Distribution of *Botia superciliaris* (Günther, 1892) ichthyoplankton in the upper mainstem of the Yangtze River preimpoundment and postimpoundment of the upstream dam cascade

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**Funding information**
National Science Foundation of China, Grant/Award Numbers: 31570420, 31700346 and 31870398; Key Strategic Program, Chinese Academy of Sciences, Grant/Award Number: ZDRW-ZS-2017-3-2

**Abstract**
Dam cascades have been a major threat to fishes of the upper Yangtze River. The remaining lotic river segment of the upper mainstem between the Xiangjiaba Dam (XJD) and the Three Gorges Reservoir (TGR) may serve as a critical refuge for endemic fishes. We investigated distribution of ichthyoplankton *Botia superciliaris*, an endemic species, at three sections preimpoundment and postimpoundment of the XJD, that is, Yibin (close to the XJD), Zhuyang (in the middle of the segment), and Mudong (in the tail of the TGR). Preimpoundment of the XJD, larvae occurred in all three sections, and their abundance tended to be highest at Yibin and lowest at Mudong. Postimpoundment, larval abundance dramatically decreased in all three sections. In particular, no larvae were found at Yibin, and larval abundance tended to be higher at Zhuyang than at Mudong. Eggs were collected from all three sections, and those from Zhuyang accounted for over 90% of the total. Initiation of egg occurrence at Yibin was approximately 1 month later than at Zhuyang and Mudong. Water temperature was lower, and water transparency was higher at Yibin than at Zhuyang and Mudong postimpoundment. We suggest that the decrease in abundance and delayed presence of ichthyoplankton at Yibin postimpoundment of the XJD reflected the impact of upstream dam discharge and that the lower abundance of ichthyoplankton at Mudong compared with Zhuyang both preimpoundment and postimpoundment of the XJD reflected the influence of inundation by the TGR. We recommend that the river sections around Zhuyang become high-priority conservation areas.

**KEYWORDS**
endemic fish, hypolimnetic discharge, larvae and eggs, remaining river segment, temporal–spatial patterns, the Three Gorges Reservoir

**1 | INTRODUCTION**

Dam construction reshapes natural riverine landscapes and has been a major threat to fish biodiversity in large river systems worldwide (Cheng, Li, Castello, Murphy, & Xie, 2015; Habit et al., 2018; Nilsson, Reidy, Dynesius, & Revenga, 2005; Poff, Olden, Merritt, & Pepin, 2007; Song, Cheng, Murphy, & Xie, 2017; Xie et al., 2007). In some river basins, large hydroelectric dams have been constructed...
downstream from each other, which is referred to as a "dam cascade" (Cheng et al., 2015). Dam cascades are thought to have greater cumulative impacts on fish biodiversity than individual dams (Cheng et al., 2015; Segurado, Branco, & Ferreira, 2013). However, the effects of dam cascades on fish diversity have rarely been investigated (Cheng et al., 2015; Petesse, Petrere, & Agostinho, 2012, 2014; X. Zhang, Gao, Wang, & Cao, 2015).

The remaining lotic river segments between two adjacent dams may provide the necessary habitats for riverine fish species to complete their life history cycle and thus serve as critical refuges (Cheng et al., 2015; Gogola et al., 2010; Lopes & Zaniboni-Filho, 2019; Suzuki & Pompeu, 2016). From a landscape perspective, such river segments are influenced by both upstream dam discharge and downstream reservoir water levels (Cheng et al., 2015). Generally, upstream hypolimnetic discharge lowers river temperatures and reduces the availability of downstream nutrients, which may induce delayed and diminished spawning patterns of fish populations (Olden & Naiman, 2010; Zhong & Power, 1996). Manipulation of the downstream reservoir water level also modifies the hydrologic parameters of the inundated river sections, which may influence the spawning of riverine fish species and nursing of fish larvae and juveniles (Agostinho, Pellicce, & Gomes, 2008; Cheng et al., 2015). The data of the temporal–spatial patterns of ichthyoplankton provide critical information about fish reproduction and nurseries (Cao, Chang, Qiao, & Duan, 2007; Ren, He, Song, Cheng, & Xie, 2016) and reflect the sensitivity of fishes to the effects of river regulation (Humphries & Lake, 2000; Humphries, Seraphini, & King, 2002; Scheidegger & Bain, 1995; Song et al., 2017). Thus, knowledge of the patterns of ichthyoplankton in such free-flowing lotic river segments may provide critical information related to understanding the influences of a dam cascade and to aid in developing efficient conservation strategies.

