

ORIGINAL ARTICLE

Spawning periodicity and synchrony of bluehead chub (*Nocomis leptocephalus*) and a nest associate, yellowfin shiner (*Notropis lutipinnis*), across local streams

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Abstract

We studied daily spawning periodicity of a nest-building species, bluehead chub (*Nocomis leptocephalus*), and a nest associate, yellowfin shiner (*Notropis lutipinnis*), in three streams in the upper Piedmont region of South Carolina, USA. Field observations were conducted for 89 consecutive days in 2016 by recording the number of active nests and environmental variables. A total of 71 nests were located across study streams; bluehead chub and yellowfin shiner spawned between April and June. Spawning was observed periodically at intervals of 4–6 days within the same stream and across different streams, indicating broad-scale influences of the same environmental factors leading to synchrony. A generalized linear auto-regressive and moving average model showed that the periodic spawning pattern was likely caused by changes in water temperature, with effects of water level varying by stream. Specifically, spawning was triggered by a short-term (2-day) increase in water temperature and was observed under stable flow conditions (i.e. a lack of precipitation). This study showed that spawning periodicity of bluehead chub and yellowfin shiner tracked daily variation in in-stream conditions, indicating that their reproduction might be affected by anthropogenic disturbances that affect the rate of change in thermal and flow regimes at the fine temporal scale (e.g. hydroelectric dams and impervious cover).

KEYWORDS

climate change, phenology, reproductive interactions, spatial synchrony, time-series analysis

1 | INTRODUCTION

Fish spawning is strongly regulated by external conditions. Timing, duration, and frequency of reproduction have evolved to maximize offspring survival in response to availability of prey abundance, competition among juveniles, and long-term environmental conditions (Bestgen, Beyers, Haines, & Rice, 2006; Divino & Tonn, 2007; Mills, 1991; Morissette et al., 2009). Spawning is often triggered by broad-scale environmental factors such as climate, which leads to spatial synchrony among local sites in a region (Cattanèo, Hugueny,

& Lamouroux, 2003; Chevalier, Laffaille, & Grenouillet, 2014; Engen & Saether, 2005). However, environmental control on spawning timing, particularly on fine-scale temporal scales (e.g. daily or over several days), is poorly understood for most nongame stream fishes.

Spawning of stream fishes is a complex process, triggered by a suite of environmental variables operating at different temporal scales (Forsythe et al., 2012; King et al., 2016; Morissette et al., 2009). Stream fish initiate and discontinue spawning under a specific range of temperatures (Bruch & Binkowski, 2002; King et al., 2016; Reid, 2006), flow conditions (Falke, Bestgen, & Fausch,

2010; Forsythe, Crossman, Bello, Baker, & Scribner, 2011; Peoples, McManamay, Orth, & Frimpong, 2014), and photoperiod (Falke, Fausch, Bestgen, & Bailey, 2010; Forsythe et al., 2012). Some of the environmental variables change predictably within a spawning season (e.g. photoperiod), but others such as temperature and flow change more stochastically from day to day (Forsythe et al., 2012; Straight, Jackson, Freeman, & Freeman, 2015). The short-term variation, including the rate of change in temperatures and flow, trigger spawning of fishes within the spawning season (Forsythe et al., 2011; Paragamian & Wakkinen, 2002). This fine-scale environmental variation can lead to spawning periodicity in which spawning occurs on some days at intervals, but not on others, within a broadly defined spawning season (Forsythe et al., 2012).

Fine-scale temporal cues of spawning have been much less studied compared to broad-scale environmental triggers in stream fishes, but this fine-scale knowledge is important to planning aquatic conservation. Studies of the timing of spawning have focused on larval emergence, reproductive migration, and their inter-annual and among-site variation (Catalano & Bozek, 2015; Falke, Fausch, et al., 2010; King et al., 2016; Krabbenhoft, Platania, & Turner, 2014; Reid, 2006; Straight et al., 2015). Direct observations of spawning are typically challenging in fishes, instead daily spawning patterns are inferred based on larval counts, the number of nests (e.g. salmonid redds), and detection of migratory adults (Divino & Tonn, 2007; Falke, Fausch, et al., 2010; Forsythe et al., 2012; Paragamian & Wakkinen, 2002; Warren, Robinson, Josephson, Sheldon, & Kraft, 2012). Few studies have linked daily spawning patterns to environmental fluctuations, particularly in stream fishes. Flow and thermal regimes in river ecosystems play vital roles in the reproductive timing and outcomes of stream fishes (Poff et al., 1997; Steel, Beechie, Torgersen, & Fullerton, 2017). Human activities (e.g. urbanization and hydropeaking dams) affect components of flow and thermal regimes on time scales of days, and lead to abnormal spawning patterns and reproductive failures (Kemp, 2017; Santucci & Wahl, 2003; Steel et al., 2017; Warren et al., 2012). Filling the knowledge gap of fine-scale spawning pattern is important for understanding environmental cues on stream fish reproduction and managing for aquatic conservation.

Bluehead chub (*Nocomis leptocephalus*) provides a unique system to study environmental influences on periodicity within a spawning season because of their prolonged spawning season (2–3 months) and conspicuous nests that make direct observations of spawning possible (Sabaj, Maurikis, & Woolcott, 2000; Wallin, 1989). Bluehead chub are widely distributed throughout the Atlantic slope of North America (Lanchner, 1952). Male bluehead chub move pebbles to construct dome-shaped nests as a host species (Wallin, 1989), and nest associates spawn on the nests with them (Jenkins & Burkhead, 1994; Johnston, 1994a). This interaction (i.e. nest association) is mutually beneficial because bluehead chub extend parental care to nest associates, which in turn provide a dilution effect when predators invade bluehead chub nests (Johnston, 1994b; Peoples, Floyd, & Frimpong, 2016;

Vives, 1990). In the upper Piedmont region of the southeastern USA, bluehead chub interact reproductively with yellowfin shiner (*Notropis lutipinnis*) via nest association (Marcy, Fletcher, Martin, Paller, & Reichert, 2005; Wallin, 1989, 1992). Both fishes spawn from spring to early summer at water temperatures of 16–23°C (Wallin, 1989, 1992). Wallin (1989) observed that spawning did not occur continuously, but exhibited a periodic pattern with clusters of days of spawning followed by consecutive days without spawning. However, little is known about how environmental cues affect spawning periodicity of bluehead chub and yellowfin shiner. Understanding spawning periodicity of a keystone species (i.e. bluehead chub) would provide valuable insights into community structure and dynamics because nest associates rely on keystone species for reproduction (Peoples et al., 2016; Peoples & Frimpong, 2016; Wallin, 1992).

