



Elevated Temperatures Shorten the Spawning Period of Silver Carp (*Hypophthalmichthys molitrix*) in a Large Subtropical River in China

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Global warming is influencing the life history traits of fishes globally. However, the impacts of elevated temperature on fish reproduction are diverse in different regions. Previous studies have revealed that the spawning timing of silver carp (*Hypophthalmichthys molitrix*) in the Pearl River, in China, has changed over the past decade. However, few studies have explored the potential reasons, which are critical for determining fishing-moratorium periods and developing sustainable fisheries. The current study used discharge suitability index (DSI), temperature suitability index (TSI), correlation and time-series analyses to determine (i) the optimal discharge and temperature for silver carp spawning; (ii) relationships among the thermal regime, hydrological parameters, and spawning timing based on an 11-year time-series dataset. Our results indicated that the most suitable discharge and temperature for silver carp spawning were 13,000–15,000 m³/s and 25–26°C, respectively. The start date of spawning fluctuated with a slight tendency to delay, while the spawning peak and end date obviously occurred earlier during the study period. Correlation analyses suggested that the increasing average temperature between January and March likely caused the initial spawning delay. Moreover, elevated temperatures in August and September probably promoted the anticipated end of silver carp spawning. However, increases in discharge did not significantly correlate with the start of spawning but were significantly and positively correlated with the spawning peak. These results indicated that elevated temperatures shorten the spawning period of silver carp in the Pearl River. Moreover, the initial spawning of silver carp seems to be triggered by temperature rather than changes in discharge; flow pulses can probably create more suitable spawning niches for *H. molitrix*. This study enhances our understanding of the effect of warming on fish reproduction in subtropical regions.

Keywords: fish reproduction, thermal regime, fish larvae, Pearl River (China), hydrological regime

INTRODUCTION

Global warming is a critical concern in spawning ecology of fishes, especially in freshwater (Alix et al., 2020; Zhang et al., 2021). By 2017, the Earth's surface temperature had increased by approximately 1.0°C relative to pre-industrial (1850–1900) levels, with average temperatures rising by 0.2°C per decade over the past three decades (IPBES, 2019). It is predicted that temperatures will rise even faster over the next 25 years than it did over the previous two decades (Smith et al., 2018). The impact of warming is likely to be stronger in freshwater than in terrestrial and marine systems, because discrete ecosystem boundaries in rivers limit fish migrations to follow optimal temperature conditions (Perry et al., 2005; Chen et al., 2011). More specifically, fish reproduction, controlled by the brain-pituitary-gonadal axis, may be more sensitive to warming than fish biodiversity, species interactions, and distributions (Walther et al., 2002; Miranda et al., 2013).

Determining the impact of global warming on fish spawning (e.g., spawning time) is challenging, since spawning characteristics are also regulated by other factors such as hydrographic parameters, spawning population stocks (Gillet and Dubois, 2007; Paumier et al., 2020). Generally, warm temperature and increases in river discharge can trigger spawning initiation (Yu et al., 2018), while spawning stock abundance mainly determines the interannual variability in larvae production (Glover et al., 2020). However, in some cases (e.g., a cold winter), temperature and river discharge affect larval abundance of some species (e.g., *Clupea harengus membras*) more significantly than spawning stock size (Ojaveer et al., 2011). Temperature and natural river floods can also affect oviposition amount and hatchability (O'Brien et al., 2012; Garcia et al., 2013; Wakefield et al., 2015). Therefore, understanding the influences of changes in temperature and hydrological conditions on fish reproduction is essential to preserving fish resources and developing sustainable fisheries practices.

For freshwater fish species that form spawning aggregations, understanding how global warming and other factors influence their spawning time is of great interest, since such information can be vital for determining management policies such as closed fishing seasons (Tuz-Sulub and Brulé, 2015; van Overzee and Rijnsdorp, 2015). Mature fishes that form transient aggregates to spawn at specific times and places are productivity hubs and vulnerable to overfishing (Erisman et al., 2017). Generally, the timing of spawning is influenced by the age of the spawning fish, water temperature, and hydrological conditions (Wang et al., 2014; Li et al., 2020). The age of mature fish slightly influences the spawning time, in that large individuals tend to produce eggs later than small ones (Gillet and Dubois, 2007; Gordo and Carreras, 2014). Low-temperature can delay fish spawning by inhibiting vitellogenesis or reducing the mature fish size (Kjesbu, 1994; Carscadden et al., 1997; Wang et al., 2014), although low temperature may contribute to earlier spawning migration in temperate fish species (Sims et al., 2004). Extreme high temperatures seem to be more readily impair or even quit some fish (e.g., *Odontesthes bonariensis*) spawning by inhibiting gene expression throughout the brain-pituitary-gonad

axis (Miranda et al., 2013). Hydrological conditions such as flood peaks during spawning seasons can promote fish spawning by favoring gonad development (Bailly et al., 2008), stimulating spawning migration (Thorstad et al., 2008), generating eddies that promote fertilization (Yi et al., 1988), and assisting the eggs and larvae in drifting downstream (Zhang et al., 2018).

Silver carp (*Hypophthalmichthys molitrix*) is a common freshwater fish that forms large spawning aggregations and is widely distributed in Asia, especially in China's rivers. As one of the four major Chinese carp, it is a commercially important fish species in the Pearl River in southern China, accounting for about 13.6% of the total weight of the catches (Zhang et al., 2020). Mature silver carp form transient aggregations in spawning grounds in flood seasons and produce semi-buoyant eggs that drift with the flow for hundreds of kilometers in Asia (Yi and Liang, 1964; Zhang et al., 2000). Spawning characteristics of silver carp populations around the world demonstrated high local adaptation. Their spawning timings vary slightly in different regions: mid-May to the beginning of July in the Caspian Basin (Abdusamadov, 1987); from mid-May to mid-June in Arkansas (Freeze and Crawford, 1983); from June to early August in the Amur River (Gorbach and Krykhtin, 1989); from May to August in the Yangtze River (Zhang et al., 2000); and early April to early October in the Pearl River in China (Shuai et al., 2018). In China, some researchers consider the occurrences of silver carp eggs and larvae to be stimulated by high water discharge (Shuai et al., 2018; Yu et al., 2018). However, this fish can reproduce in the Wabash River without changes in discharges (Coulter et al., 2016). Notably, the spawning of silver carp in China is impacted by changes in thermal and hydrological regimes caused by the construction of dams (Wang et al., 2014; Li et al., 2016). In general, thermally stratified reservoirs releasing hypolimnetic water could reduce the temperature below large dams (Preece and Jones, 2002; Wang et al., 2014), while small surface-release dams could increase downstream temperatures by releasing warm epilimnetic water (Lessard and Hayes, 2003).