The upper Yangtze River, located upstream from Yichang (30°41′N, 111°17′E), contains three free-flowing lotic river segments, that is, the headstream, the Jinsha segment, and the upper mainstream (Cheng et al., 2015). The upper mainstream of the Yangtze River is between Yichang and Yibin (YB, 28°42′N, 104°34′E) and is approximately 1,030 km in length (Cheng et al., 2015; Liu & Cao, 1992). This section harbours diverse fish fauna, with 154 species recorded, including 67 endemic species of the Yangtze River (Cheng et al., 2015). Since 2003, the impoundment of the Three Gorges Reservoir (TGR) has inundated approximately 600 km of this river segment (Zhao, Ye, Xie, & Cheng, 2015). Upstream from YB in the Jinsha segment, 10 other dams are under construction or have been completed (Cheng et al., 2015). Among these dams is the Xiangjiaba Dam (XJD), which is the most downstream dam and is approximately 30 km upstream from YB. The XJD has been fully impounded since October 2012 and was the first dam constructed along the Jinsha segment. The Xiluodu Dam is approximately 157 km upstream from the XJD and has been impounded since May 2013 (Zhao et al., 2015). The river segment between the XJD and the tail water section of the TGR is riverine and lotic. The length of this segment ranges from approximately 440 km (when the water level of the TGR is 175 m) to 580 km (when the water level is 145 m), and this segment serves as a critical refuge for fishes of the upper Yangtze River, specifically endemic species, which are mainly rheophilic fishes (Cheng et al., 2015).

*Botia superciliaris* is an endemic fish of the Yangtze River that is distributed in the middle and upper parts and is relatively abundant in the Jinsha and upper mainstream segments (Institute of Hydrobiology (IHB), 1976). However, the abundance of this species has decreased since the impoundment of the XJD (Li et al., 2016). This fish is a typical demersal and rheophilic species and is a high-value commercial species (Ding, 1994; IHB, 1976; M. S. Yang & Ding, 2010). In this study, we investigated the distribution of larvae and eggs of *B. superciliaris* in this river segment preimpoundment and postimpoundment of the XJD. Our objectives were to reveal the temporal–spatial patterns of *B. superciliaris* ichthyoplankton in this river segment and to reveal the potential impacts of the dam cascade. We hypothesized that both the upstream dam discharge and the downstream reservoir water level regime shape the distribution and temporal dynamics of *B. superciliaris* ichthyoplankton in the river segment between the XJD and the tail water section of the TGR. Conservation measures of endemic species in the upper mainstream of the Yangtze River are proposed based on our results.

## Methods

### Sampling sites

Ichthyoplankton were sampled from the upper mainstream of the Yangtze River in three sections, at YB (approximately 30 km from the XJD), Zhuyang (ZY, 29°03′N, 105°55′E, approximately 285 km from the XJD), and Mudong (MD, 29°34′N, 106°50′E, approximately 470 km from the XJD; Figure 1). The sampling site at MD was in the tail water section of the TGR, which is inundated when the water level of the TGR is higher than 150 m and is riverine when the water level is lower.