In this study, we conducted field observations for 89 consecutive days to characterize daily spawning patterns of bluehead chub and yellowfin shiner at three streams in the Piedmont region of South Carolina, USA. The study species enabled us to understand their daily spawning periodicity because field observations were facilitated by conspicuous pebble mound nests constructed by bluehead chub, which attracted swarms of the brilliantly-colored breeding nest associate (Peoples, Blanc, & Frimpong, 2015; Sabaj et al., 2000; Wallin, 1989). The objectives of this study were to (a) document reproductive periodicity of both species, (b) examine reproductive synchrony among local streams, and (c) assess whether daily variation in spawning is explained by environmental variables. We expected that spawning would take place synchronously among local streams if regional factors, such as weather patterns (i.e. temperature and precipitation), are the key drivers of bluehead chub and yellowfin shiner reproduction.

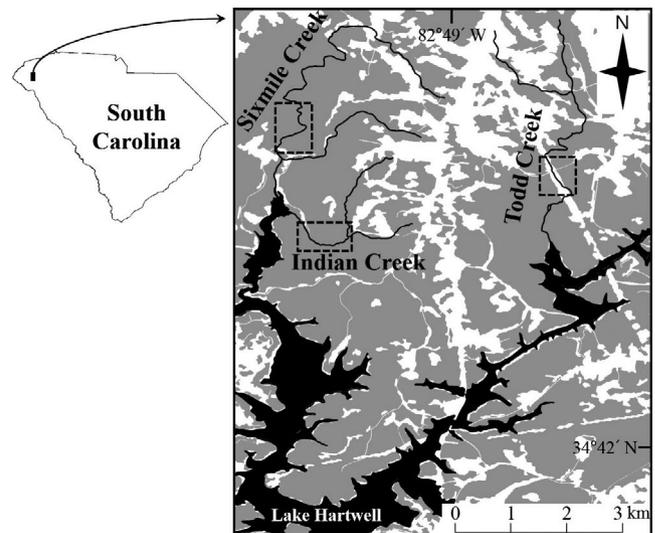


FIGURE 1 Map of study streams in the Savannah River Basin in the upper Piedmont region of South Carolina, USA. Waterways (lakes and streams) are shown in black, forested areas are gray, and developed areas and roads are white. Dotted rectangles indicate the study area in each stream

TABLE 1 Habitat characteristics of each study stream

Stream	Mean wetted width (m) ^a	Mean depth (cm) ^a	Dominant substrate ^b	Canopy cover
Indian Creek	2.8	16.6	PE, SD	High
Todd Creek	3.8	24.7	PE, CO	Low
Sixmile Creek	7.4	32.1	SD, GV	Intermediate

^aMean wetted width and depth were based on measurements at transects, which were evenly distributed across study sites (Indian Creek: 48, Todd Creek: 32, Sixmile Creek: 20).

^bDominant substrate was visually estimated at transects. CO: cobble (64–256 mm); GV: gravel (2–16 mm); PE: pebble (16–64 mm); SD: sand (0.01–2 mm).

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in three streams in the Clemson University Experimental Forest located in the upper Piedmont region of South Carolina, USA (Figure 1). Study streams were selected to represent a gradient of stream size and habitat characteristics in which both species occurred. Indian Creek was the smallest stream based on mean wetted width (2.7 m; Table 1). The stream canopy was mixed hardwoods and dominant substrates were pebble (16–64 mm) and sand (0.01–2 mm; Table 1). Todd Creek was intermediate in size (wetted width = 3.8 m) with an open canopy (Table 1; Figure 1). Substrate was composed of a combination of bedrock, cobble, pebble, and sand. Sixmile Creek was the largest of the three streams (wetted width = 7.3 m), and was mainly covered by overhanging trees but some parts of the stream had little shade from riparian shrubs (Table 1). The dominant substrate was sand and gravel (2–16 mm). The length of study area was 1.6 km in Indian Creek, 1.0 km in Sixmile Creek, and 0.8 km in Todd Creek. Common species found in all streams were bluegill (*Lepomis macrochirus*), creek chub (*Semotilus atromaculatus*), green sunfish (*L. cyanellus*), redbreast sunfish (*L. auritus*), and striped jumprock (*Moxostoma rupiscartes*). Rosyface chub (*Hybopsis rubrifrons*), another known nest associate (Marcy et al., 2005), was found in Indian and Sixmile Creeks, but they were much less common than yellowfin shiner.

2.2 | Field sampling

Spawning activity of bluehead chub and yellowfin shiner was observed for 89 consecutive days from April 4th to July 1st, 2016. The study period encompassed an entire spawning season because the field observation had started nearly two weeks before the first nests were observed and it ended one week after the last nests had been observed (see Section 3). Observations were conducted between 10 a.m. and 5 p.m. To avoid a bias introduced by observation hour, the order of visits to streams were randomized daily. Based on observations of the first five nests every 4 hr for 24–48 hr, we determined that nests stayed active for more than a day (S. Kim unpublished data), and our sampling protocol was unlikely to miss active nests. Two observers walked on the bank or in the stream channel to locate bluehead chub nests. Male bluehead chub prefer shallower runs covered by gravel and pebble for nesting (Bolton, Peoples, & Frimpong, 2015; Sabaj et al.,

2000; Wallin, 1989), but observers checked all habitat types including runs, riffles, pools and undercut banks. Observers confidently identified bluehead chub nests because pebbles mounds were conspicuous and easily viewed in the clear water. When a new nest was located, a marker was placed on the nearest bank with a unique identification number. Observers checked marked nests daily until they were destroyed by high flows or male bluehead chub stopped attending nests. Yellowfin shiner display brilliant breeding colors (i.e. red body color with yellow fins) while spawning on bluehead chub nests (Marcy et al., 2005), and yellowfin shiner spawn only when bluehead chub spawn or attend their nests (Wallin, 1989, 1992). Thus, we recorded an active nest when yellowfin shiner with breeding color were schooling or spawning on the nest. The number of active nests was recorded daily at each study stream.

Regional- and stream-scale environmental data were collected daily including precipitation (mm) and air temperature (°C) measurements from the nearest weather station (Clemson-Oconee County Airport Weather Station by the National Weather Service), approximately 10 km from the study area. Water temperature (°C) and level (m) were recorded hourly by deploying loggers (Model U20L-004, HOBO Onset Computer Corp.) at the downstream end of each stream. Stream flows were not gaged in any of our study streams, and we considered that water level represented temporal variation in stream flows.

2.3 | Statistical analyses

2.3.1 | Spawning synchrony among streams

The degree of reproductive synchrony among three streams was analyzed using the nonparametric Spearman's rank correlation test with a Bonferroni correction of a statistical significance level (adjusted $\alpha < 0.017$, or 0.05 divided by three pairwise comparisons). The test was based on the cumulative number of daily active nests between each pair of streams. Statistical significance was set at $\alpha < 0.05$ for all analyses that follow.