Currently, we lack a clear understanding of the impacts of global warming and other factors upon the spawning characteristics of silver carp in one of its largest habitats, the Pearl River in China (Shuai et al., 2018). First, there is a debate on the change of spawning timing of silver carp (delayed vs. advanced) in the Pearl River. Based on fish larvae data from 2006 to 2008, Tan et al. (2010) reported silver carp spawning delays in the Pearl River. In contrast, Shuai et al. (2018) reported that the spawning peak of this fish occurred at an earlier date from 2006 to 2013 in the same region. The spawning processes of fish have natural fluctuations, and long-term data are required to reveal the dynamics. Second, few studies have examined the possible reasons that drive the changes in spawning characteristics of silver carp in this river (Shuai et al., 2016).

The present study uses a long time-series dataset (2006–2013 and 2017–2019) to reveal the changing spawning characteristics of silver carp in the Pearl River and the underlying drivers. We focus on answering the following three questions: (1) what are the temperature and hydrological requirements for spawning of silver carp in the river; (2) how has their spawning timing varied (delayed or advanced) over the past decade; (3) which factors

(e.g., global warming, river discharge) were mainly correlated with such variation?

MATERIALS AND METHODS

Study Area

The Pearl River is the largest river in southern China, with a total length of 2,214 km and a mean annual discharge of $3.3 \times 10^{11} \text{ m}^3$. The sampling location, i.e., Zhaoqing section, is in the lower reach of the Pearl River, about 180 km upstream from the estuary (Figure 1). The annual average air temperature, annual rainfall, and annual discharge of this section are about 22.0°C, 1,644.5 mm, and 6,810 m³/s, respectively (Lu, 1990). There are 76 fish species recorded in the lower reach of the Pearl River, excluding the estuary area (Zhang et al., 2020). Over the past century, 18 spawning grounds of silver carp have been reported in the middle and upper reaches of the Pearl River (Committee of Pearl River Fishery Resources Investigation, 1985), and approximately 26 dams had been built near the spawning grounds by 2007. Our long-term monitoring results (unpublished data), along with a recent study (Gao et al., 2020), indicate that only the spawning grounds in the lower reaches of the tributary Liujiang River and the Laibin–Pingnan section of the mainstream still exist after 2007.

For our samples, the spawning grounds are located in the Guiping–Pingnan section, estimated by the development periods of captured larvae and water velocity (Pearl River Water Resources Commission, unpublished data). Eleven dams have been constructed in the mainstream of the Pearl River. All these dams were completed before 2005 and are located at the upper reaches, except for two downstream dams: Changzhou Dam and Datengxia Dam (Chen et al., 2018). The Changzhou Dam is a low head dam (height < 30 m, highest water level = 16 m) built in 2007 with only a daily discharge regulation. The Datengxia Dam began to impound in 2020, with a maximum water level of 61 m expected in 2023. Taken together, all large dams were located in the headwater and upper reaches of the Pearl River before 2019, far away from the current silver carp spawning grounds. Therefore, the impoundment would not influence the water temperature in the current spawning grounds during the study period (2006–2019).

Data Collection

We sampled three times a day (06:00–08:00, 13:00–15:00, and 19:00–21:00) every other day throughout the year. Larval fish were collected using a pyramid trap net (mesh size = 0.5 mm, length = 6 m). The net had a rectangular mouth (width × height: 1.5 m × 1.0 m), and the end opened to a larval collection cage (0.8 m × 0.4 m × 0.4 m) (Shuai et al., 2018). A cup-type flowmeter (LS45-2) was fixed at the net mouth center to measure the water volume flowing through the net. The net was submerged in the water with mouth open and facing the river flow. The net position would change slightly with the rise and fall of the water level, but it was kept 10–15 m away from the bank, where the flow velocity was approximately 0.3 m/s. Sampling was initially conducted at S1 (23°2′40″ N, 112°27′5″ E) from 2006 to 2013. But the location

was changed to S2 (23°9′54″ N, 112°16′58″ E, about 28 km upstream of S1) from 2017 to 2019, because cargo ships anchored near S1 (Figure 1). No samples were collected from 2014 to 2016.

Larvae samples were kept in a 5% formalin solution immediately after collection. The larvae of silver carp were identified (based on morphological characteristics) and counted by an experienced researcher in the laboratory (Yi et al., 1988). The abundance of larvae was calculated as the number of larvae per 24 h. The collected silver carp larvae were mainly at two developmental stages: the emergence of air bladder and one-chamber air bladder. Spawning dates of larvae were estimated using back-calculation methods from the captured dates (Yi et al., 1988). The spawning date of larvae was defined as the day of spawning occurrence.

We collected daily water temperatures and discharges at the Dahuangjiangkou (DHJK) gauge station to represent the environmental conditions of the spawning ground from 2006 to 2019 (Figure 1). Daily water temperature was collected by an automatic water temperature monitor, which recorded the temperature at least four times a day. Daily river discharge (Dis) was obtained from the Pearl River Water Resources Commission.

