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Responses of spawning thermal suitability to climate change and hydropower operation for typical fishes below the Three Gorges Dam

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ABSTRACT

River thermal regime is a critical factor affecting the initiation of spawning and breeding success in freshwater fish species. The four main domestic carps (FMDCs) and Chinese sturgeon are representative warm-water and cool-water fishes with different spawning thermal requirements in the Yangtze River Basin, China. This study focused on these two types of fish species below the Three Gorges Dam (TGD), and thermal response curves of fish spawning were constructed. The daily thermal suitability index (TSI) was simulated based on scenario analysis of climate-induced water warming and cooling. The variation in four TSI-based spawning indicators was then analyzed to evaluate the response of fish spawning to climate change and hydropower operation. The results showed that the spawning time is likely to be advanced by 1.3 days on average for the FMDCs and delayed by 2.1 days on average for the Chinese sturgeon with a 0.2 °C increase in the water temperature. For the FMDCs, climate warming would narrow the spawning window, although it may advance the spawning time that has been postponded by TGD operation, and climate cooling would widen the spawning window but further postpone spawning. For the Chinese sturgeon, climate warming would aggravate the negative impacts of TGD operation by further narrowing the spawning window and delaying spawning, while climate cooling would likely offset the negative impacts of TGD operation on fish spawning. We suggest that adjusting hydropower operation rules, e.g., elevating the water temperature in the early spawning period of the FMDCs to expand the spawning window and reducing the water temperature by at least 1.2 °C during the spawning period of the Chinese sturgeon, is essential for maintaining and restoring the natural spawning process and populations. Our study is also beneficial for inferring the cumulative impacts of cascading hydropower operations and provides insights for the management and conservation of fish species with different thermal tolerances in other hotspot regions.

1. Introduction

The thermal and flow regimes of rivers are key aspects in environmental flow management for the restoration or conservation of ecological health (Acreman & Dunbar 2004), with the thermal regime considered a fundamental ecological variable (Olden & Naiman 2010, Parker & Abatzoglou 2018). Freshwater fish species are ectothermic river organisms, and the thermal regime therefore affects their metabolic rates, growth, development, and survival as well as their distribution and abundance within fluvial environments (Kedra & Wiejaczka 2018). Thermal regime alteration (e.g., the increases and decreases in water temperature and changes in the timing of the maximum and minimum temperatures) may bring about a wide variety of detrimental consequences (Olden & Naiman 2010), such as the slow growth and reduced survival of larval and juvenile fish (Pörtner & Farrell 2008), delays in migration and spawning, declines in native fish production, and even the extirpation of native fishes and invasions of exotic fish species (Hari et al. 2006, Olden & Naiman 2010). Overall, the thermal regime strongly affects the productivity of river ecosystems (Chadwick 2008).

In natural rivers, the thermal regime is primarily determined by heat exchange between the water body and the overlying air, which is affected by air temperature, solar radiation, relative humidity, cloud cover, and wind speed (Sinokrot & Stefan 1993). However, the

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construction of hydroelectric dams, a type of anthropogenic activity directly impacting rivers, appears to have multiple effects on the fluvial environment, with specific effects on the thermal regime of rivers. Dams affect downstream temperature through hypolimnetic (bottom layer) water release, which modifies natural thermal conditions, reduces habitat quality, and changes aquatic community structure (Poff et al. 2007). In addition to the construction of hydroelectric dams, climate change affects the thermal regimes of rivers, which in turn have a direct impact on freshwater ecosystems. As the temperature of water bodies is directly influenced by heat exchange with air, river water temperature is expected to increase as a result of the increase in air temperature induced by a changing climate. Global predictions project that mean river water temperatures will increase by 0.8–1.6 °C on average under climate change (van Vliet et al. 2013), and such an increase is expected to cause adverse changes in river thermal patterns, endangering native aquatic wildlife (Mohseni et al. 2003, Hari et al. 2006). Several studies have predicted the impacts of climate change on fish habitat quality (Sievert et al. 2016, Wang et al. 2018), fish species distributions (Kwon et al. 2015), and fish spawning behavior in regional rivers (Tillotson & Quinn 2017, Zhang et al. 2018a).

As a fundamental physical factor in all life stages of fishes, water temperature has particularly strong effects on reproductive processes (Pankhurst & Munday 2011). Driven by breeding behavioral mechanisms, fishes select and remain in waters within thermal ranges that benefit their gonad development and spawning activity in their spawning season. The thermal regime alteration induced by climate change and dam operation shifts the spawning timing, duration and scale of freshwater fishes. For instance, the water temperature decrease induced by hydropower operation is found to be the main factor that resulted in the decrease of the spawning habitat and the delay of spawning months of the endemic fish *Coreius guichenoti* in the upper Yangtze River (Zhang et al. 2018a, Zhang et al. 2018b), while future climate change is expected to reduce such negative effects on fish spawning(Zhang et al. 2018a). The effects of temperature variation can be differentially expressed depending on when spawning normally occurs in the annual thermal cycle (Shimizu 2003, Pankhurst & King 2010). The four main domestic carps (FMDCs, namely, grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), black carp (*Mylopharyngodon piceus*) and bighead carp (*Aristichthys nobilis*)) and the Chinese sturgeon (*Acipenser sinensis*) are representative of two kinds of fish species in which reproductive activities are stimulated by increasing temperatures in spring and early summer and by falling temperatures in autumn, respectively, in the Yangtze River, China. The FMDCs are the most important commercial freshwater species in the middle and lower reaches of the Yangtze River, and the Chinese sturgeon is ancient and among the world's largest freshwater fishes, with historical spawning sites widely distributed along the Yangtze River. Because of hydropower development, especially the construction and operation of the Three Gorges Dam (TGD) in the Yangtze River, thermal habitat quality in the surrounding river reaches has seriously deteriorated in response to the changes in the thermal regimes (e.g. cooler river water temperatures in spring and summer, and warmer temperatures in autumn and winter), and the spawning activity of fishes has been adversely affected, resulting in a significant decline in the stock of the FMDCs and severe degradation of the Chinese sturgeon population in recent decades (Zhang et al. 2019). The Chinese sturgeon has been classified for first-grade state protection in China and is listed as a critically endangered species on the IUCN Red List.

