 82 – 98%).

We observed generally minimal recruitment synchrony between species when limiting the data to paired observations of year classes within lakes. While mean percent agreement in year-class strength was greater than 50% in 5 of 10 possible species pairs, only bluegill and black crappie recruitment agreement agreed significantly more often than 50% of the time (Table 2). Supporting this, there was only one species pair, bluegill – black crappie, that had a significant, positive correlation between year-class strengths (Figure 2a). There were, however, three species pairs (black crappie – largemouth bass, bluegill – redear sunfish, and redear sunfish – yellow perch) that exhibited significant, negative correlations in year-class strength (Table 2; Figure 2b-d). There were few significant effects of in-lake habitat or water quality characteristics on recruitment agreement between species – bluegill and largemouth bass synchrony was positively related to the ratio of maximum to mean depth, and bluegill and yellow perch synchrony was negatively related to lake area (Table S4, Fig. S1).

3.2. Among lake synchrony within species

e-folding scale regression indicated very low spatial synchrony in year-class strength among Indiana glacial lakes (Table 3), as indicated by small (or negative) and non-significant effects of υ, suggesting either no synchrony at all, or synchrony limited to less than 10 km among lakes (Figure 3).

Due to the lack of spatial synchrony, we then sought to evaluate whether environmental similarity was driving year-class strength agreement between lakes for each species. Model performance was generally very poor (low McFadden's R^2 and low Hosmer-Lemeshow test p-values; Table S5). Bluegill year-class strength agreement was significantly, positively related to differences in lake depth, and redear sunfish year-class strength agreement was significantly, negatively related to differences in temperature at 1.5m depth (Figure S2). No other species yielded significant relationships between recruitment synchrony and lake environmental similarity (Table S5).

3.3. Among lake synchrony between species

Examinations of correlations in year-class strength at the regional level revealed a similar lack of synchrony as within-lake analyses. Although 6 of 10 possible species pairs exhibited positive correlations of mean year-class strength across lakes, only one correlation was even marginally significant: a positive correlation between redear sunfish and largemouth bass (Table 5; Figure S3).

3.4. Climatic drivers of year-class strength

There were relatively few significant relationships between binary year-class strength and regional climatic variables across all species (Table S6). Bluegill and black crappie recruitment exhibited a significant positive relationship with annual mean daily wind speed, and yellow perch recruitment was positively related to spring precipitation. No other species exhibited significant relationships between year-class strength and climatic variables. In addition, model performance was generally poor, with AUC less than 0.8 and generally small Hosmer-Lemeshow p-values, indicating the predictive ability of our selected climatic variables was limited for the recruitment of these species.

4. Discussion

Examining recruitment patterns in five species across 130 lakes allowed us to evaluate several potential predictions for how environmental variables at multiple spatial scales influence and potentially synchronize fish population dynamics. We observed surprisingly few instances of synchrony in recruitment either between species inhabiting the same lakes, within species inhabiting different (even environmentally similar lakes), or among species at a regional scale. In addition, there was inconsistent evidence of environmental or climatic variables influencing recruitment of each species. These results give strongest support to our third prediction: that interactions between species-specific traits and local-scale environmental variation, both abiotic and biotic, are most important in driving recruitment variation in these types of small glacial lakes. Our results support the paradigm that the scale of recruitment synchrony and importance of climatological variables is correlated to system size (Myers et al., 1997).