2.3.2 | Environmental effects on spawning

The link between daily spawning and environmental variables was examined by using time-series models. A generalized linear auto-regressive moving average (GLARMA) model (Benjamin, Rigby, & Stasinopoulos, 2003) was applied to assess the effect of

environmental variables on spawning periodicity. The GLARMA model includes auto-regressive moving average (ARMA) components to account for the serial dependence in time series data using regressors that are conditional on past values (Dunsmuir & Scott, 2015). Unlike the conditional ARMA model, the GLARMA model is a non-Gaussian state space model which can apply link functions (e.g. Poisson distribution), analogous to the generalized linear model (GLM), by using time-series explanatory variables to account for temporal variation in a response variable (Benjamin et al., 2003; Dunsmuir & Scott, 2015). Let Y_t represent a serial observation over time t ($t = 1, \dots, 89$: the number of daily observations in this study) and an array $(x_{t,k})$ containing regressor k (i.e. explanatory variables) at time t . Let $F_t = (Y_{1:t-1}; x_{1:t,k})$ be the past information on the response series and the past and present information on the regressors. For the Poisson GLARMA, the conditional distribution of Y_t given F_t is assumed to follow a Poisson distribution with mean μ_t :

$$Y_t | F_t \sim \text{Poisson}(\mu_t) \quad (1)$$

$$\log(\mu_t) = \alpha + \beta_k x_{t,k} + Z_t \quad (2)$$

where α is an intercept, β_k is a vector of regression coefficient of length k , and Z_t accounts for a serial dependence in the response process. The binomial GLARMA model assumes that the distribution of the Y_t given $x_{t,k}$ and F_t is denoted by:

$$P(Y_t = 1 | F_t) = p_t \quad (3)$$

$$\text{logit}(p_t) = \alpha + \beta_k x_{t,k} + Z_t \quad (4)$$

where $Y_t = 1$ denotes the presence of active nests and p_t is the probability of presence during time t . The GLARMA model includes auto-regressive (AR) and moving average (MA) components by specifying Z_t as follows:

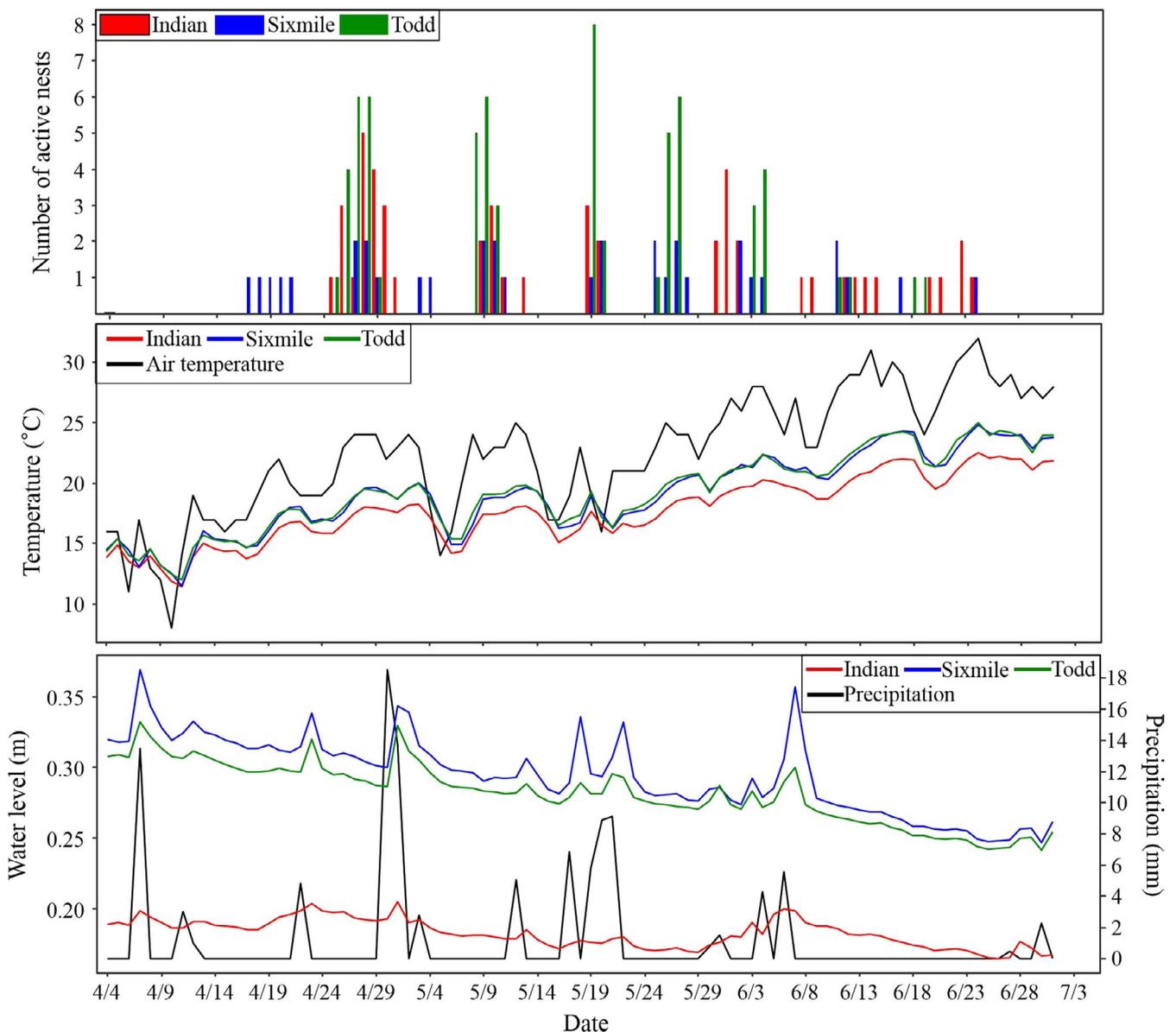


FIGURE 2 Time series plots of the number of active nests (top), temperature (middle), and water level and precipitation (bottom) from April 4th to July 1st in 2016

$$Z_t = \sum_{j=1}^{\infty} \gamma_j e_{t-j} = \sum_{j=1}^r \theta_j (Z_{t-j} + e_{t-j}) + \sum_{j=1}^q \theta_j e_{t-j} \quad (5)$$

where e_{t-j} is the predictive residual, γ_j is given as coefficients on ARMA term, and r and q are the orders of polynomial AR (θ) and MA (θ) terms respectively.