Data Analysis

We back-calculated the earliest birth date of the captured larvae, date of the spawning peak, and the end date of spawning by subtracting their development periods from the capturing dates of the larvae. These variables were used to describe the spawning period across our study. A previous study reported that the minimum discharge required to observe the occurrence of silver carp larvae was 10,000 m³/s in the Pearl River (Shuai et al., 2018). Thus, we used the first date of the discharge increased to 10,000 and 13,000 m³/s to index the possible flow-related reasons for changes in spawning timing. The minimum water temperature for silver carp spawning was 18°C (Yi et al., 1988). We counted the number of days with a temperature not lower than 18°C (hereafter, N₁₈) prior to the spawning season (from January to March). The threshold temperature for initial gonad development of adult silver carp was 15°C. We thus regarded the date when the water temperature reached 15°C during spring as the start date of stage IV (Wang et al., 2014). The end date of stage V denoted the date when larval abundance reached 5% of the total observed annual abundance. The cumulative temperature from stages IV to V was calculated by the sum of daily water temperature from stages IV to V in the year. The above variables and the mean monthly water temperature of the spawning ground were used to describe the changes in water temperature of spawning and cumulative temperature. Using the day of year calendar, the date is a sequential day number starting with day 1 on January 1.

The discharge suitability index (DSI) and the temperature suitability index (TSI) were applied to define the discharge and temperature suitability for silver carp spawning (Yu et al., 2018). The DSI was calculated as $DSI_i = \frac{D_i}{D_{max}}$, where DSI_i is the discharge suitability index of the discharge bin i , D_i is the value of larvae abundance weighted by the number of spawning

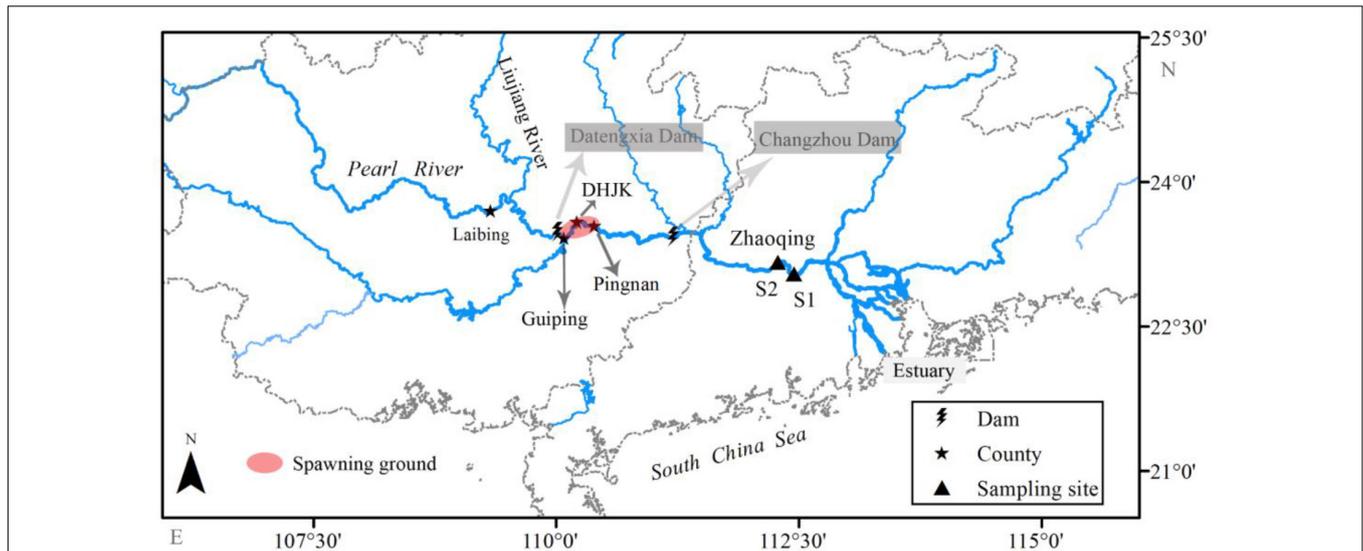


FIGURE 1 | Locations of dams near the spawning ground, sampling sites, and spawning ground of the collected larvae in the Pearl River (China). Sampling of larvae was conducted during 2006–2013 and 2017–2019. The daily temperatures and discharges of the spawning ground were collected from the DHJK gauge station from 2006 to 2019.

occurrences of the discharge bin i , D_{max} is the maximum value of larvae abundance weighted by the number of spawning occurrences across all discharge bins. The TSI was calculated as $TSI_j = \frac{T_j}{T_{max}}$, where TSI_j is the temperature suitability index of the temperature bin j , T_j is the value of larvae abundance weighted by the number of spawning occurrences of the temperature bin j , T_{max} is the maximum value of larvae abundance weighted by the number of spawning occurrences across all temperature bins.

All datasets of discharge, temperature, and abundance of larvae have normal distributions. The analysis were performed using Shapiro–Wilk tests in the “stats” package in R 3.6.1 (R Core Team, 2019). Pearson correlation analysis was used to determine the statistical significance of correlations between the spawning timing, discharge increase, and monthly temperature variables. The correlation analysis was performed using SPSS 13.0. Data for daily temperature (from January to March, August to September) was converted to weekly time-series for trend analysis using the “stats” package in R. The structural change in a time-series was detected by the chow test/F statistic using the “strucchange” package in R to plot the corresponding p -values (Zeileis et al., 2002). Differences were considered statistically significant at $p < 0.05$.