An assessment of the effects of water temperature variation on fish spawning is the basis to formulate mitigation measures. Previous studies have mainly focused on the impacts of temperature variation resulting from TGD operation on fish spawning, while the combined impacts of climate change and hydropower operation have hardly been explored for the spawning of FMDCs and Chinese sturgeon (Gao et al. 2014, Wang et al. 2014). As the nature of the effects will depend on the amplitude of water temperature variation, this study employs a water temperature sensitivity method to evaluate the response of spawning activities of the FMDCs and Chinese sturgeon to climate change and hydropower operation. First, the thermal response curves of fish spawning were constructed based on spawning occurrence and water temperature data. Simulations of scenarios based on water warming and cooling were then conducted to analyze the responses of the thermal suitability index (TSI) to climate-induced and TGD-impacted temperature variation. Finally, the impacts of climate change and hydropower operation on fish spawning were evaluated based on shifts in TSI-based spawning indicators.

2. Materials and methods

2.1. Study sites, fish species and data

The Yangtze River is China's longest river, spanning 6,300 km, with latitudes ranging from 25°N to 35°N. It flows from west to east and empties into the East China Sea in Shanghai. The span from the source of the river to Yichang (the TGD site) is classified as the upper reach, the span from Yichang to Hukou (Fig. 1) is classified as the middle reach, the span from Hukou to Datong is classified as the lower reach, and the span below Datong is classified as the estuary. The middle reach of the Yangtze River is 898 km long and has a drainage area of approximately 680,000 km^2. The Gezhouba (GZB) Dam, which is located in Yichang (Fig. 1), is the first dam along the mainstream of the Yangtze River and began operation in 1981. It has blocked migration routes for many fish species (Wang et al. 2014). As the Gezhouba Dam is a low-head dam with less regulation of river flow, its impacts on the downstream water environment have been limited (Song et al. 2018). The TGD is located 38 km upstream of the GZB Dam. It started filling in 2003, began full operation in 2012, and has since had various negative impacts on fish resources and aquatic ecosystems in the downstream middle Yangtze River and adjacent areas, especially for the Chinese sturgeon and FMDCs (Zhang et al. 2020).

The FMDCs grow and mature in Yangtze floodplain lakes. The adult fishes migrate upstream to spawn during the flood season, and then the larvae are passively transported to the lakes, which serve as a nursery. Since these four species have very similar reproductive behaviors, the same spawning time, and almost identical environmental requirements and their eggs or larvae are often caught together, they are usually investigated together (Yi et al. 1988). Stimulated by increased water temperature (a minimum spawning temperature of approximately 18 °C) and rising water levels during the flood season (a daily water increase greater than 0.15 m/d), adults naturally migrate into the river during the spawning season (April-July) (Yi et al. 1988). The middle Yangtze River from Yichang to Chenglingji (380 km) is one of the most important reproductive areas for the FMDCs. Twelve spawning sites for the carp species occur within this reach, and two of the sites, namely, Yanzhiba and Huyatan, are near the Yichang River reach (Fig. 1). Since the Three Gorges Reservoir (TGR) impoundment began in 2003, the larval abundance of the FMDCs in the middle reach of the Yangtze River has sharply declined to less than 20% of the pre-dam abundance, and the spawning of these species has been delayed gradually with the increase to the maximum impoundment level of the TGR (Duan et al. 2009). Since TGD operation began, the flood pulse frequency has been sharply reduced, and the discharge of cool water has decreased the water temperature, which is thought to be linked with the larval abundance declines and spawning delays of the FMDCs (Duan et al. 2009).

The Chinese sturgeon is the largest anadromous fish in the Yangtze River. After the population matures in coastal waters, individuals swim into the Yangtze River mouth and continue moving upriver while fasting along the way. The individuals breed in the upper spawning ground in the next autumn (December-November) and then quickly return to the sea (Huang & Wang 2018). The spawning grounds of Chinese sturgeon were historically distributed in the upper reaches of the Yangtze River. Since 1981, the GZB Dam has blocked their migratory path and