Prior to the GLARMA analysis, we conducted three steps of data examination and preparation. First, we restricted the analysis period to range from 7 days before the first nest was observed and until 7 days after the last nest was observed to focus on spawning periodicity and remove unintended influences that observations outside the spawning period may have on this time-series analysis. Second, we only selected in-stream variables such as water temperature and level as explanatory variables; water temperature was highly correlated with air temperature, and precipitation was only weakly correlated with precipitation (see Section 3). The variance inflation factor (VIF) was used to assess multicollinearity between water temperature and level. Pairwise VIF values in three streams were lower than three thus both explanatory variables were retained in all streams (O'Brien, 2007). Third, the GLM was fit to obtain initial values for the regression coefficient of explanatory variables and AR and MA terms, which were later used in the GLARMA analysis (Dunsmuir & Scott, 2015). Response variables were the daily number of active nests in Indian and Todd Creeks, thus the Poisson GLM was applied to both streams. The binary (presence/absence) response was used in the Binomial GLM for Sixmile Creek because the maximum daily number of active nests was two (single active nest on 17 days and two active nests on 9 days: Figure 2), and the Poisson GLARMA model did not converge. Fish typically have optimum breeding conditions bound by the lower and upper environmental thresholds (Falke, Bestgen, et al., 2010; King et al., 2016; Krabbenhoft et al., 2014), thus quadratic terms (in addition to linear terms) were included as predictors to account for a potentially unimodal response of spawning to environmental variables.

The GLARMA model was applied in each stream independently. Similar to the GLM, the Poisson GLARMA models were used for Indian and Todd Creek, and the Binomial GLARMA model was used for Sixmile Creek. The GLARMA models were fit using the Fisher Scoring iterative method and Pearson residuals were used to assess residual temporal auto-correlation. The initial AR and MA terms were chosen by the auto-correlation function (ACF) and partial auto-correlation function (PACF) plots using the residuals from the results of GLMs in each stream (Appendix S1). Lower orders of AR and MA terms were chosen based on the patterns and significant residuals in the ACF and PACF plots, and polynomial terms were selected to improve model fit (Dunsmuir & Scott, 2015). Candidate polynomial AR and MA terms were applied into GLARMA models, and were compared using Akaike's information criterion corrected for small sample size (AIC_c) and Akaike weights were used to identify the top-ranked and competing models (i.e. $\Delta AIC_c \leq 2$: Burnham & Anderson, 2002: Appendix S2). For the model diagnostics, the

Wald test was applied to test whether the serial dependent parameters (ψ) were equal to zero ($H_0: \psi = 0$ vs. $H_a: \psi \neq 0$), and the likelihood-ratio test was used to compare likelihoods between the GLARMA and GLM (Appendix S2). In addition, the ACF of Pearson residual plot was examined to evaluate residual temporal auto-correlation in GLARMA models (Appendix S3). Residual deviances of the Poisson GLARMA model were checked against the residual degree of freedom to assess evidence of overdispersion (Dunsmuir & Scott, 2015). Overdispersion was declared if residual deviance of the GLARMA model exceeded residual degree of freedom (Hilbe, 2007).

To facilitate interpretation of covariate effects in GLARMA models, explanatory variables were visually examined to discern whether spawning was correlated with their raw values or the rate of change over time. This analysis was similarly conducted using data ranging from 7 days before the first nest observed to 7 days after the last nest was observed in each stream. The rate of change was calculated as the difference between the present day versus the previous 1–3 days. Since the inferences varied only subtly among the intervals chosen, we reported results from the 2-day interval. The scatter plot was used to visualize the relationships between the daily number of active nests and raw value and rate of change of water temperature and level. Additionally, t tests were used to assess if water temperature and level and their rates of change differed between days with or without active nests in each stream.

All statistical analyses were conducted in the R version 3.5.1 (R Development Core Team, 2018), and GLARMA models were fit using the *glarma* package (Dunsmuir & Scott, 2015).

3 | RESULTS

3.1 | Environmental conditions

Water temperature increased gradually over the study period and highly correlated with air temperature in all streams (Spearman $\rho = 0.90$ – 0.92 , p -value < .001: Figure 2). Water temperature differed significantly among streams (one-way ANOVA: $F_{2, 183} = 6.5$, p -value = .002). Specifically, Indian Creek (mean = 17.7°C, range = 11.4–22.5) was colder than Sixmile Creek (mean = 19.1°C, range = 11.5–24.8) and Todd Creek (mean = 19.2°C, range = 12.0–25.0; Tukey's honestly significant difference post hoc test: p -value = .003 and .011 respectively), but there was no significant difference between Sixmile and Todd Creeks (Tukey's honestly significant difference post hoc test: p -value = .846). Precipitation was recorded on 18 days, and the mean daily value across these days was 6.01 mm. Water level generally declined during the study period (Figure 2). Water level was not correlated with precipitation (Spearman $\rho = 0.06$ – 0.17 , p -value = .13–.55), but higher water levels coincided with rain events (Figure 2). In addition, water level in Indian Creek (mean = 0.18 m, CV = 5.41) was more temporally stable than other streams (Sixmile Creek, mean = 0.29 m, CV = 9.31; Todd Creek, mean = 0.28 m, CV = 7.61).

3.2 | Spawning timing and periodicity

A total of 71 active nests (Indian Creek: 21, Sixmile Creek: 16, Todd Creek: 34) were located during the study period (Figure 2). The first active nests were observed on April 17th in Sixmile Creek (14.7°C) and on April 25th in Indian (15.8°C) and Todd Creek (17.1°C). Spawning was last observed on June 19th in Todd Creek and June 24th in Indian and Sixmile Creeks (Figure 2). More than fifty per cent of active nests were observed between April 25th and May 20th (Indian Creek, 51%; Sixmile Creek, 60%; Todd Creek, 65%) (Figure 2). Active nests were recorded when water temperature ranged between 14.7 and 24.8°C, but the range of temperature during the peak time (April 25th–May 20th) was narrower and varied by stream (Indian Creek, mean = 18.8°C, range = 15.8–18.1; Sixmile Creek, mean = 19.2°C, range = 17.6–20.5; Todd Creek, mean = 18.8°C, range = 17.1–20.4; Figure 2). Each nest was active for a median of 2 days (range = 1–4). Multiple active nests were typically documented on a single day in Todd Creek (median = 3 nests, range = 1–8), but a single active nest was most frequently located in Indian (median = 1 nest, range = 1–5) and Sixmile Creek (median = 1 nest, range = 1–2; Figure 2). Spawning was observed periodically (Figure 2) at median intervals of 4 days