RESULTS

Discharge and Temperature Suitability for Silver Carp Spawning

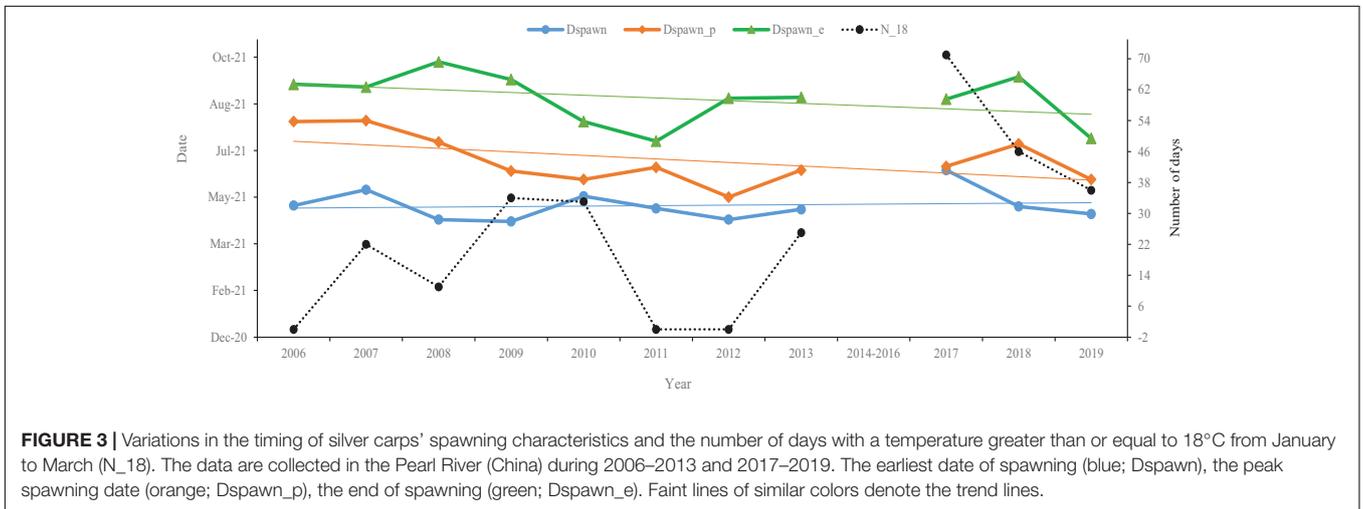
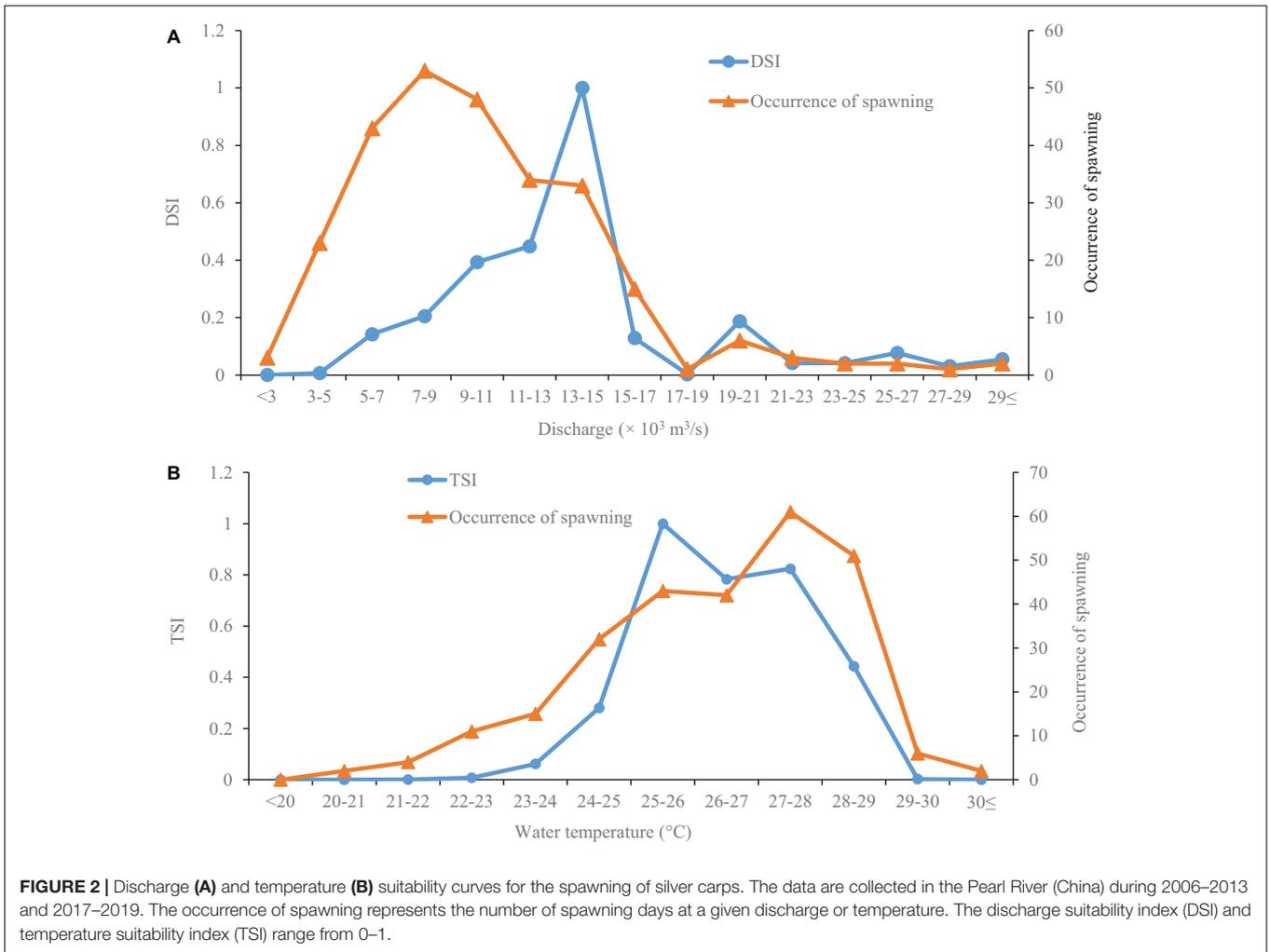
The silver carp started to spawn when the river discharge reached $2,310 \text{ m}^3/\text{s}$ (Figure 2A). The occurrence of spawning gradually increased with increased discharge before $7,000\text{--}9,000 \text{ m}^3/\text{s}$, and then decreased (Figure 2A). However, the highest discharge

suitability index (DSI) was observed at a discharge of $13,000\text{--}15,000 \text{ m}^3/\text{s}$ (Figure 2A). Moreover, there was a relatively lower peak of DSI at a discharge of $19,000\text{--}21,000 \text{ m}^3/\text{s}$ (Figure 2A).