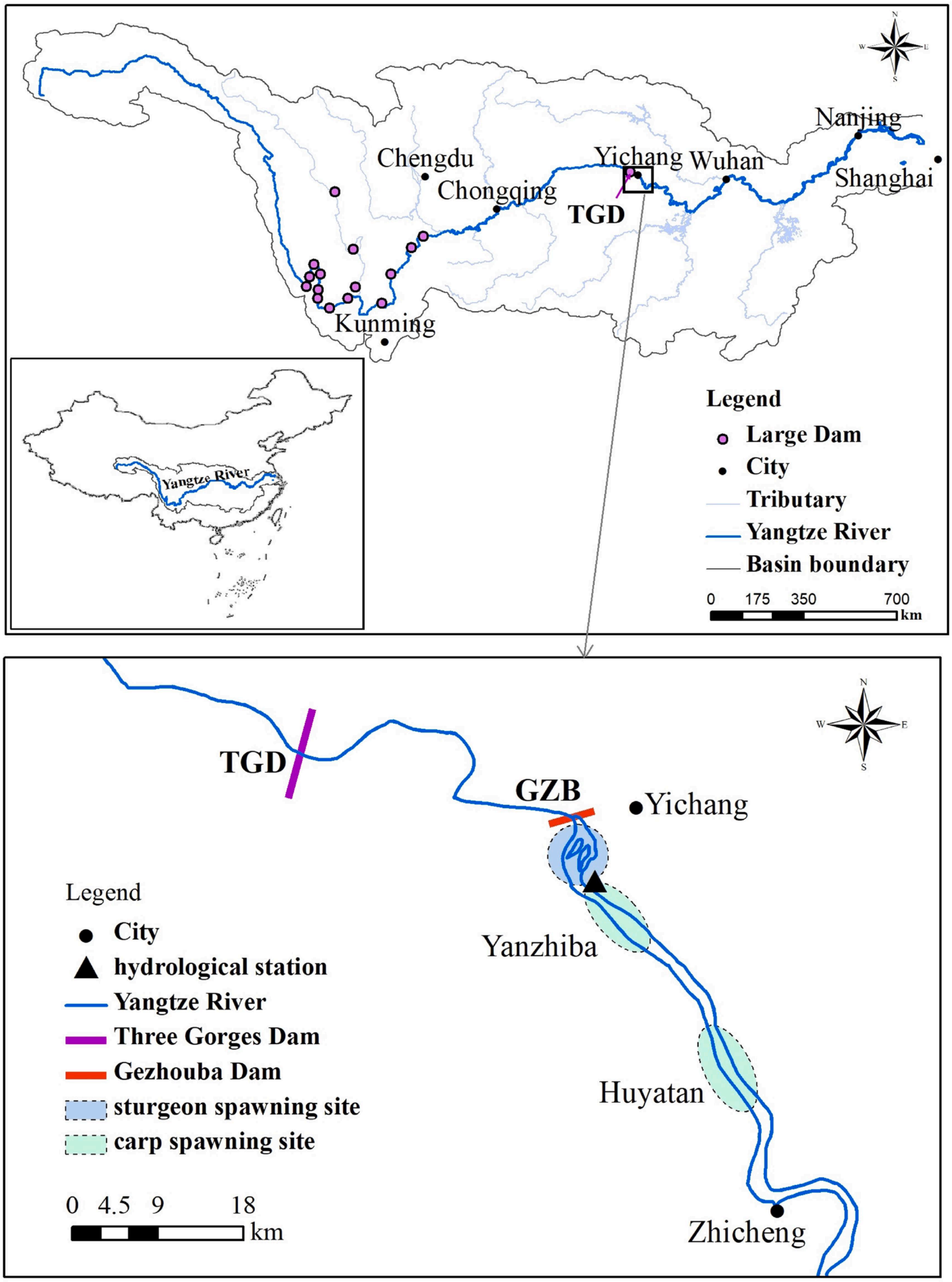

Fig. 1. The study sites.

prevented them from swimming to their spawning grounds in the upper Yangtze River. Over the next few years, continual monitoring showed that this fish species was forced to propagate in a new spawning ground along the 4-km-long main stream below the GZB Dam (Fig. 1). As a result, the population size of Chinese sturgeon has fallen gradually since 1990 (Yang et al. 2007b). The species was listed as critically endangered by the IUCN in 2010 and included in Appendix II of CITES in 2015. Water temperature and discharge have been suggested as the main factors impacting Chinese sturgeon spawning (Yang et al. 2007a, Xiao & Duan 2011). Field measurements and studies have shown that the Chinese sturgeon initiate spawning when the water temperature decreased to approximately 18 °C, and the optimal spawning water velocity and depth are approximately 1.2 ~ 1.6 m/s and 7.5 ~ 13.5 m, respectively (Yang 2007). As TGD operations further altered the flow and thermal regimes and deteriorated the spawning environment, the spawning habitat was seriously degraded, and spawning was postponed. However, the water temperature increase caused by TGR impoundment was suggested to be the primary cause of spawning delay and population degradation (Shen et al. 2017).

The site addressed in this study is the river reach downstream of the GZB Dam, which is an important spawning ground for the Chinese sturgeon and contains two important spawning sites for the FMDCs as discussed above (Fig. 1). Water temperature data from the Yichang hydrological station were collected, including monthly mean water temperature before GZB Dam operation from 1965 to 1980, daily water temperature after GZB Dam operation and before TGD construction from 1983 to 1992, and daily water temperature after TGD operation from 2007 to 2016. The date that spawning activity occurred in the fishes was collected from the literature. Finally, 33 and 45 spawning occurrence data were obtained for the FMDCs (Yi et al. 2010, Cai et al. 2017) and the Chinese sturgeon(Jiao et al. 2019), respectively.

2.2. Thermal response curve construction

To characterize the thermal suitability and availability of habitats, thermal response curves for fish spawning were constructed. The values of the curves were defined by the TSI, which ranges from 0 to 1, with 0 and 1 representing the lowest and the highest thermal habitat suitability, respectively. First, the number of groups of water temperature when spawning occurred was classified by Sturges' rule (Scott 2009), and the distribution of spawning occurrence frequency was obtained. Second, the relationship between spawning occurrence frequency and water temperature was fitted in the form of a polynomial function. Finally, the polynomial curve was normalized to a range from 0 to 1 by dividing by the maximum value of the function, and then the thermal response curves for the spawning FMDCs and Chinese sturgeon were obtained.

2.3. Scenario setting

A comparison of monthly mean water temperature among the three periods showed that TGD operation induced an obvious hysteresis effect on water temperature (Fig. 2). TGD operation imposed significant changes in downstream thermal regimes, decreasing the water temperature from March to June and increasing it from September to February in the next year, while the GZB Dam had little impact on the downstream water temperature regime. For this reason, and because daily water temperature data from 1965 to 1980 were not collected in this study, 1983 to 1992 was treated as the baseline (B), representing the scenario with no impact of hydropower, and the period from 2007 to 2016 was regarded as the scenario with TGD operation impacts (H). The daily mean water temperature in the two periods (Fig. 3) was calculated for B and H and used for scenario analysis.