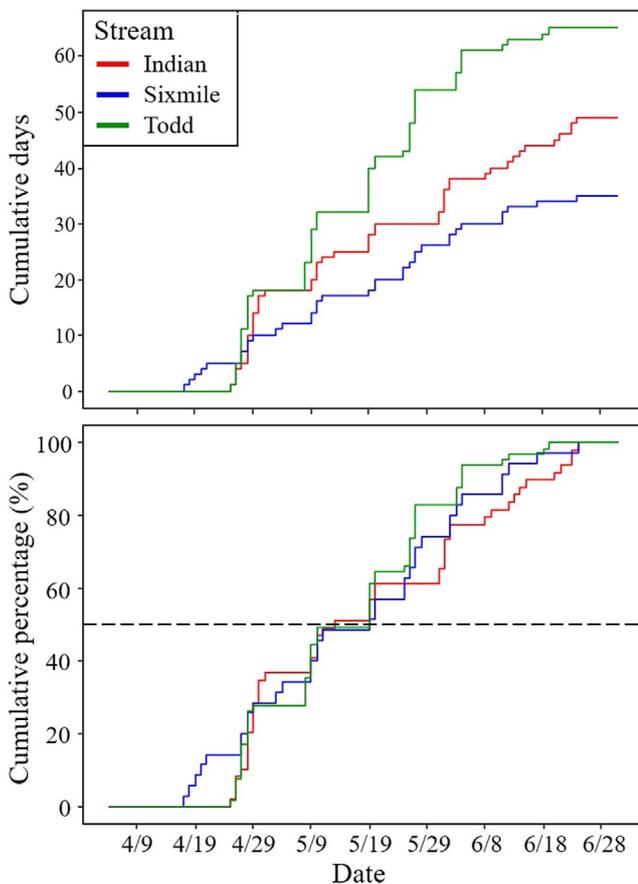


FIGURE 3 Cumulative days (top) and percentage (bottom) of active nests in each study site during the 2016 spawning season. Cumulative days were a sum of number of days that each nest was active up to the observation date. The black dashed line indicates the mid-point (50%)

in Indian Creek (range = 1–10) and Sixmile Creek (range = 3–7) and 6 days in Todd Creek (range = 3–7).

3.3 | Spawning synchrony among streams

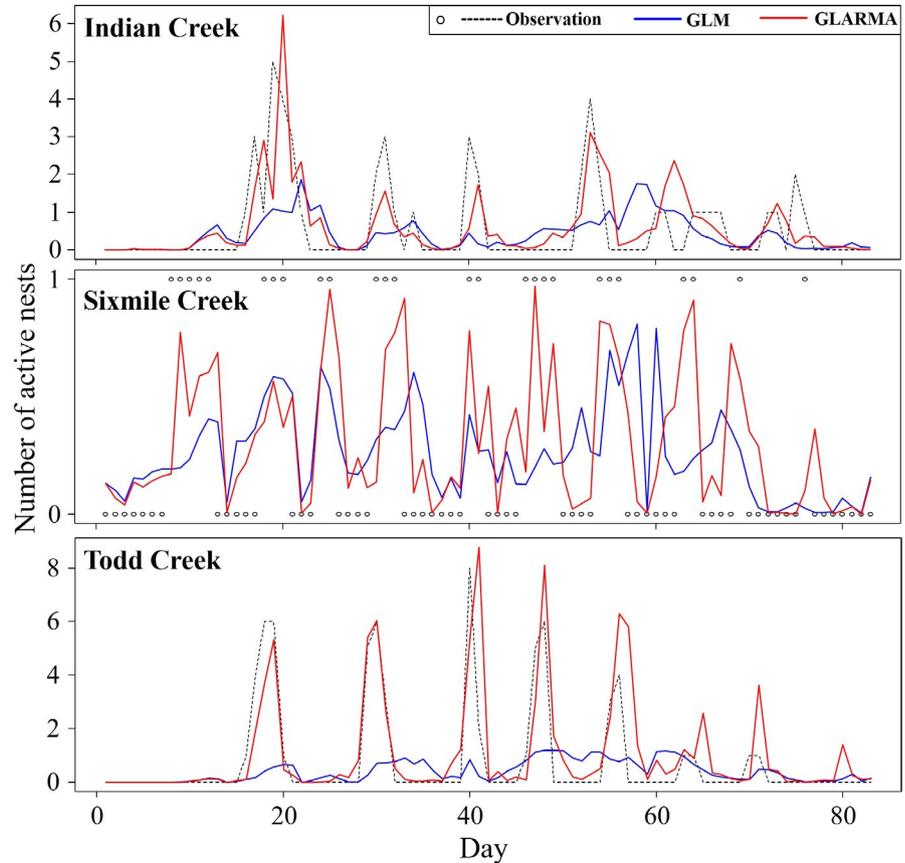
The total cumulative days that nests were active were 49 in Indian Creek, 35 in Sixmile Creek, and 65 in Todd Creek (Figure 3). The cumulative percentage of daily active nests indicated that the periodicity of spawning between all stream pairs was strongly and positively synchronized (Spearman $\rho = 0.99$, p -value < .001; Figure 3). Trends of water temperature and level were likely to affect local synchrony. In particular, spawning activity was hampered by increasing flows and declining temperatures caused by precipitation (May 1st in Indian and Todd Creeks, May 12th in Sixmile and Todd Creek, May 21st in all streams, and June 4th in Sixmile and Todd Creek; Figure 2).

3.4 | Environmental effects on spawning

The top-ranked GLARMA models explained the periodic pattern of spawning better than competing models and GLMs (Figure 4; Appendix S2). Residual autocorrelation was not observed in all top-ranked GLARMA models (Appendix S3). Additionally, the Poisson GLARMA models had no sign of overdispersion (Indian Creek, 75.4 on 76 degree of freedom; Todd Creek, 66.4 on 73 degree of freedom), thus we focus on the description of the top-ranked model in each stream (Table 2). Fish spawned more frequently with increasing water temperature (i.e. positive linear effects) in all streams (Indian Creek, coefficient = 11.734, p -value < .001; Todd Creek, coefficient = 8.887, p -value < .001; Sixmile Creek, 13.897, p -value = .019; Table 2), but up to a point (i.e. unimodal effects) with quadratic terms significant in Indian (coefficient = -15.340, p -value = .009) and Todd Creek (coefficient = -12.597, p -value < .001). Negative quadratic effects of water level were significant in Sixmile (coefficient = -10.206, p -value = .027) and Todd Creek (coefficient = -15.818, p -value = .021), indicating that fish spawned at the intermediate range of stream discharge but not in Indian Creek (Table 2).