### Ichthyoplankton sampling and data analysis

Ichthyoplankton were collected using a 0.5-mm mesh ichthyologic trap net, which is commonly used for ichthyoplankton surveys in the Yangtze River (Duan et al., 2009; Ren et al., 2016; Song et al., 2017). The net has a rectangular mouth with an area of 4.9 m² (width × height: 2.9 m × 1.7 m), and its end opens to a 0.5-mm mesh cage (width × width × height: 60 cm × 35 cm × 35 cm; Duan et al., 2009). The additional details of the trap used in this study are provided by Duan et al. (2009). The net was set 8–30 m from the left river bank at water depths >2.5 m. The mouth of the net was set facing the river flow and was 0.3 m below the water surface. The net was regularly cleaned to remove fine materials from the mesh. Ichthyoplankton samples were collected at 8-hr intervals from each site over a 24-hr period at all three sampling sites.

Water temperature (°C) and Secchi depth (cm) were measured from the time the net was set and at each time ichthyoplankton were collected from the cage (i.e., four measurements per sample). The mean value of these four measurements was then calculated as the
Ichthyoplankton were sampled from late April through early July 2012; late April through mid-July 2013; and from mid-April 2015 through late March 2016. Sampling in 2012 was preimpoundment of the XJD, whereas sampling in 2013 and 2015–2016 was postimpoundment of the XJD. Sampling in 2012 and 2013 was carried out once in April, twice per month in May and June, and once in July. Sampling in 2015–2016 was carried out twice monthly in May, June, and July, and once a month in the other months. Among the samples in 2015–2016, ichthyoplankton of *B. superciliaris* were present only during mid-June through early August 2015 (see Section 3).

Ichthyoplankton collected in 2015–2016 were immediately fixed in a 4% formalin solution for 2.5 hr, then preserved in 75% ethanol, and stored in 4°C in refrigerator (Song et al., 2017). The Secchi depth was measured using a Secchi disk. The daily river discharge in the three sampling sections during the sampling period was obtained from the China Hydrology Information Network (http://xxfb.hydroinfo.gov.cn/).

Ichthyoplankton were sampled from late April through early July 2012; late April through mid-July 2013; and from mid-April 2015 through late March 2016. Sampling in 2012 was preimpoundment of the XJD, whereas sampling in 2013 and 2015–2016 was postimpoundment of the XJD. Sampling in 2012 and 2013 was carried out once in April, twice per month in May and June, and once in July. Sampling in 2015–2016 was carried out twice monthly in May, June, and July, and once a month in the other months. Among the samples in 2015–2016, ichthyoplankton of *B. superciliaris* were present only during mid-June through early August 2015 (see Section 3).

Ichthyoplankton collected in 2015–2016 were immediately fixed in a 4% formalin solution for 2.5 hr, then preserved in 75% ethanol, and stored in 4°C in refrigerator (Song et al., 2017). Larvae were determined to the species level through a combination of morphological and molecular analyses (Cheng, Li, Wu, Murphy, & Xie, 2013; Ren et al., 2016), and in this process, morphological keys for species identification of *B. superciliaris* larvae at different developmental stages were developed to perform morphological analysis. Ichthyoplankton collected in 2012 and 2013 were fixed in a 4% formalin solution immediately after collection. Molecular analysis could not be performed for species identification of these samples. Instead, *B. superciliaris* larvae in these samples were identified based on the morphological keys that were developed for the 2015 specimens.

*B. superciliaris* eggs collected in 2015 were identified through molecular analysis, and the embryonic stages were determined based on the work of He, Chen, Wen, Long, and Li (2014). The eggs collected in 2012 and 2013 could not be identified to the species level through molecular analysis and were not analysed in the present study.

The numbers of *B. superciliaris* larvae (in 2012, 2013, and 2015) and eggs (in 2015) were determined for each sample. The catch per unit effort (CPUE) for each sample was calculated as the number of eggs or larvae collected by a net over 24 hr (ind. net$^{-1}$ 24 hr$^{-1}$).