In recent years, the most significant change in the global climate and environment has been global warming. Climate model prediction revealed that all of China will experience summer and winter warming (Li et al. 2018), which is expected to increase the water temperature in the summer and winter months. Vliet (2013) used a global, physically based, hydrological water temperature modeling framework to predict the global daily river discharge and water temperature under future

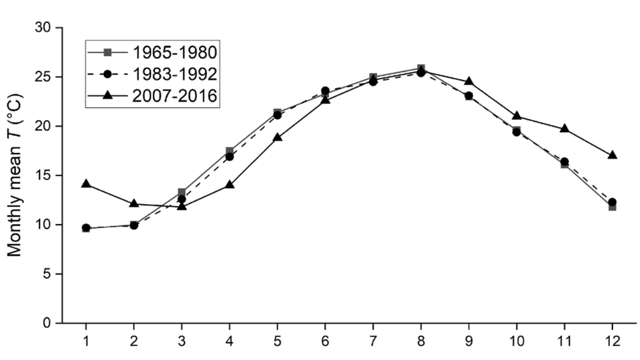

Fig. 2. Comparison of monthly mean water temperature in the natural period (1965–1980), the period before TGD construction (1983–1992), and the period after TGD operation (2007–2016).

climate conditions. The results showed that the global mean and high (95th percentile) river water temperatures are projected to increase by 0.8–1.6 (1.0–2.2)°C on average under climate change, and the future mean water temperature increase in the Yangtze River is expected to be 1.8 °C for the period 2071–2100. The daily predictions of Vliet (2013) also revealed an overall water temperature increase throughout the year. While the global average temperature will rise with future climate change, different regions may experience different conditions. Evidence from the analysis of observed data from the Yangtze River Basin in recent years (1990–2002) revealed that air temperature variations in the basin show large regional differences (Su et al. 2005). For example, the mean maximum air temperature in the summer showed a rising trend and a falling trend in 24% and 8% of the observer stations in the upper Yangtze River Basin, respectively, while 4.2% of stations showed a rising trend and 29% of stations showed a falling trend in the middle and lower Yangtze River Basin, respectively (Su et al. 2005).

Considering the caveats regarding the uncertainties of climate change noted above, future climate warming and cooling were both analyzed and assumed to occur throughout the spawning months of the target fish species in this study. Future climate change scenarios (CC) were established by increasing and decreasing daily mean water temperature in scenario B (Fig. 3). Scenarios of climate change and hydropower operation (CC + H) impacts were created based on the daily mean water temperature data in scenario H (Fig. 3). To explore the sensitivity of spawning thermal suitability to climate change, ten climate warming and ten climate cooling scenarios in which the water temperature increased and decreased by 0.2 °C, 0.4 °C, 0.6 °C, …, 2.0 °C, were selected. Thus, twenty scenarios each were constructed for CC and CC + H. The TSI for each scenario was simulated based on the thermal response curves of the spawning FMDCs and Chinese sturgeon.

2.4. Evaluation based on the TSI

To evaluate the effects of climate change and hydropower operation on fish spawning, four indicators were defined based on the TSI: the initial suitable spawning day (ISD) when the TSI increased to greater than 0 represented the commencement of spawning activity; the first optimal spawning day (OSD) was regarded as the first day when the TSI was greater than 0.8; the length of the normal spawning period (NSP) was calculated as the total number of continuous days with TSI values greater than 0; and the length of the optimal spawning period (OSP) was calculated as the total number of continuous days with TSI values greater than 0.8. The ISD and OSD were used to assess the temporal change in spawning time, and the NSP and OSP were used to quantify the durations of the suitable and optimal spawning periods, respectively.

3. Results

3.1. Thermal response curves of fish spawning

Spawning occurrence frequency exhibited a unimodal distribution for the FMDCs (Fig. 4a) and the Chinese sturgeon (Fig. 4b). The relationship between the spawning occurrence frequency and water temperature was well fitted with quadratic functions, with R^2 values of 0.91 and 0.93 (p less than 0.05) for the FMDCs and the Chinese sturgeon, respectively (Fig. 4a and 4b). The thermal response curves and functions are shown in Fig. 4c and 3d. For the FMDCs, the TSI was above 0 when the water temperature was greater than 17.8 °C and less than 24.4 °C, indicating that spawning activity normally occurred when the water temperature was in this range. For the Chinese sturgeon, the TSI was greater than 0 when the water temperature was in the range of 16.4 ~ 21.1 °C. The optimal spawning water temperatures (T_{opt} in Fig. 4c and 4d) revealed by the thermal response curve were 21.1 °C and 18.7 °C (TSI = 1) for the FMDCs and the Chinese sturgeon, respectively. As ectotherms that breed in different seasons, the FMDCs and the Chinese sturgeon have different thermal niches. Another difference that should

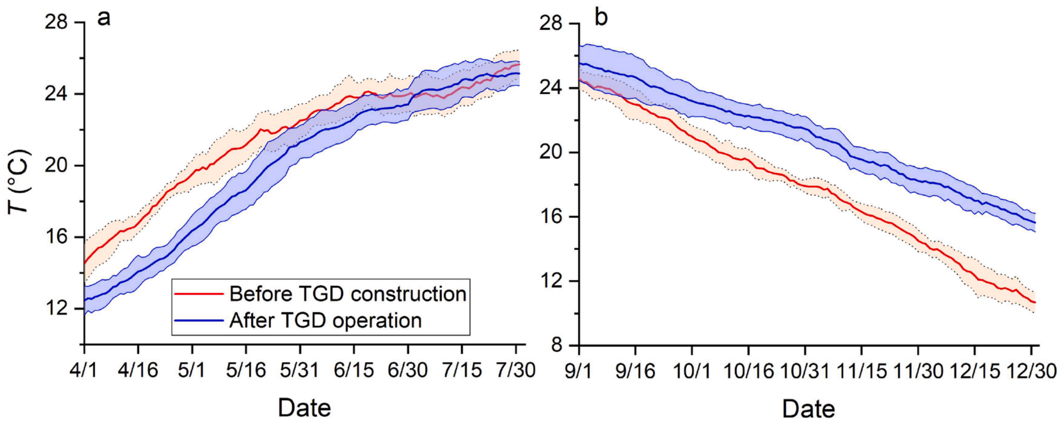

Fig. 3. Daily mean water temperature and standard deviation area around the spawning months for the FMDCs (a, April-July) and the Chinese sturgeon (b, September-October) before TGD construction (Scenario B, 1983–1992) and after TGD operation (Scenario H, 2007–2016).