Scatter plots showed that the number of active nests peaked at the intermediate range of water temperature in Indian and Todd Creeks, as supported by GLARMA models (Table 2; Figure 5). Fish spawned at higher water temperatures in Indian Creek (t test $t = -2.308$, $df = 74$, p -value = .024; Figure 5), but not in Sixmile (t test $t = -0.086$, $df = 65$, p -value = .932) and Todd Creek (t test $t = -0.682$, $df = 52$, p -value = .498). Notably, the majority of spawning occurred when water temperature had risen over the previous 2 days in all streams (Indian Creek, t test $t = -2.331$, $df = 54$, p -value = .024; Sixmile Creek, t test $t = -5.063$, $df = 70$, p -value < .001; Todd Creek, t test $t = -3.149$, $df = 33$, p -value = .004), as indicated by the range of positive rate of change not overlapping or just barely overlapping with zero on days when spawning was observed (Figure 5). Water level had a significant effect on the number of active nests in GLARMA models (Table 2), but there was no significant difference between days with and without active nests (Indian Creek, t test $t = -0.850$, $df = 51$, p -value = .399; Sixmile Creek, t test $t = -0.008$, $df = 73$,

FIGURE 4 Observed versus expected count (Indian and Todd Creeks) and presence (Sixmile Creek) of active nests using GLM and GLARMA models



p -value = .994; Todd Creek, t test $t = 0.520$, $df = 51$, p -value = .606; Figure 6). Similarly, the rate of change of water level was not significantly different across all streams (Indian Creek, t test $t = 0.048$, $df = 52$, p -value = .633; Sixmile Creek, t test $t = 1.622$, $df = 79$, p -value = .108; Todd Creek, t test $t = 1.123$, $df = 56$, p -value = .225; Figure 6). However, a notable pattern was that spawning concentrated when there was little change in water level in Sixmile and Todd Creeks, as indicated by narrower ranges of water level changes centered around zero on days with active nests (Figure 6). This result indicated that flow stability was an important criterion for bluehead chub to spawn and flow fluctuation caused by precipitation hampered spawning (Figure 2).

4 | DISCUSSION

Bluehead chub and yellowfin shiner displayed a periodic spawning pattern that was synchronized among local streams. Water temperature affected the timing of spawning in all streams, whereas effects of water level varied by stream. Intriguingly, spawning concentrated when temperature had increased over the previous two days and flow changed little (i.e. under stable flow conditions). Our findings elucidate how multiple environmental drivers determine daily spawning periodicity of stream fishes and concur with previous studies that document temperature and flow as key factors in the timing of spawning (Forsythe et al., 2012; King et al., 2016; Krabbenhoft et al., 2014; Reid, 2006) and reproductive synchrony

triggered by regional drivers such as weather patterns (Chevalier et al., 2014; Engen & Saether, 2005; Warren et al., 2012).

Our findings suggest that water temperature is likely a primary environmental cue for spawning. A fish species may spawn across a range of stream temperatures (Falke, Fausch, et al., 2010; Krabbenhoft et al., 2014). Likewise, bluehead chub and yellowfin shiner spawned when water temperature ranged between 14.7 and 24.8°C in our study, and a similar range (16–23°C) was reported in a study conducted in the same major basin (i.e. Savannah River Basin; Wallin, 1989, 1992). Water temperature in Indian Creek was colder than the other streams (Figure 2). However, the mean and range of water temperature when fish spawned were similar to the other streams because stream temperature on days with active nests was significantly higher than that on days without active nests in Indian Creek but not in others (Figure 5), supporting the idea that spawning is bound by the lower and upper thermal thresholds. Additionally, the peak spawning occurred in a narrower range of temperature (15.8–20.4°C), and it was nearly identical to a study of bluehead chub (15–21°C) conducted in various river basins located in Georgia, North Carolina, and Virginia (Sabaj et al., 2000). Consistent ranges of water temperatures among studies suggested that stream temperature provided a thermal template that defined their spawning period. However, this alone could not address the observed periodic patterns within the spawning season. The timing of spawning of fishes is also affected by a short-term increase in water temperature (Forsythe et al., 2011, 2012; Paragamian & Wakkinen, 2002). For instance, reproductive activities of lake sturgeon (*Acipenser fulvescens*)

Stream	Term	Parameter	Estimate	SE	Z-ratio	p-value
Indian Creek	AR	1	0.482	0.071	6.757	<.001
	AR	16	-0.432	0.110	-3.941	<.001
	Intercept		-1.836	0.437	-4.199	<.001
	Water temperature	Linear	11.734	5.010	2.342	.019
	Water temperature	Quadratic	-15.340	5.900	-2.600	.009
	Water level	Linear	3.941	2.881	1.368	.171
	Water level	Quadratic	-0.580	1.643	0.353	.724
Todd Creek	AR	2	0.274	0.101	2.716	.007
	AR	4	-0.573	0.089	-6.446	<.001
	AR	6	-0.537	0.107	-5.007	<.001
	AR	15	0.136	0.055	2.494	.013
	MA	1	0.712	0.040	17.998	<.001
	Intercept		-2.195	0.331	-6.641	<.001
	Water temperature	Linear	8.887	2.614	3.400	<.001
	Water temperature	Quadratic	-12.597	2.319	-5.432	<.001
	Water level	Linear	-3.746	3.770	-0.993	.321
	Water level	Quadratic	-10.206	4.953	-2.222	.027
Sixmile Creek	AR	3	-0.199	0.083	-2.401	.016
	AR	6	-0.297	0.107	-2.777	.005
	AR	11	-0.822	0.116	-7.101	<.001
	MA	1	1.070	0.321	3.334	<.001
	Intercept		-1.455	0.407	-3.572	<.001
	Water temperature	Linear	13.897	5.940	2.337	.019
	Water temperature	Quadratic	3.467	4.087	0.848	.396
	Water level	Linear	15.259	7.033	2.170	.030
	Water level	Quadratic	-15.818	6.827	-2.317	.021

Note: Significant environmental covariates (p -value < .05) are shown in bold. Abbreviations: AR, auto-regressive term; MA, moving average term.

and white sturgeon (*A. transmontanus*) are strongly associated with a temporal change in water temperature; the onset of spawning is associated with the rate of increase in temperature but a rapid decline causes fish to leave nesting sites (Forsythe et al., 2012; Paragamian & Wakkinen, 2002). Similarly, the majority of spawning occurred when water temperature had risen by 2.0°C over the previous 2 days, while there was little evidence that temperatures themselves differed between days with or without active nests in Sixmile and Todd Creeks (Figure 5).

Whereas short-term warming in stream temperature triggered spawning, bluehead chub and yellowfin shiner were more likely to spawn under stable flow conditions over the course of two days. Flow plays a vital role in providing optimal habitat conditions for spawning (King et al., 2016; Peoples et al., 2014). Bluehead chub prefer to spawn in distinct mesohabitats (e.g. pool tails and shallower runs covered by gravel and pebble; Jenkins & Burkhead, 1994; Peoples, Tainer, & Frimpong, 2011) and microhabitats based on depth and velocity (Bolton et al., 2015; Peoples et al., 2016). Specifically, the range of water velocity is important for depositing eggs (Maurakis, Woolcott, & Sabaj, 1992) and shallower depths

TABLE 2 Parameter estimates of the Generalized Linear Auto-Regressive Moving Average model (GLARMA) to predict spawning periodicity of bluehead chub in three study streams

enable bluehead chub to avoid large-bodied predators (Bolton et al., 2015). Male bluehead chub move thousands of pebbles to construct nests as a form of parental care (Wallin, 1989, 1992). Stable flows may make it easier for male bluehead chub to locate and maintain suitable nesting sites, whereas higher fluctuations following precipitation events could hamper spawning activities. This conclusion was further supported by the finding that water level was not significant in the most hydrologically stable creek (Indian Creek: Table 2), but was significant in the other two creeks that experienced higher variation in flow (Figure 6).