The lowest temperature observed for the occurrence of silver carp spawning was 20.7°C (Figure 2B). The occurrence of spawning gradually increased with increasing temperature before $27\text{--}28^\circ\text{C}$, slowly declined after that, and then plummeted (Figure 2B). The temperature suitability index (TSI) stayed at a low level when the temperature was lower than 22°C , then sharply increased to the peak at $25\text{--}26^\circ\text{C}$. Then TSI rapidly declined and remained at a relatively stable level at temperatures of $26\text{--}28^\circ\text{C}$ after that; finally, it sharply decreased at temperatures above 28°C (Figure 2B).

Increased Temperature Shortening Spawning Period of Silver Carp Variation of Spawning Timing and Temperature Variables

Silver carp’ spawning began with the onset of floods at the end of April, peaking by June/July (Figure 3). The onset of spawning (spawning start; Figure 3) fluctuated from 2006 to 2017, with a delay of 55 days in 2017 relative to 2009 (the trough). By 2019, the onset of spawning was 47 days earlier than in 2017. In contrast, there were relatively stronger temporal trends in peak and end of spawning dates in that they were both earlier (Figure 3). For instance, peak spawning occurred earlier stepwise from 2006 to 2012, with the earliest peak occurring in 2012. Specifically, peak spawning was 80-days earlier in 2012 than 2006; in 2019, peak spawning was delayed by 18 compared to 2012. A similar temporal trend was also observed for the end of the spawning season, which tended to occur earlier stepwise from 2006 to 2011, with the earliest end date in 2011. This 2011 end date was 61-days earlier than 2006 and



only 3 days earlier than in 2019. Consequentially, the interval between the onset and the end of spawning decreased from 130 days in 2006 to 81 days in 2019. In contrast, the number of days temperatures were greater than or equal to 18°C from

January to March (N₁₈) generally increased. The N₁₈ first gradually increased from 0 in 2006 to 71 in 2017 (the peak), although there were two zeros in 2011 and 2012 and the peak value halved by 2019.

Correlation Between Flow and Temperature Variables and Spawning Timing

Pearson correlation coefficients between timings of silver carp spawning, thermal regime, and discharge variables are shown in **Table 1**. The number of days with a temperature greater than or equal to 18°C from January to March (N_{18}) and the mean temperature in January (T_1) were significantly and positively correlated with the initial spawning date (D_{spawn}) ($p < 0.05$), but significantly and negatively correlated with the days of spawning occurrence ($Occu$) ($p < 0.05$). Spawning peak (D_{spawn_p}) was significantly and positively correlated with (i) the end of spawning (D_{spawn_e}), (ii) the onset of the discharge increased to 10,000 m³/s (D_{dis_1}), and (iii) the cumulative temperature from stages IV to V ($D_{degdayIV-V}$) ($p < 0.05$). The D_{spawn_e} was positively correlated with the mean temperature in April (T_4 , $p < 0.05$), but negatively correlated with mean temperatures in August (T_8) and September (T_9) (both $p < 0.05$). The onset of the discharge increased to 13,000 m³/s (D_{dis_13}) was positively correlated with D_{dis_1} , $D_{degdayIV-V}$, and mean temperatures in January (T_1), April (T_4), May (T_5), and December (T_{12}) (all $p < 0.05$). The D_{dis_1} was positively correlated with D_{spawn_p} , D_{dis_13} , $D_{degdayIV-V}$, and mean temperature in May (T_5) (all $p < 0.05$). The $Occu$ was negatively correlated with D_{spawn} , N_{18} , and mean temperatures in January (T_1) and February (T_2) (all $p < 0.05$).

Interannual Fluctuations of Temperature

The temperature before the spawning season (from January to March) fluctuated and can be generally viewed from two periods: before and after 2012 (**Figure 4**). Prior to 2012, the temperature fluctuated without significant trends. After 2012, there was a warming trend by 2019 (all p values < 0.05 , except those in 2019). During 2006–2019, the average minimum and maximum temperatures from January to March increased by approximately 0.95 and 1.76°C, respectively.

The temperature from August to September (during the late period of the spawning season) can be viewed from three periods: 2006–2011, 2011–2015, and 2015–2019 (**Figure 5**). The temperature during the late period of the spawning season showed a generally significant increase trend between 2006 and 2011, when the minimum and maximum temperatures increased by approximately 1.61 and 2.39°C, respectively (**Figure 5**). In contrast, the temperature fluctuated without a significant trend from 2011 to 2015, when the minimum and maximum temperatures decreased by approximately 1.91 and 2.44°C, respectively. From 2015 to 2019, however, there existed another warming trend, and the minimum and maximum temperatures increased by approximately 1.73 and 2.49°C, respectively.

DISCUSSION

Discharge and Temperature Suitability for Silver Carp Spawning

Spawning environment suitability of fish in rivers is determined by hydrodynamic, geomorphological, and biological interactions that generate complex and localized linkages

(Alvarez-Mieles et al., 2019). The same species distributed over a variety of environmental conditions could probably demonstrate different ecological and hydrological requirements for spawning. The silver carp is distributed all over the world and has high local adaptation in reproduction characteristics. The initiation of silver carp spawning without changes in discharge was noted in the Wabash River, but the occurrences of eggs and larvae of this fish seemed to be triggered by flood pulses in the Yangtze River and Pearl River (Coulter et al., 2016; Shuai et al., 2018; Yu et al., 2018). The most suitable discharge and temperature of silver carp spawning habitats in the middle and lower reaches of the Yangtze River were 15,000–21,300 m³/s and 21–24°C, respectively (Yi et al., 1988; Yu et al., 2018). In contrast, the current study demonstrated that spawning in the Pearl River was initiated when discharge was much lower, approximately 2,310 m³/s, indicating that the fish can start to spawn without significant increases in discharge. The most suitable discharge for silver carp spawning in this study (13,000–15,000 m³/s) was also lower than that in the Yangtze River. The distance between the middle and lower reaches of the Yangtze River and those of the Pearl River is approximately 800 km, and there is a relatively high genetic distance between these two silver carp populations (Ji et al., 2009). Therefore, different hydrological requirements for silver carp spawning in those two large rivers in China could probably attribute to local adaptation.