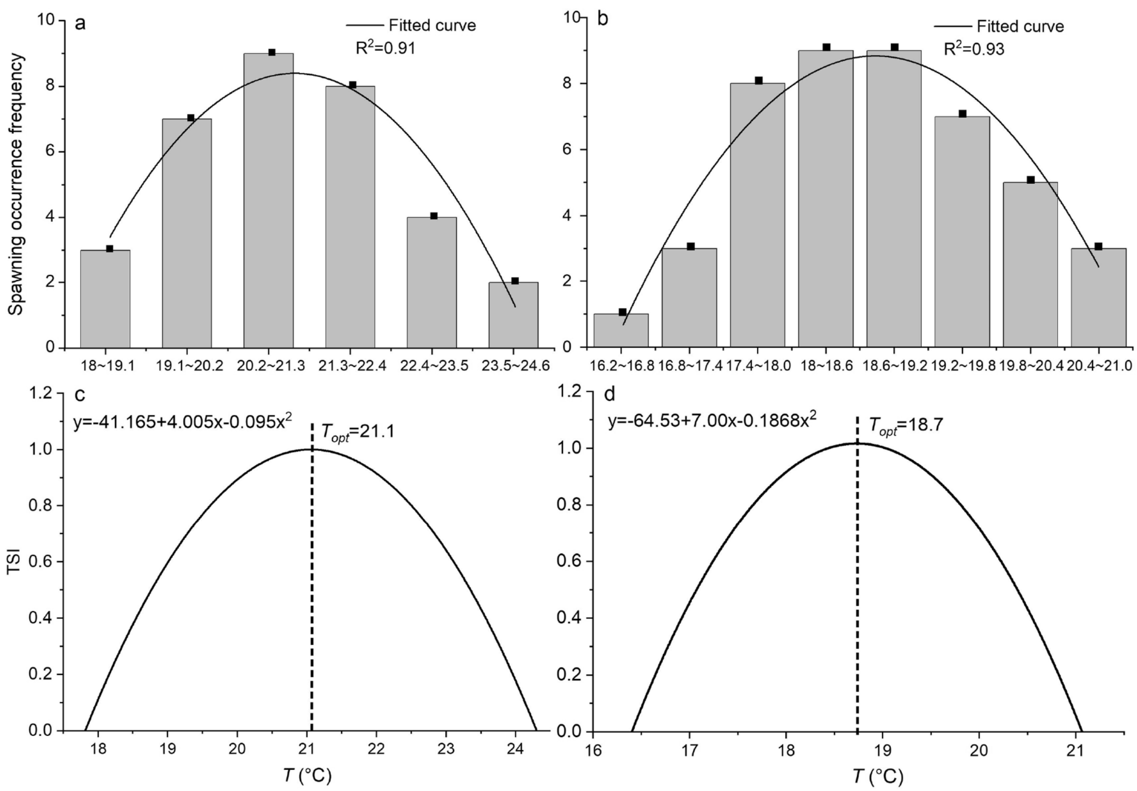

Fig. 4. Relationship between spawning occurrence frequency and water temperature for the FMDCs (a) and Chinese sturgeon (b) and the constructed thermal response curves for the spawning FMDCs (c) and Chinese sturgeon (d).

be noted is that the spawning activity of the FMDCs occurred as the water temperature increased to above 17.8 °C in late spring and then reached the optimal thermal range, while spawning of the Chinese sturgeon was stimulated by the decrease in the water temperature to below 21.1 in late autumn.

3.2. *TGD-induced thermal suitability variation*

The comparison in Fig. 3 shows obvious changes in the daily water temperature impacted by the TGD, and the difference before TGD construction and after TGD operation decreased over time for the FMDCs and increased for the Chinese sturgeon, which resulted from the temporal variations in the TSI. The monthly mean TSI of the FMDC spawning before TGD construction and after TGD operation revealed obvious changes impacted by TGD operation (Fig. 5a). In the period before TGD construction, high TSIs (above 0.6) mainly appeared in May and June, the two main spawning months. Under the impact of TGD operation, the mean TSI decreased from 0.81 ± 0.11 to 0.47 ± 0.19 in May, while it increased from 0.39 ± 0.18 to 0.66 ± 0.22 in June. The mean TSIs in April were all 0 in the years from 2007 to 2016, indicating that the suitable thermal habitat for spawning in late April under natural conditions disappeared because of the TGD. Overall, TGD operation altered the thermal suitability regimes, with high TSI values moving from May to June, and reduced the mean TSI by 22.5% during the spawning period.