Environmental influences on spawning led to reproductive synchrony among local streams (Figure 3), driven primarily by short-term increase in water temperature. Daily trends of water temperature and level were linked to weather conditions (i.e. air temperature, precipitation), which was most likely responsible for local synchrony. Our data also point to potential synchrony in spawning within the same stream, as inferred from temporarily clustered spawning patterns. This conclusion should be only incomplete because individuals could not be uniquely identified during spawning and we could not discern if individuals spawned

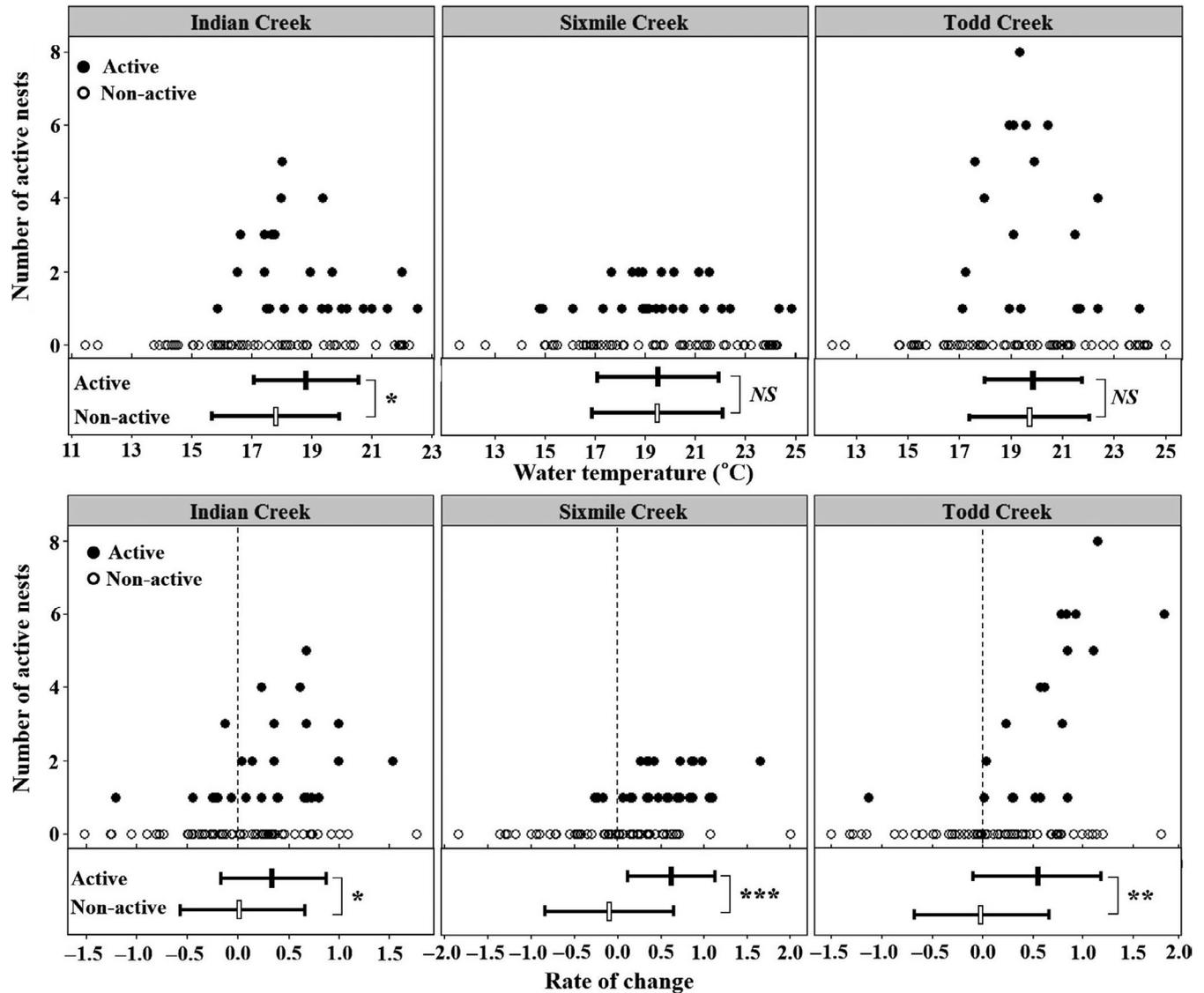


FIGURE 5 Scatter plots showing relationships between the daily number of active nests and water temperature (top) and its rate of change over 2 days (bottom). Each scatter plot is accompanied by error bars that summarizes the mean and standard deviation on days with or without active nests with *t* test results (NS, *p*-value \geq .05; **p*-value $<$.05; ***p*-value $<$.01; ****p*-value $<$.001)

repeatedly in a single spawning season. Reproductive synchrony in the same local habitat is prevalent across many taxa, including mass spawning of corals, plant seeding, and spawning aggregations of fishes (Harrison et al., 1984; Kelly & Sork, 2002; Koizumi, Yamamoto, Nomoto, & Maekawa, 2008). Reproductive synchrony within the same stream, but not among isolated streams, may be driven not only by abiotic cues but also by intra-specific interactions among individuals (Bruch & Binkowski, 2002; Chevalier et al., 2014; Engen & Saether, 2005; Forsythe et al., 2011; Harrison et al., 1984; Koizumi et al., 2008). Reproductive synchrony within the same streams may have evolved as an adaptive strategy to maximize offspring survival (Harrison et al., 1984; Kelly & Sork, 2002), a topic which is beyond the scope of this paper but warrants further investigations.