Two-factor factorial analysis of variance was conducted to test the effects of the sampling year, sampling site, and their interactions (Year × Site) on the CPUE of *B. superciliaris* larvae. One-way analysis of variance was conducted to test the effect of the sampling site on the CPUE of *B. superciliaris* eggs collected in 2015. When the effects were significant, a Duncan multiple comparison was conducted to compare the differences among the means. *B. superciliaris* larvae were present in samples from late May through early July in 2012 and 2013 and from late June through early August in 2015; *B. superciliaris* eggs were present from early June through late July (see Section 3). We included the CPUE of the samples in these corresponding periods in the statistical analyses. CPUE data were log-transformed to reduce heteroscedasticity. Differences were regarded significant when *p* < .05. The analyses were conducted using STATISTICA 10 software (StatSoft Inc., USA).

### 2.3 Determining egg spawning sites

The location of the spawning site of each egg collected in 2015 was estimated by calculating the distance the egg drifted to the sampling site based on the embryonic stage using the following formula:

$$L = V \times T,$$

where $V$ is the average drifting velocity of the embryonic stage and $T$ is the developmental time, which is defined as the duration (hr) that an egg took to develop from the initiation of fertilization to the embryonic stage at collection. The flow in a meandering river such as the upper mainstem of the Yangtze River is complex (IHB, 1976; Yi, Liang, & Yu, 1988), and the average drifting velocity ($V$) of *B. superciliaris* eggs in the upper mainstem of the Yangtze River was set at 0.5 m/s as recommended by Yi et al. (1988). Developmental time ($T$) is dependent on water temperature. In the present study, water temperature varied among the samples, but the average water temperature when eggs were collected at each sampling site was approximately 23°C. Thus,
we estimated the development time (T) for each collected egg under a water temperature of $23 \pm 0.5^\circ C$ following He et al. (2014).

3 | RESULTS

3.1 | Environmental factors

Water temperature ranged from 17.8 to 26.3°C across all sampling sites over the sampling period (Figure 2a–c). In 2012, the temperature was similar among the three sampling sites (Figure 2a). In 2013, the temperature was similar between YB and ZY, whereas that at MD was higher than those at YB and ZY from late May on, with the difference ranging from 0.8 to 1.8°C (Figure 2b). In 2015, the temperature at YB was consistently lower than that at ZY, which was, in turn, lower than that at MD (Figure 2c). The monthly difference between YB and ZY ranged from 0.9°C to 3.2°C, with a mean of 1.4°C; the difference between YB and MD ranged from 1.1°C to 5.5°C, with a mean of 2.6°C; and the difference between ZY and MD ranged from 0.1°C to 2.3°C, with a mean of 1.2°C.

Secchi depth ranged from 2.2 to 225.0 cm across all sampling sites over the sampling period (Figure 2d–f). In 2012, the Secchi depth was similar at all three sites (Figure 2d). The Secchi depth was higher in 2013 compared with that in 2012 (Figure 2e). The Secchi depth at YB tended to be higher than those at ZY and MD on some occasions (Figure 2e), and the difference ranged from 3.4 to 75.0 cm, with a mean of 30.9 ± 27.1 cm. The Secchi depth ranged from 10.0 to 225.0 cm from mid-April through early August in 2015 (Figure 2f). The temporal patterns at ZY and MD were similar to those in 2013 (Figure 2f). The Secchi depths at YB ranged from 57.5 to 225.0 cm, which was much higher than those in 2012 and 2013 (Figure 2f).

The difference of the Secchi depth at YB to those at ZY and MD ranged from 38.5 to 198.8 cm, with a mean of 115.3 ± 50.3 cm.

Discharge was lower at YB than at ZY, which was, in turn, lower than that at MD for all 3 years (Figure 2g–i). Discharge was generally low before late June or early July and increased thereafter (Figure 2g–i). Discharge tended to fluctuate to a greater degree in 2012 and 2013 than in 2015, specifically at ZY and MD. Fluctuation at YB was very minimal, typically occurring in 2013 and 2015 (Figure 2h,i).