For the Chinese sturgeon, the occurrence of high TSI values was shifted from October to November by TGD operation (Fig. 5b). In the period before construction, the monthly mean TSI in October was

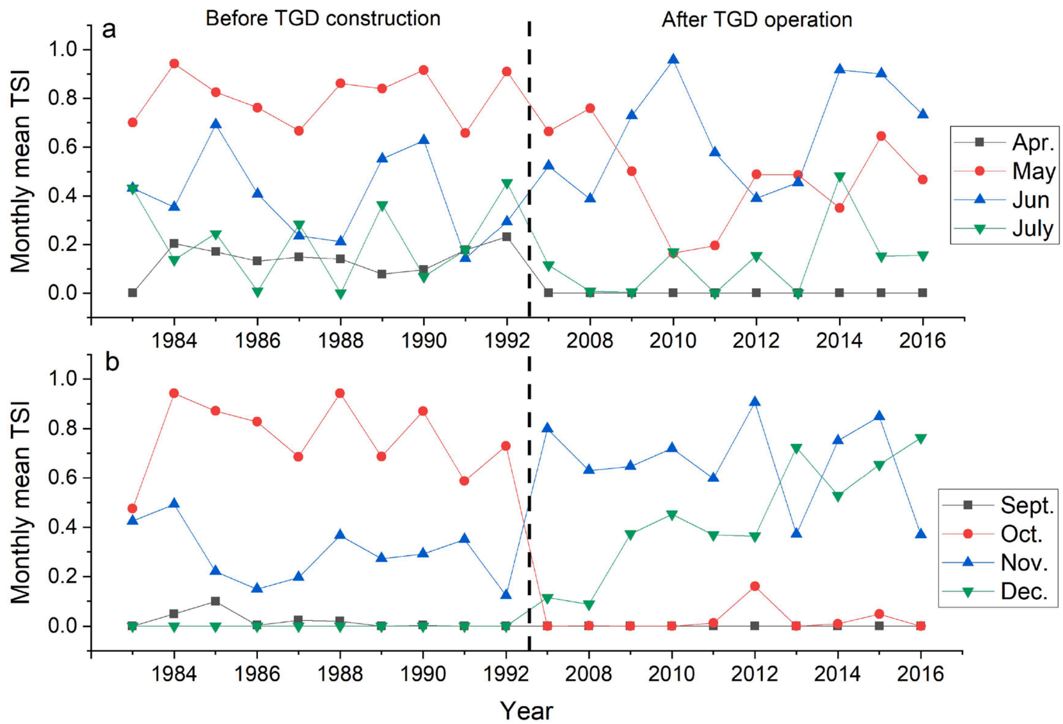

Fig. 5. Monthly mean thermal suitability index (TSI) of fish spawning for the FMDCs (a) and Chinese sturgeon (b) before TGD construction (1983–1992) and after TGD operation (2007–2016).

generally above 0.7 with a mean of 0.77 ± 0.16, while it dramatically decreased to 0 after TGD operation. However, the mean TSI in December significantly increased from 0.29 ± 0.12 to 0.67 ± 0.18 after TGD operation. Elevated TSI values even appeared in December, especially in later years of the TGD operation period. The overall relative reduction in the TSI was 38% in the normal spawning months (October-November).

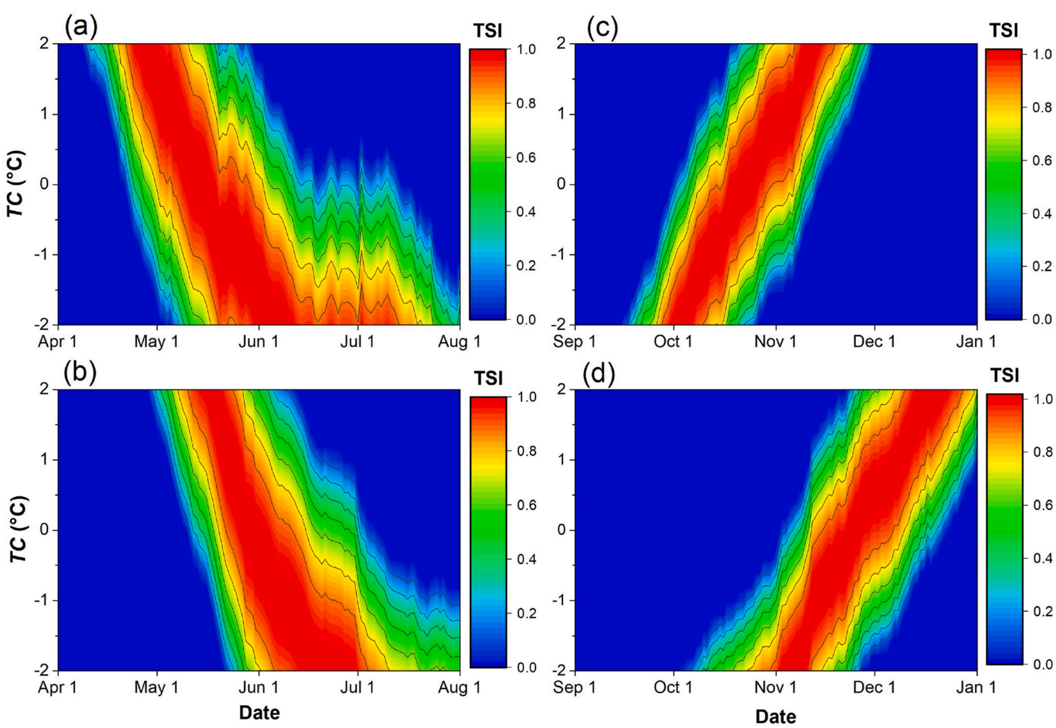

Fig. 6. Thermal suitability distribution for spawning fishes under climate-induced water warming and cooling effects with different temperature change (*TC*) scenarios. (a) and (c) are scenarios of independent climate change impacts on the FMDCs and the Chinese sturgeon, respectively, and (b) and (d) are scenarios of combined impacts of the climate change and TGD operation on the FMDCs and the Chinese sturgeon. The scenarios of $TC = 0$ in (a) and (c) represent natural conditions, and the scenarios of $TC = 0$ in (b) and (d) represent the TGD-impacted conditions without future climate change impacts.