In general, spatial synchrony among populations of the same species is thought to be limited between small, disconnected lakes. The lack of dispersal between water bodies and variable biotic, habitat, and environmental conditions among these types of systems would seem to reduce the amount of potential environmental similarity fish populations would experience, even if broad-scale climatic conditions were correlated across large geographic areas. The few published studies examining recruitment synchrony in our target species, in concert with our findings, would seem to support this hypothesis, especially in the sunfishes. Bluegill recruitment has been shown in multiple studies to be largely determined by biotic conditions (Kaemingk et al., 2013; Parkos et al., 2011; Santucci Jr. and Wahl, 2011), with limited influence of abiotic variables and minimal among-population synchrony (Edwards et al., 2007; Tomcko and Pierce, 2011). Similarly, largemouth bass recruitment has been related to system productivity, prey and habitat availability, and density-dependent effects (Michaletz and Siepker, 2012; Miller and Storck, 1984; Paukert and Willis, 2004; Post et al., 1998), with few observed relationships to climate patterns (but see Rypel, 2009). Similar dynamics appear to influence black crappie recruitment (Bunnell et al., 2011; Guy and Willis, 1995; Maceina, 2003). The evidence for synchrony in yellow perch populations is mixed. Honsey et al., (2016) and Dembkowski et al., (2016) both observed extensive recruitment synchrony in the Great Lakes and inland lake systems, respectively, but yellow perch between Muskegon Lake and Lake Michigan, and in this study, showed little concordance even at short geographic distances (Janetski et al., 2013). In addition, yellow perch recruitment has been extensively related to biotic conditions like predator abundance and density-dependent dynamics (Forney, 1971; Irwin et al., 2009). Thus, we conclude that, within species, recruitment synchrony is likely to be minimal across inland lake populations.

One species pair, black crappie and bluegill, exhibited synchronous dynamics in their correlations of year-class strength when coexisting and in their regional positive response to mean annual wind speed. Both bluegill and black crappie prefer nesting sites sheltered from wind (Pope and Willis, 1997; Stahr et al., 2013); thus, altered spawning site selection in windy years may affect recruitment success similarly in both species. Wind speeds may also alter lake mixing, primary production, and zooplankton phenology and distribution, influencing potential forage for larval and juvenile fishes (de Souza Cardoso and da Motta Marques, 2009; Gauthier et al., 2014). However, a precise mechanism remains unclear, as wind speeds have not been strongly linked to larval distribution or abundance in either species (Kaemingk et al., 2011; Post et al., 1995), although Pope et al., (1996) also found a positive relationship between black crappie recruitment and wind speed. Beyond wind, similar responses to biotic conditions may structure synchrony between species. Black crappie and bluegill responded similarly to largemouth bass removals in Alabama lakes (McHugh, 1990), and juveniles of both species share similar habitat and trophic niches (Holland and Huston, 1985; Knights et al., 1995; Werner et al., 1977). Thus, a combination of within-lake interactions and regional climatic patterns may result in similar population dynamics between these two species, where conditions benefitting black crappie recruitment, a goal of fishery biologists seeking to improve fisheries for this recreationally popular species (Boxrucker and Irwin, 2002), may also benefit bluegill populations.

Habitat availability and water quality can act as important regulators of fish population dynamics, influencing everything from spawning site preferences to larval growth and survival (Sass et al., 2017). Therefore, despite limited geographic synchrony within or among species, we also attempted to discern whether environmental characteristics could potentially drive recruitment synchrony. Evidence was limited, but there was an indication that agreement between bluegill and largemouth bass was positively related to littoral habitat availability within lakes (maximum:mean depth), and similarity in lake depth and water temperature were significantly related to within-species agreement in bluegill and redear sunfish recruitment among lakes, respectively. Bluegill generally spawn at depths less than 2 m (Gosch et al., 2006) – steep sided (i.e., high ratio of maximum to mean depths), deep lakes may offer less littoral habitat, limiting bluegill to smaller areas or making them more susceptible to environmental variability by offering lower quality habitat to juvenile bluegill and largemouth bass, thereby increasing synchrony compared to lakes with abundant and variable littoral habitats (Gaeta et al., 2014; Sass et al., 2006; Werner and Hall, 1974). There have been few investigations of redear sunfish recruitment, but studies on similar species (e.g., bluegill) have shown some importance for spring temperatures to improve growth and promote overwinter survival (Santucci Jr. and Wahl, 2011). Therefore, lakes with similar thermal conditions may generally produce similar effects on redear sunfish recruitment success, while differences between thermally distinct lakes may result from interactions with other abiotic or biotic variables. Similar nonlinear or interacting effects in recruitment dynamics have been observed in other species. For instance, walleye recruitment was found to be more resilient to warming temperatures when largemouth bass abundance was low in Wisconsin lakes (Hansen et al., 2017), and water transparency interacted with zooplankton abundance to structure bluegill recruitment in a Nebraska reservoir (Kaemingk et al., 2013). These results suggest that the interplay of abiotic and biotic conditions can complicate the assessment of recruitment patterns in lentic species under dissimilar environmental conditions.