3.2 | Dynamics of ichthyoplankton preimpoundment and postimpoundment of the dam

A total of 102 B. superciliiis larvae were collected in 2012, including 63 at YB (on May 29, June 11, and June 24), 31 at ZY (on June 14, June 25, and July 10), and eight at MD (on May 26, June 7, and July 3; Figure 3a). By comparison, 64 B. superciliiis larvae were collected in 2013, including zero at YB, 58 at ZY (on May 27, June 26, and July 17), and six at MD (on June 28; Figure 3b). In addition, a total of 36 B. superciliiis larvae were collected in 2015, including zero at YB, 21 at ZY (on June 28, July 9, July 28, and August 11), and 15 at MD (on July 26; Figure 3c). The sampling site had a significant effect ($p < .05$) on the CPUE of B. superciliiis larvae, whereas the sampling year and the interaction of the sampling site and year did not significantly influence the CPUE ($p > .05$). The CPUE at ZY was significantly higher than those at YB and MD in 2015 ($p < .05$; Figure 4). The annual average of the CPUE (mean ± SD) from data including the three sampling sites was $8.5 \pm 17.5$ ind. net$^{-1}$ 24 hr$^{-1}$ in 2012, which tended to be higher than those in 2013 ($5.3 \pm 15.4$ ind. net$^{-1}$ 24 hr$^{-1}$) and 2015 ($3.0 \pm 5.1$ ind. net$^{-1}$ 24 hr$^{-1}$) but was not significantly different ($p > .05$).
A total of 225 *B. superciliaris* eggs were collected in 2015, including 10 at YB (on July 12 and July 30), 212 at ZY (on June 17, June 28, July 9, and July 28), and three at MD (on June 11; Figure 3d). The sampling site also had a significant effect \((p < .05)\) on the CPUE of *B. superciliaris* eggs. The CPUE at ZY was significantly higher than those at YB and MD \((p < .05; \text{Figure 4d})\).

The developmental stages of the eggs at YB varied from the cleavage stage to the organogenesis stage, with most eggs at the gastrula stage, and the spawning sites were estimated to be 5.3–25.7 km upstream of the sampling site (Table 1). The eggs at ZY ranged from the cleavage stage to the hatching stage, with most eggs at the organogenesis stage, and the spawning sites were estimated to be 3.8–59.9 km upstream of the sampling site (Table 1). The eggs at MD were all at the organogenesis stage, and the spawning sites were estimated to be 34.3 km upstream of the sampling site (Table 1).

4 | DISCUSSION

The distribution of *B. superciliaris* ichthyoplankton in the upper mainstem of the Yangtze River showed clear preimpoundment and postimpoundment variations related to the XJD. Preimpoundment, larval abundance tended to be highest at YB and lowest at MD. Postimpoundment, larval abundance dramatically decreased in all three sampling sections. Specifically, there were no larvae collected at YB, and the abundance of larvae was greater at ZY than at MD. Eggs of *B. superciliaris* were collected in all three sections in 2015, and those collected at ZY accounted for over 90% of the total number of eggs; in addition, the initiation of egg occurrence at YB was approximately 1 month later than at ZY and MD. We suggest that the dramatic decline in larval abundance in all three sections, the lack of larvae at YB, and the lower abundance and later occurrence of eggs at YB than at ZY postimpoundment of the XJD reflect the cumulative impacts caused by the construction and operation of the upstream dams. These impacts include loss of spawning grounds, modified hydrological regimes, lower water temperatures, and lower nutrient concentrations. The lower abundance of ichthyoplankton at MD than at ZY both preimpoundment and postimpoundment of the XJD reflects the influence of inundation of the TGR by modifying...
the originally lotic habitat to a relatively lentic one. *B. superciliaris* is a typical, small demersal, and rheophilic species that produces drifting eggs (Cheng et al., 2015; He et al., 2014). There are several other endemic species, for example, *Sinibotia reevesae*, *Leptobotia elongata* and *Jinshaia sinensis*, in the upper mainstream of the Yangtze River with life history characteristics similar to those of *B. superciliaris* (Ding, 1994; IHB, 1976). The results observed for *B. superciliaris* in the present study may also occur in these species.