3.3. Thermal suitability responses to climate change and hydropower operation

For the FMDCs, with the increase in water temperature induced by climate warming (Fig. 6a), the TSI gradually increased in late April and decreased from late May to July compared with baseline conditions (Fig. 6a, temperature change (*TC*) = 0). The range of periods with suitable thermal suitability (TSI greater than 0) narrowed under the effects of water warming. In contrast, the decrease in water temperature gradually decreased the TSI in the first half of May (Fig. 6a). The suitable thermal range extended to June and early July, especially when the water temperature was reduced by over 1 °C, resulting in a thermal range that was nearly double that observed under natural conditions. When also considering the impact of TGD operation (Fig. 6b), increasing climate-induced water temperatures advanced the suitable thermal ranges that were delayed by TGD operation, as revealed by the comparison with the no water TC scenario in Fig. 6a and 6b (also indicated in 3.2). However, only under the maximum climate-induced water warming of 2 °C did the suitable thermal periods nearly return to that observed under natural conditions (Fig. 6a, *TC* = 0). Greater water warming further reduced the periods of high TSI values. Under the combined impacts of TGD operation and climate-induced water cooling, although the range of suitable and high TSI periods tended to gradually extend with a water temperature reduction, further backward movement of the suitable thermal period occurred in response to TGD operation.

For the Chinese sturgeon, in the absence of hydropower operation, both climate-induced water warming and cooling hardly changed the duration of suitable thermal habitat for spawning but did altere the temporal regimes of thermal suitability (Fig. 6c). Increasing water warming advanced the suitable TSI to late September, while increased water cooling delayed the suitable TSI until the second half of November. In the scenarios of TGD operation with climate change (Fig. 6d), the postponed suitable thermal period (from October to November) caused by TGD operation (Fig. 6d, *TC* = 0) tended to advance to October as a result of climate-induced water cooling. However, the suitable thermal periods were far from reaching those observed under natural conditions (Fig. 6c, *TC* = 0), especially for the periods with high TSI values. Water warming further delayed the suitable thermal period until December.

3.4. Changes in spawning indicators

Distinct temporal changes in the TSI in response to TGD operation and climate-induced water temperature changes are likely to dramatically shift the spawning indicators. Under the baseline conditions without TGD impacts shown in Fig. 7, climate-induced water cooling and water warming tended to postpone the two spawning timing indicators (ISD and OSD) of the FMDCs and the Chinese sturgeon, respectively, as the former prefer to spawn in warm waters while the latter prefer to reproduce in relatively cool waters. TGD operation postponed the ISD (from late April to middle May) and OSD (from early May to late May) of the FMDCs by 18 and 19 days, respectively (Fig. 7a, *TC* = 0), because of the discharged cooling water and delayed the ISD (from early October to early November) and OSD (from middle October to middle November) of the Chinese sturgeon by 33 and 32 days, respectively (Fig. 7b, *TC* = 0) because of the discharged warming water. Therefore, under the combined impacts, climate warming reduced the postponement of the ISD and OSD of the FMDCs but further delayed the ISD (further to late November) and OSD (further to early December) of the Chinese sturgeon, and climate cooling is expected to have further negative impacts on the ISD and OSD for the FMDCs but positive effects on the Chinese sturgeon. Overall, with every increase in the water temperature of 0.2 °C, the ISD and OSD will likely be advanced by 1.3 days on average for the FMDCs and delayed by 2.1 days on average for the Chinese sturgeon.

The responses of the NSP and OSP to climate change and TGD operation varied greatly (Fig. 8). For the FMDCs, climate-induced water cooling alone did not increase the NSP and OSP, except in the scenario where the water temperature decreased by more than 1.2 °C, in which the OSP increased from 35 to 60 days (Fig. 8a). Increases in water warming slightly decreased the OSP and significantly decreased the NSP by 30 days until an increase of 0.6 °C, and greater water temperature increases hardly changed the NSP. Comparisons showed that TGD operation significantly decreased the NSP by 26 days but only slightly decreased the OSP (see Fig. 7a, *TC* = 0). Under the combined impacts of climate warming and TGD operation, a further decrease in the NSP did not occur, despite the negative impacts of water warming on the NSP, and both the NSP and OSP only slightly decreased. In contrast, climate-induced water cooling eliminated the negative impacts to some extent by increasing the NSP and OSP by a maximum of 14 and 11 days, respectively.

For the Chinese sturgeon, compared with those observed for the baseline without TGD impacts (Fig. 8b, *TC* = 0), both the NSP and OSP showed decreasing trends as the water became cooler, but they remained almost unchanged as the water became warmer, indicating the negative impacts of climate cooling and the lack of serious negative impacts of climate warming on spawning. However, both the NSP and OSP showed decreasing trends under the combined impacts of TGD operation and increasing climate-induced water warming. These results

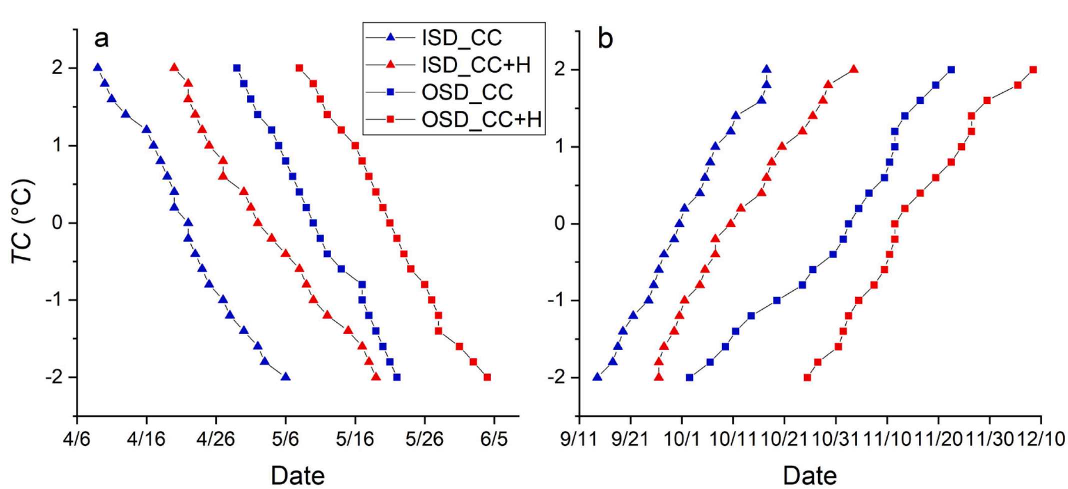

Fig. 7. Comparison of the ISD and OSD under climate change (CC) and the combined impacts of climate change and hydropower operation (CC + H) with different climate-induced water temperature change (*TC*) scenarios for the FMDCs (a) and the Chinese sturgeon (b).