More broadly, our results suggest that biotic interactions between species likely represent critical drivers of recruitment success. While there was only a single positive correlation in relative year-class strength between species, there were significant negative correlations between black crappie and largemouth bass, bluegill and redear sunfish, and yellow perch and redear sunfish relative year-class strength. The observed negative correlations primarily occurred between species that inhabit relatively similar trophic niches. Both black crappie and largemouth bass transition from benthic invertebrate prey to fish prey during their ontogeny, and an inability to switch to fish prey can significantly reduce juvenile performance (Ellison, 1984; Mittelbach and Persson, 1998; Olson, 1996). In addition, negative relationships between black crappie populations and largemouth bass abundance have been observed elsewhere, suggesting that strong largemouth bass year classes may depress black crappie recruitment (McHugh, 1990; Schultz et al., 2008). Similarly, bluegill, redear sunfish, and yellow perch all prey on a combination of zooplankton and benthic invertebrates during their first year of life (Feiner and Höök, 2015; Huckins, 1997; Werner and Hall, 1974). Potentially, competitive interactions between these species may have led to these negative correlations, where strong year classes for one species limited year-class success by others and vice versa. Additional work to uncover the mechanisms by which these species potentially interact could further elucidate whether these types of biotic interactions may influence their recruitment.

Our conclusions contrast some recent work suggesting that freshwater species can exhibit recruitment synchrony on geographic scales approaching those observed in large, marine systems, including percids (Beard et al., 2011; Dembkowski et al., 2016; Honsey et al., 2016), cyprinids (Grenouillet et al., 2008; Marjomäki et al., 2004; Phelps et al., 2008), and coregonids (Bunnell et al., 2010; Myers et al., 2015). The differences we observed may have resulted from differences in life history, system size, or desynchronization during ontogeny. First, most species previously shown to exhibit recruitment synchrony are broadcast spawning fishes with no parental care, which may expose their offspring to stronger influences of spatially-correlated climatic conditions (Pope et al., 1996; Beard et al., 2011; Honsey et al., 2016; Janetski et al., 2013). This contrasts the centrarchids included in this study, which exhibit parental care and show stronger effects of biotic variables on recruitment (Edwards et al., 2007; Post et al., 1998; Santucci Jr. and Wahl, 2011). Secondly, the systems in our study were generally much smaller than those within which other freshwater species have exhibited broad-scale synchrony, most notably in the Great Lakes, where potential larval dispersal and connected habitats may boost potential recruitment synchrony similarly to large marine systems (Bunnell et al., 2016; Honsey et al., 2016). Finally, within-lake conditions may act to desynchronize populations later in life. Our catch curve analysis was estimating year-class strength based on the abundances of adult (age 2+) fish. Recruitment synchrony in inland lakes has previously been observed in analyses indexing recruitment using the abundances of early life stages (larvae or young-of year; Beard et al., 2011; Dembkowski et al., 2016; Marjomäki et al., 2004). Potentially, early life abundances may be synchronized by climatic conditions, but become unlinked by within-lake processes during ontogeny. For instance, Grenouillet et al., (2008) observed synchrony in the abundance of age-0 roach (*Rutilus rutilus*) along the Rhône River, but little synchrony in age-1 abundances. In small systems, therefore, biotic or other in-lake environmental variation is likely most important to recruitment variability and may act to decouple adult abundances. Thus, our observations of minimal spatial synchrony are potentially typical for these study species.

Findings of spatial synchrony in fish populations have been identified as a potential avenue for determining the proper spatial scale for management actions or in predicting the responses of species to climatological events or climate change at broader regional scales (Hansen et al., 2015; Tonkin et al., 2017). While these are useful goals when recruitment synchrony is present, our results underscore the importance of understanding how habitat and biotic interactions at the lake level regulate recruitment success. Our observations of at least some within-lake environmental influences on recruitment or recruitment synchrony and a near-complete lack of spatial synchrony or regional climate effects would indicate that, in smaller lakes, spatial variability in habitat may be more important than geographic proximity. Therefore, after assessing recruitment synchrony within and among lakes and species across more than a hundred systems, we suggest that recruitment dynamics for the species included in this study are more a function of the interplay between species traits, biotic interactions, and habitat rather than any large-scale climatic disturbances. Thus, inferences about recruitment may be limited in the absence of data taken at sufficiently fine temporal and spatial scales.