Dams interrupt the longitudinal connectivity of rivers, modify natural hydrological regimes, and lower water temperature and nutrient concentrations downstream of the dams by controlling discharge and releasing hypolimnetic and clean water (Cheng et al., 2015; Poff et al., 1997). As a consequence, the recruitment success of fish populations below dams may be diminished through the loss of their main spawning grounds, delay in the gonad development of spawning stocks, and decreased survival rate of offspring (Normando, Santiago, Gomes, Rizzo, & Bazzoli, 2014; Pringle, Freeman, & Freeman, 2000; Song et al., 2017; G. Zhang et al., 2012). The locations of the spawning grounds of *B. superciliaris* in the upper Yangtze River have not been previously documented. Larvae collected at YB in 2012 preimpoundment of the XJD might primarily originate from the spawning grounds in the Jinsha segment above the dam. Following the impoundment of the XJD and the Xiluodu Dam, the spawning grounds were inundated (Cheng et al., 2015). No larvae were collected at YB postimpoundment of the XJD in either 2013 or 2015. Thus, the loss of the upstream spawning grounds may partly account for the decrease in the abundance of *B. superciliaris* larvae postimpoundment of the XJD. Similar phenomena of diminishing recruitment success of fish populations due to the loss of upstream spawning grounds due to dam impoundment have been widely documented (Cheng et al., 2015; Gogola et al., 2010; Zhong & Power, 1996). Inundation of the upstream spawning grounds by a dam cascade in the upper Paraná River reduced the recruitment success of several migrating fishes (Agostinho et al., 2008). Impoundment of the TGR led to the loss of a major component of the spawning grounds for the four major Chinese carps (i.e., black carp *Mylopharyngodon piceus*, grass carp *Ctenopharyngodon idella*, silver carp *Hypophthalmichthys molitrix*, and bighead carp *Aristichthys nobilis*) above the dam, which is considered a major reason for the dramatic decreases in the larval production and population size of these fishes in the middle reach of the Yangtze River (Duan et al., 2009; Wang et al., 2014; Xie et al., 2007).

The serial discontinuity concept predicts that a river continuum disruption by dams could be reset by intersection with downstream tributaries (Ellis & Jones, 2013; Ward & Stanford, 1983). Both abiotic and biotic variables downstream of the dams may form longitudinal gradients based on the distance from the dam (Helfman, 2007). In the present study, the distances from the XJD to the three sampling locations at YB, ZY, and MD are 30, 285, and 470 km, respectively, and there are three major tributaries, that is, the Minjiang River, the Tuojiang River, and the Chishui River, flowing into the river section between YB and ZY (Figure 1). We observed apparent environmental gradients among the three sampling sections relative to their distance to the XJD in 2015. The lowest water temperature and highest water transparency at YB reflected the impacts of the hypolimnetic and clean water discharge from the XJD; the water temperature and discharge increased; and the water transparency decreased at ZY and then further decreased at MD, which reflects the gradual elimination of the negative impacts due to the increase in the distance to the dam and the conjunction of the tributaries (Ellis & Jones, 2013; Song et al., 2017). The lower water temperature at YB may delay gonad development of adult fish there (Normando et al., 2014; Song et al., 2017). At the same time, the higher water transparency at YB indicated that this area had lower nutrient concentrations (Garner et al., 2002; Song et al., 2017), which combined with the lower water temperature, may consequently lead to lower primary productivity and poorer prey availability for fish at YB than at ZY and MD, and may further delay fish spawning (Song et al., 2017). Furthermore, flow peaks provide critical cues and stimulate the spawning of drifting-egg fishes (Cheng et al., 2015; Humphries et al., 2002). The lack of flow peaks at YB during spawning seasons may also negatively influence spawning. Thus, the lower abundance and later occurrence of *B. superciliaris* eggs at YB than at ZY could be due to the negative impacts of discharge control and hypolimnetic and clean water discharge from the XJD. Negative impacts of hypolimnetic and clean water discharge from dams on fish populations have been documented in many river systems (Clarkson & Childs, 2000; Koehn & Harrington, 2006; Normando et al., 2014; Song et al., 2017; Wang et al., 2014; Zhong