Our study provides some new insights about the mechanisms of how river discharge affects the spawning characteristics of silver carp. First, our findings suggest that the spawning peak of silver carp, rather than the initial spawning, is probably triggered by flow increase in the Pearl River. This was evidenced by the fact that the start date of spawning was not significantly correlated with high discharge (D_{dis_1} and D_{dis_13}), while the spawning peak was significantly and positively correlated with high discharge (D_{dis_1}). Second, we showed that spawning occurrence of silver carp occurred at a relatively low discharge level, but with relatively lower daily larvae abundance. This finding is likely because only part of the mainstream is suitable for fish spawning when the discharge is at a low level. Then as the discharge gradually increases, some hydro-fluctuation zones become suitable for spawning, which explains why the highest average daily larvae appeared at high discharge. Flow pulses can probably create more suitable spawning niches for fish.

We indicate that the minimum and most suitable temperatures for silver carp spawning in the Pearl River were higher than those in the Yangtze River (Yi et al., 1988). Temperature can both affect the development of gonad and trigger spawning of fish (Morgan et al., 2013). In the present study, silver carp spawned at 20.7–30.1°C in the Pearl River, while they spawned at 18–28°C in the Yangtze River (Chen et al., 2009). Fish are very capable of finding habitat patches with suitable spawning temperature (Górski et al., 2010), which might explain why silver carp can spawn at a wide range of temperatures. The lowest temperature for silver carp spawning is 18°C indicating that water temperature is not a limiting factor in the Pearl River where average annual water temperature in spawning grounds is approximately 23°C (Yi et al., 1988). Although there is a wide range of temperatures for silver carp

TABLE 1 | Pearson correlation coefficients among thermal, discharge, and spawning timing variables in the Pearl River (China) during 2006–2013 and 2017–2019.