The GLARMA model was a useful framework to account for daily spawning periodicity of bluehead chub and yellowfin shiner. Unlike

other time-series models using ARMA components, the GLARMA model incorporates polynomial AR and MA terms that increase flexibility when analyzing serial data (Benjamin et al., 2003; Dunsmuir & Scott, 2015). Bluehead chub and yellowfin shiner exhibited periodic spawning patterns, but intervals of spawning events varied over the spawning season (Figure 3). Furthermore, although the peak timing was May, fish still spawned intermittently until late June (Figure 2). Despite these complex serial data, the GLARMA model was capable of accounting for spawning periodicity (Table 2; Figure 4). Data on spawning timing of fishes are frequently collected to estimate reproduction, larval emergence, and migration at daily, monthly, or annual intervals (Catalano & Bozek, 2015; Forsythe et al., 2011; Krabbenhoft et al., 2014; Reid, 2006; Straight et al., 2015). Several models (e.g., a generalized linear mixed model with time-series components) have been successfully applied to study the reproductive timing when fish spawn intensively in a short period or exhibit a

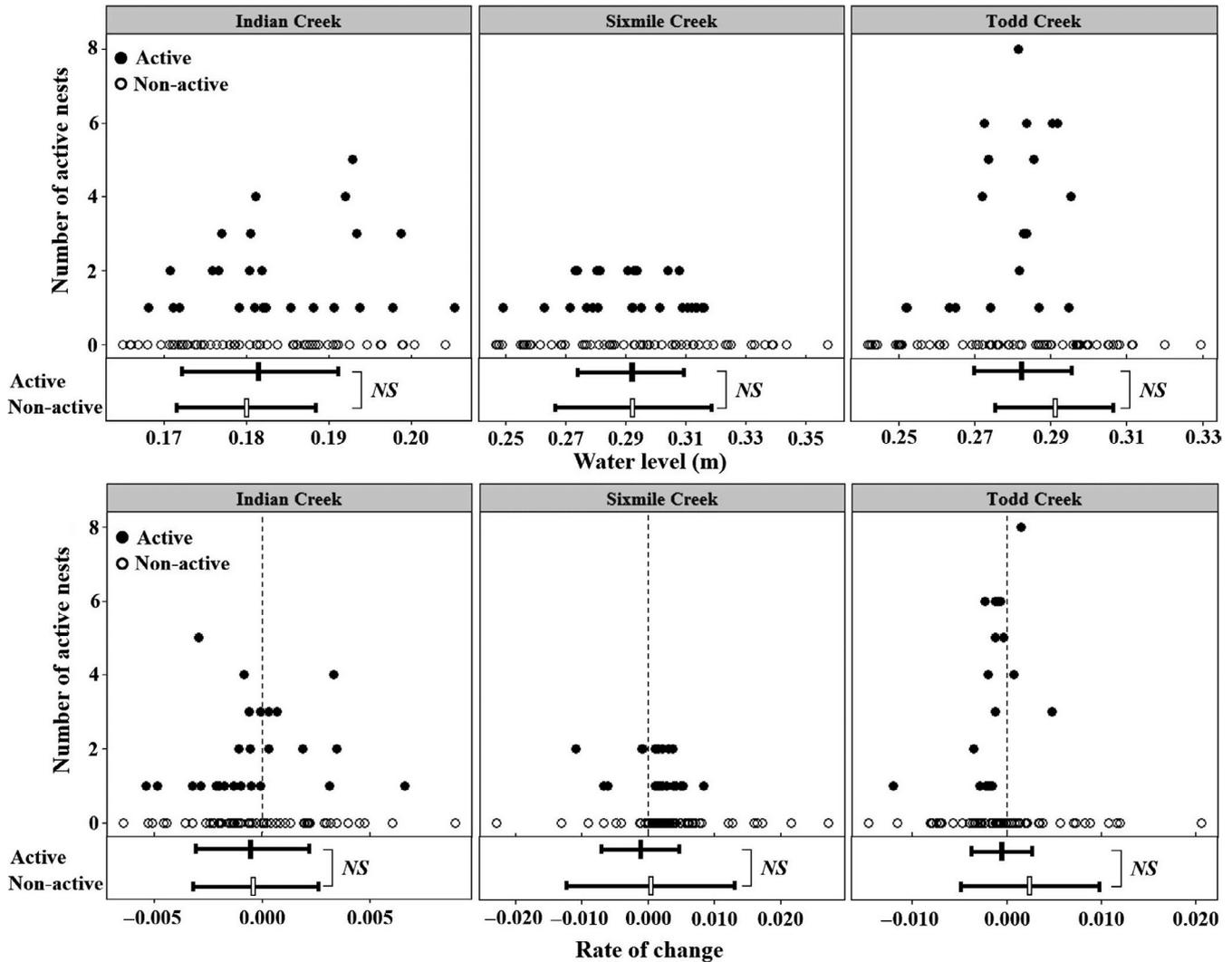


FIGURE 6 Scatter plots showing relationships between the daily number of active nests and water level (top) and its rate of change over 2 days (bottom). Each scatter plot is accompanied by error bars that summarizes the mean and standard deviation on days with or without active nests with *t* test results (NS, *p*-value $\geq .05$; **p*-value $< .05$; ***p*-value $< .01$; ****p*-value $< .001$)

consistent periodic pattern (Falke, Fausch, et al., 2010; Forsythe et al., 2012; Straight et al., 2015). However, if a time-series data set deviates from a regular pattern, the GLARMA model can noticeably improve model fit. A potential caveat of the GLARMA model lies in interpreting ecological significance of their covariates and inherent structural components (i.e. AR and MA terms). To facilitate ecological understanding, we found it useful to start with a simpler model (e.g. GLM) and add complexities gradually, complemented with visualization of raw data (Figures 5 and 6).

Nest association among freshwater fishes is common throughout North America (Johnston, 1994a). We never observed yellowfin shiner spawning solitarily without bluehead chub, a phenomenon similarly observed by Wallin (1989, 1992). Spawning timing of nest associates has evolved concurrently with host species, thus understanding the reproductive ecology of keystone species is crucial for community- and ecosystem-wide conservation (Johnston, 1994b; Peoples et al., 2015; Peoples & Frimpong, 2016; Vives, 1990). Our findings demonstrate that daily variation in

environmental variables affects spawning periodicity of bluehead chub and their nest associate (i.e. yellowfin shiner). Consequently, anthropogenic activities and climate change that disrupt the daily environmental patterns may affect spawning periodicity and population viability of multiple species (Falke, Bestgen, et al., 2010; King et al., 2016; Krabbenhoft et al., 2014; Lohse, Newburn, Opperman, & Merenlender, 2008; Peoples et al., 2014). Frequent changes in stream discharge in flow-regulated rivers (e.g. hydroelectric dams) may not provide an optimal range of water depth and velocity for a sufficiently long period, preventing successful reproduction of bluehead chub (Kemp, 2017; Peoples et al., 2014; Poff et al., 1997). Modified land cover (i.e. impervious surface) leads to flashier flow and thermal regimes, which causes reproductive failures (Kemp, 2017; Lohse et al., 2008; Steel et al., 2017). Anthropogenic stressors are likely to act synergistically with climate change to affect spawning phenology of hosts and associates (Bestgen et al., 2006; Morissette et al., 2009; Warren et al., 2012). Knowledge of reproductive periodicity associated with environmental cues is

paramount as we attempt to conserve stream fish assemblages in the face of multiple anthropogenic stressors.

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DATA AVAILABILITY STATEMENT

The data set that support the findings of this study are available from the corresponding author upon reasonable request.

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