### Table 1

<table>
<thead>
<tr>
<th>Developmental stage</th>
<th>Number of eggs</th>
<th>Drifting distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yibin</td>
<td>Zhuyang</td>
</tr>
<tr>
<td>Cleavage</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Blastula</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Gastrula</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Neurula</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Organogenesis</td>
<td>2</td>
<td>179</td>
</tr>
<tr>
<td>Hatching</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>10</td>
<td>212</td>
</tr>
</tbody>
</table>
Hypolimnetic discharge from the Garrison Dam in the Missouri River delayed spawning and reduced the larval abundance of Catostomidae species downstream (Wolf, Willis, & Power, 1996). Cold and clean water discharge from the Danjiangkou Dam delayed the spawning of some fish species in the Hanjiang River (a large tributary of the Yangtze River) below the dam by 20–30 days, and the growth of young fish was dramatically slower than that of their counterparts from the middle reach of the Yangtze River (Zhong & Power, 1996).

We observed a lower abundance of B. supercilialis ichthyoplankton at MD than at ZY both preimpoundment and postimpoundment of the XJD. This result might reflect the influence of the inundation of this river section by the TGR. MD is in the tail range of the TGR, which is inundated from November through the following April and lotic from May through October (S. R. Yang, Gao, Li, Ma, & Liu, 2012). Inundation during winter and spring might make this river section unfavourable for rheophilic species such as B. supercilialis (M. S. Yang & Ding, 2010). In addition, B. supercilialis is demersal in riverine sections with substrates of various-sized pebbles, gravels, and sands (Ding, 1994; IHB, 1976; Liu & Cao, 1992). Inundation of the tail range of the TGR facilitates the retention of sediments, which may modify the structure of the substrates and make the habitat unsuitable for B. supercilialis, even during the lotic period. Even if the tail range is lotic during the major spawning seasons of this species, we observed a lower abundance of larvae and eggs in that area.

Our results suggest that the river section around ZY was less directly impacted by the upstream dam discharge and downstream inundation of TGR, and this section substantially contributed to the spawning and population recruitment success of B. supercilialis. Thus, the river section around ZY should be considered a priority for conservation. We roughly estimated the locations of the spawning sites based on the developmental stages of the collected eggs, which were generally less than 60 km upstream of the sampling sites. Further research should be conducted to investigate egg distribution at a fine scale (e.g., every 60 km or less) for multiple species to determine the spawning grounds of fishes across the upper mainstem of the Yangtze River. Such information will contribute to the development of efficient conservation strategies. Dam cascades are common in large river systems worldwide, such as the Amazon, Mekong, and Yangtze River basins (Cheng et al., 2015; Nilsson et al., 2005; Ou & Winemiller, 2016). Our research provides a framework for evaluating the impacts of a dam cascade on the remaining lotic river sections of these large river systems by considering both the impacts of upstream dam discharge and downstream inundation.

ACKNOWLEDGEMENTS

This research was financially supported by the National Science Foundation of China (31570420, 31700346, and 31870398) and Key Strategic Program, Chinese Academy of Sciences (ZDRW-ZS-2017-3-2). Thanks to Dr. Bjorn V. Schmidt for the English revision.

AUTHOR CONTRIBUTIONS

F. C. and S. X. conceived the ideas and designed the methodology; Z. W., F. C., A. T. S., and Y. S. performed the field and laboratory work; Z. W., F. C., and G. H. analysed the data; and Z. W. and F. C. led the writing of the manuscript. All the authors contributed to the revisions and approved the final draft for publication.

CONFLICT OF INTERESTS

The authors have no conflict of interests.

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