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Table 1. Lake and species sample sizes used in analyses. Below the diagonal are the number of lakes with species pairs, and above the diagonal are the total number of species pair observations across lakes and years. Values on the diagonal represent the number of lakes for that species, with total number of year classes observed across lakes listed in parentheses.

Species	Black crappie	Bluegill	Largemouth bass	Redear sunfish	Yellow perch
Black crappie	13 (46)	31	31	2	9
Bluegill	10	107 (499)	271	64	64
Largemouth bass	10	71	98 (502)	53	52
Redear sunfish	1	19	15	23 (95)	16
Yellow perch	3	19	16	5	24 (91)

Table 2. Upper: weighted mean (SE) proportion agreement in year-class strength (below diagonal) and p-value from one-way weighted t-test testing whether proportion agreement was > 0.5 (above diagonal). Lower: repeated-measures Spearman rank correlation coefficients between paired observations of year-class strength within lakes (below diagonal) and associated p-values (above diagonal). Dashes (--) indicate insufficient sample size for a comparison and bolded values are significant at $p < 0.05$. See Table 1 for sample sizes.

Mean proportion agreement in year-class strength					
Species	BLC	BLG	LMB	RES	YEP
BLC		**0.006**	0.829	--	0.409
BLG	**0.74 (0.08)**		0.355	0.970	0.500
LMB	0.39 (0.11)	0.51 (0.03)		0.279	0.934
RES	--	0.36 (0.07)	0.55 (0.08)		0.928
YEP	0.56 (0.21)	0.50 (0.07)	0.40 (0.06)	0.31 (0.10)	
Correlation of year-class strength within lakes					
	BLC	BLG	LMB	RES	YEP
BLC		**0.006**	**0.042**	--	0.690
BLG	**0.567**		0.651	**0.008**	0.928
LMB	**-0.436**	-0.032		0.187	0.094
RES	--	**-0.388**	0.216		**0.041**
YEP	0.186	0.014	-0.279	**-0.595**	

Table 3. *e*-folding scale model results to determine extent of spatial synchrony in the recruitment of five sportfish species in northern Indiana, including model coefficients (SE) ρ_0 (the expected correlation when distance is zero) and υ (the distance (km) required to decrease synchrony by e^{1}), model degrees of freedom (df), and residual standard error (RSE). Minimal spatial synchrony was observed across all species.

Species	ρ_0	υ	df	RSE
Bluegill	-0.307 (1.644)	0.574 (2.245)	2261	1.050
Largemouth bass	0.375 (0.784)	1.012 (1.96)	2059	1.045
Redear sunfish	0.545 (0.323)	8.992 (9.835)	81	1.174
Black crappie	0.176 (0.178)	-90.867 (77.246)	20	1.146
Yellow perch	0.007 (0.031)	-31.572 (35.311)	90	1.103

Table 4. Weighted Spearman rank correlation coefficients (*r*) for mean annual binary year-class strength between species (below diagonal). Observations were weighted by the number of lakes sampled each year. The number of years included in the analysis are shown in parentheses, and p-values for correlations are listed above the diagonal.

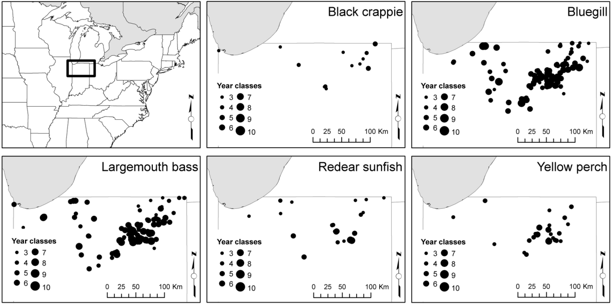
	Black crappie	Bluegill	Largemouth bass	Redear sunfish	Yellow perch
Black crappie		0.551	0.624	0.787	0.414
Bluegill	0.148 (20)		0.497	0.545	0.961
Largemouth bass	0.122 (20)	0.145 (26)		**0.049**	0.902
Redear sunfish	0.072 (18)	-0.142 (22)	**0.434** (22)		0.806
Yellow perch	-0.221 (17)	0.012 (22)	-0.029 (22)	0.059 (21)	