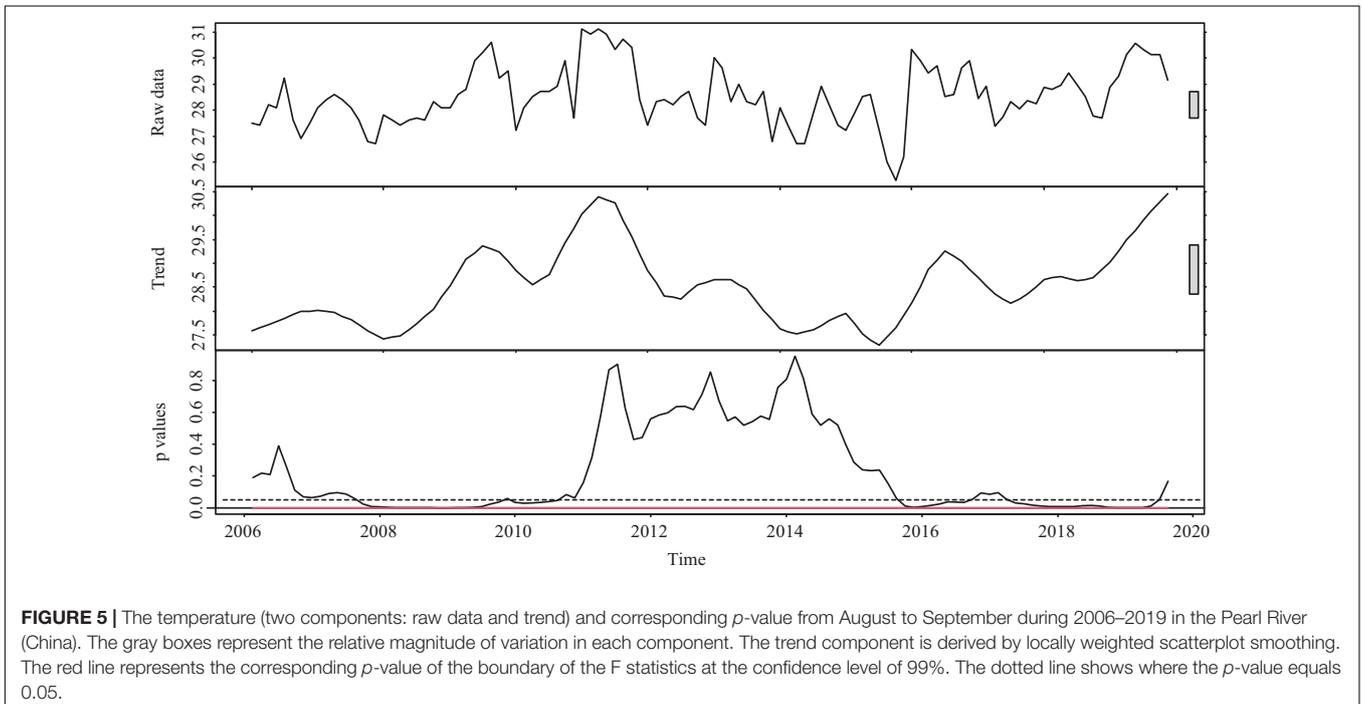
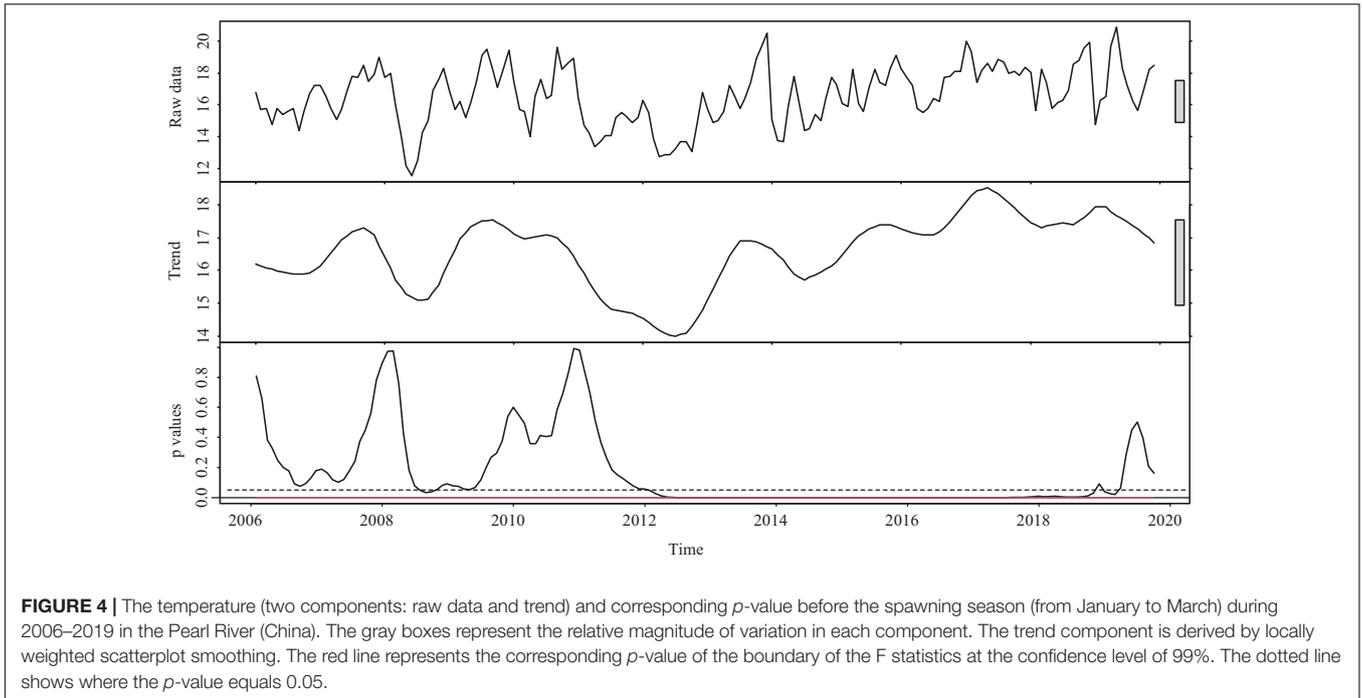
	Dspawn	Dspawn_p	Dspawn_e	Ddis_13	Ddis_1	N_18	DdegdayIV-V	Occu	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	
Dspawn	1																				
Dspawn_p	0.22	1																			
Dspawn_e	-0.11	0.53*	1																		
Ddis_13	0.46	0.37	0.23	1																	
Ddis_1	0.07	0.60*	0.34	0.75**	1																
N_18	0.59*	-0.13	0.02	0.52	0.12	1															
DdegdayIV-V	0.38	0.79**	0.45	0.75**	0.75**	0.26	1														
Occu	-0.56*	-0.09	0.40	-0.49	-0.21	-0.56*	-0.41	1													
T1	0.61*	0.24	0.25	0.76**	0.34	0.85**	0.62*	-0.54*	1												
T2	0.50	-0.03	-0.21	0.31	0.06	0.77**	0.19	-0.61*	0.55*	1											
T3	0.33	0.16	0.22	0.25	0.32	0.72**	0.29	-0.26	0.50	0.65*	1										
T4	0.02	0.27	0.55*	0.56*	0.44	0.46	0.50	-0.16	0.59*	0.30	0.49	1									
T5	0.20	0.28	0.35	0.70*	0.57*	0.26	0.44	-0.26	0.40	0.10	0.21	0.76**	1								
T6	0.17	0.26	0.09	0.31	0.27	0.38	0.17	-0.48	0.33	0.40	0.42	0.57*	0.65*	1							
T7	-0.06	0.19	-0.13	-0.29	0.11	-0.23	-0.14	-0.10	-0.44	0.02	0.27	-0.02	0.23	0.54*	1						
T8	-0.17	-0.26	-0.65*	-0.42	-0.29	-0.09	-0.47	-0.34	-0.32	0.07	-0.10	-0.47	-0.36	0.31	0.42	1					
T9	-0.34	-0.54	-0.63*	-0.31	-0.32	0.07	-0.44	-0.20	-0.15	0.25	-0.13	-0.41	-0.60*	-0.17	-0.22	0.67*	1				
T10	0.01	0.20	0.18	0.32	0.06	0.16	0.34	-0.13	0.34	0.45	-0.04	0.50	0.23	0.11	-0.38	-0.40	0.00	1			
T11	-0.06	0.26	-0.37	0.19	0.14	-0.20	0.20	-0.52	0.00	0.09	-0.44	-0.10	0.07	0.32	0.04	0.50	0.37	0.34	1		
T12	0.29	0.12	-0.32	0.58*	0.45	0.33	0.22	-0.37	0.40	0.32	0.04	-0.08	0.10	0.18	-0.25	0.23	0.33	0.08	0.46	1	

Dspawn, *Dspawn_p*, and *Dspawn_e* denote the earliest date of spawning, date of the spawning peak, and the end date of the spawning, respectively; *Ddis_1* and *Ddis_13* denote the first date of the discharge increased to 10,000 m³/s and 13,000 m³/s, respectively; *N_18* denotes the number of days with a temperature greater than or equal to 18°C from January to March; *DdegdayIV-V* denotes the cumulative temperature from stages IV to V; *Occu* denotes the days of spawning occurrence in a whole year; *T1*–*T12* denote the mean monthly water temperature of spawning ground across the year.

Significant results using a one-tailed test of significance are shown in bold.

**Significant at the 0.01 level.

*Significant at the 0.05 level.



spawning in the present study, the most suitable temperature was closely related to the flood season.

Increased Temperature Shortening Spawning Period of Silver Carp

We showed that the spawning period of silver carp has been gradually shortened, given the start date of spawning fluctuated

with a slight tendency to delay, while the spawning peak and end date obviously occurred earlier over the years. The start date of spawning of silver carp in the Pear River was largely regulated by water temperature, and warmer temperature prior to the spawning season can delay the spawning (Warren et al., 2012). The temperature-related changes in spawning timing are evident in a large number of freshwater fish species. For example, elevated water temperatures caused earlier spawning of rainbow

smelt (*Osmerus mordax*) in the Great Lakes (O'Brien et al., 2012). Warmer temperatures prompted earlier phenology that led to 17 species of larval fishes occurring earlier in the year in southern California (Asch, 2015). In the Yangtze River, a water temperature decline of 2–4°C between March and May resulting from the Three Gorges Dam impoundment led to a delay in silver carp spawning (Wang et al., 2014). However, the rising temperature can also delay fish spawning. It has been reported that the elevated summer temperature caused delayed spawning of brook trout (*Salvelinus fontinalis*) and reduce spawning activities in Rock Lake (Warren et al., 2012). Likewise, in our study, the results suggest that rising temperature from January to March (prior to the spawning season) may delay the spawning start date and decreases the occurrence of spawning. Given the uncertainty between 2014 and 2016 and the limited time-series points, our analyses and conclusions on the trend of Dspawn should be viewed with caution.

We indicated that water temperature increases before the spawning season may be the principal reason for the initial spawning delay in the present study. However, an observed delay in silver carp spawning in the Yangtze River was caused by water temperature declines before spawning (Wang et al., 2014). This could attribute to the reasons that when the mean temperature before the spawning season is lower than 15°C (threshold temperature for gonad development of silver carp), the increase of temperature may favor body growth and promoted gonad development (Yi et al., 1988). However, when the mean temperature substantially exceeds 18°C (threshold temperature for silver carp spawning), we speculated that the elevated temperature would increase metabolism, diverting energy from the fat accumulation, which is needed to complete gonad development, ultimately causing spawning delay (Luksiene and Svedang, 1997; Pankhurst and Munday, 2011). The mean water temperature before and during the spawning season in the spawning ground (DHJK) in the Pearl River were approximately 18 and 26°C, respectively. However, in the spawning grounds of silver carp in the Yangtze River, the mean water temperatures before and during the spawning period were approximately 13 and 21°C, respectively (Wang, 2016). These differences in ambient temperatures might be the principal reason for the divergence in warming effects on the onset of spawning. Although temperature-dependent adaptation allows parents to adjust the spawning time so that the larvae match the timing of the food source (Neuheimer et al., 2018), most studies consider that temperature-related spawning time variations can be attributed to changes in effective accumulated temperature (Robinson et al., 2010; Chezik et al., 2014; Hansen et al., 2017). The initiation of spawning in the present study did not significantly correlate with cumulative temperature. Although cumulative degree-day is an important factor affecting spawning initiation, it is not the main limiting factor in a subtropical river with high temperatures (Wang et al., 2014; Hansen et al., 2017).

The average temperature in August and September was significantly and negatively correlated with the end of spawning, indicating that high temperature in August and September promotes the earlier termination of silver carp spawning. The mean water temperature in the Pearl River between August and

September is approximately 28.6°C, which is higher than mean temperatures in other months. The optimum temperature for embryo development of silver carp is 22–28°C (Chen et al., 2009). Therefore, it is likely that silver carp in the Pearl River complete spawning early to avoid the adverse effects of rising temperature on embryo development in a freshwater system with limited thermal refugia (McCullough et al., 2009; Warren et al., 2012).

We revealed that the temperature before the spawning period (from January to March) and near the end of spawning (August and September) were increased during the study period. According to the relationships between the timing of spawning and thermal regime, this warming trend was likely the principal reason for the decreasing trend of the spawning time of silver carp in the present study. Given there was no large dam near the spawning ground during the sampling period, the temperature variation could not be attributed to dam impoundment. It has been reported that the Pearl River basin has been undergoing air temperature increases since the 1950s caused by climate change (Zhang et al., 2012; Tian and Yang, 2017). Therefore, the upward trend in the water temperature in the present study is most likely due to global warming.

CONCLUSION

The discharge suitability index for spawning of silver carp in the Pearl River showed a peak at the discharge of 13,000–15,000 m³/s. While the temperature suitability index peak was observed at temperatures of 25–26°C, the most suitable temperature for spawning was between 25 and 28°C. In general, the start date of spawning fluctuated with a slight tendency to delay, while the spawning peak and end date obviously occurred earlier during the study period. The initial spawning delay mainly attributed to the increasing temperatures between January and March. In addition, the end date of the spawning became earlier, likely due to elevated temperatures in August and September. Increases in discharge did not significantly correlate with the start of spawning but significantly positively correlated with the spawning peak. These results indicated that (i) the initial spawning of silver carp seems to be triggered by temperature rather than changes in discharge; (ii) flow pulses can probably create more suitable spawning niches for fish; and (iii) elevated temperature has shortened the spawning period of silver carp in the Pearl River.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

All experiments were performed under the approval of the Ethics Committee of Pearl River Fisheries Research Institute, Chinese Academy of Fishery Sciences. These policies align

with the Chinese Association for the Laboratory Animal Sciences and the Institutional Animal Care and Use Committee (IACUC) protocols.

AUTHOR CONTRIBUTIONS

YX: data analysis, writing—original draft, writing—review and editing, and visualization. XL: conceptualization, methodology, and funding acquisition. JY, SZ, ZW, and JL: sampling collection and data curation. YL: conceptualization, methodology, investigation, and supervision. All authors contributed to the article and approved the submitted version.

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