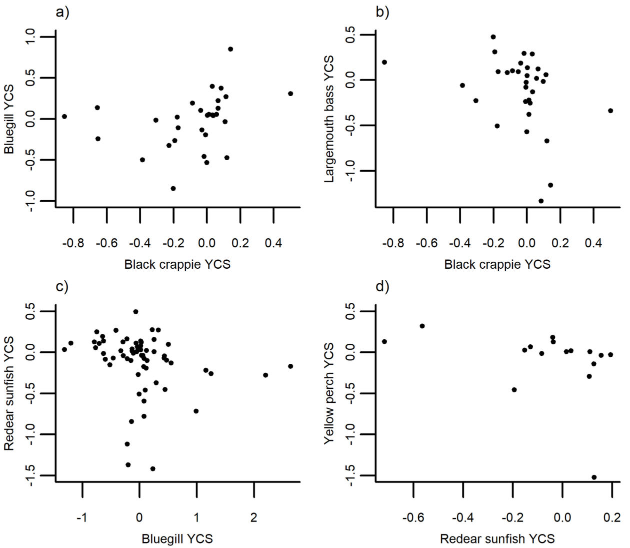
Figure Captions

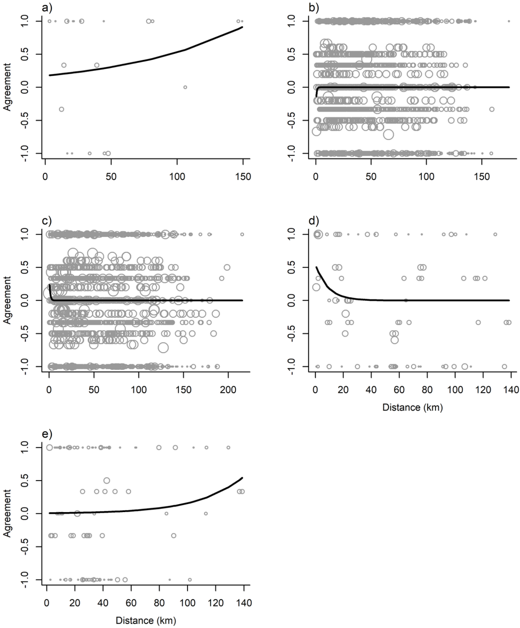
Figure 1. Location of northern Indiana, USA, lakes where black crappie, bluegill, largemouth bass, redear sunfish, and yellow perch were sampled by the Indiana Department of Natural Resources from 1982 to 2010. Size of dots correspond to number of year classes observed in each lake.

Figure 2. Significant, repeated measures Spearman correlations of relative year-class strength (YCS) were observed between a) bluegill and black crappie, b) largemouth bass and black crappie, c) redear sunfish and bluegill, and d) yellow perch and black crappie. Only bluegill and black crappie recruitment was positively correlated.

Figure 3. Relationships between mean scaled proportional agreement in relative year-class strength and geographic distance (km) between lakes for a) black crappie, b) bluegill, c) largemouth bass, d) redear sunfish, and e) yellow perch sampled in northern Indiana, USA, glacial lakes. Circles (gray) represent observed agreement, with symbol size denoting the number of overlapping year classes for each lake pair. Solid black line is the predicted *e*-folding scale relationship for each species. Minimal spatial synchrony was observed across species.


Black crappie
Bluegill
Largemouth bass
Redear sunfish
Yellow perch
Year classes
3 4 5 6 7 8 9 10
0 25 50 100 Km
N


a)
Bluegill YCS
Black crappie YCS
b)
Largemouth bass YCS
Black crappie YCS
c)
Redear sunfish YCS
Bluegill YCS
d)
Yellow perch YCS
Redear sunfish YCS



a)
b)
c)
d)
e)
Agreement
Agreement
Agreement
1.0
0.5
0.0
-0.5
-1.0
0
50
100
150
200
20
40
60
80
100
120
140
Distance (km)
Distance (km)