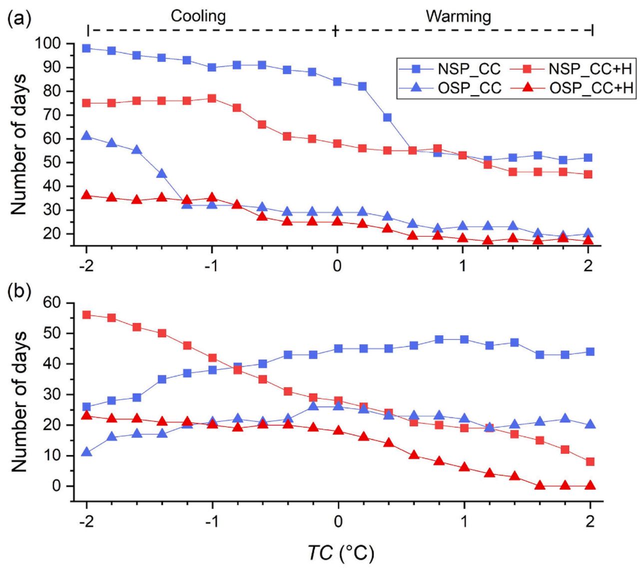

Fig. 8. Comparison of the NSP and OSP under climate change (CC) and the combined impacts of climate change and hydropower operation (CC + H) with different climate-induced water temperature change (*TC*) scenarios for the FMDCs (a) and the Chinese sturgeon (b) in their normal spawning periods.

imply that future climate warming will exacerbate the negative impacts resulting from TGD operation, as the NSP and OSP were obviously reduced by TGD operation compared with the baseline scenarios. By contrast, future climate cooling will enhance the NSP (to a maximum of 56 days) to be greater than that under the baseline condition (45 days) after water cooling exceeds 1.2 °C, indicating the positive effects of climate cooling resulting from the synergistic influences of TGD operation and climate change. However, climate-induced water cooling had only a minor positive impact on the OSP under the combined impacts, while TGD operation tended to reduce the negative effect of climate cooling when the climate-induced water cooling was greater than 1.2 °C.

4. Discussion

4.1. Differences in the impacts of climate change and hydropower operation

The spawning responses of the FMDCs and Chinese sturgeon, two kinds of fish species that spawn in different seasons with different spawning thermal tolerances, to TSI variation are distinct. Our study showed that the elevated water temperatures induced by climate warming are likely to advance spawning of the FMDCs while delaying the spawning onset of the Chinese sturgeon (Fig. 7). Despite these effects, the suitable and optimal spawning windows do not widen but obviously narrow for the FMDCs and change only slightly for the Chinese sturgeon during its NSP (Fig. 8). The former response could be due to the decreasing TSI with increasing water warming in the late spawning period (Fig. 6a). Unsurprisingly, climate-induced water cooling is projected to have the opposite effect of water warming on the initial spawning time of both kinds of fish species (Fig. 7). However, the variation trend of spawning duration in response to the water cooling effect was not consistent with that in response to the water warming effect. This was especially evident for the Chinese sturgeon, for which the suitable spawning window progressively decreased as water temperatures decreased. In general, although warmer waters are preferred for spawning by the FMDCs and cooler waters are preferred by the Chinese sturgeon, climate-induced water warming and cooling are likely to have negative impacts on the spawning of these two kinds of fish species,. Climate-induced water cooling seems to have positive impacts on the FMCC spawning by elongating the spawning window (Fig. 8a), while slightly narrowing the spawning window of the Chinese sturgeon.

Our results showed that TGD operation led to similar temporal variation in the TSI of the FMDCs and Chinese sturgeon (Fig. 6 and Fig. 7, $TC = 0$), which is likely to postpone and truncate the suitable spawning windows of the two kinds of fish species (Fig. 7 and Fig. 8). These results are consistent with those of previous research showing that spawning of the FMDCs downstream of the TGD began in early to late May, which was approximately 25 days later than that observed before construction of the TGD (Li et al. 2013), and field monitoring showing that the spawning onset of the Chinese sturgeon was postponed until early November at the earliest after TGD construction (Gao et al. 2014, Jiao et al. 2019). As a result of delayed spawning and narrowing of the spawning window, the prey availability of the spawning fish may have been reduced, the predation pressures on the eggs and larval fishes may have increased, and another important factor, flow discharge, may have become less suitable for spawning (e.g., excessively high flow discharge in the upcoming flood period for the FMDCs and low environmental flow in the winter for the Chinese sturgeon), largely causing the significant decline in egg and larval abundance of the FMDCs (Duan et al. 2009, Li et al. 2016) and the decreased spawning scale and frequency of the Chinese sturgeon (Wu et al. 2017, Huang & Wang 2018) below the TGD.

Although future climate-induced water warming is likely to somewhat mitigate the delay of spawning in the FMDCs (Fig. 7a) caused by TGD operation, the spawning window would be further narrowed under the combined impacts of climate change and TGD operation. In contrast, climate-induced water cooling would further postpone the spawning date but extend the spawning window of the FMDCs when coupled with the impact of TGD operation. However, considering all the adverse effects of spawning date delays on spawning activity and offspring survival discussed above, climate cooling could be considered to have a negative influence. Overall, both climate warming and cooling during the spawning period are expected to aggravate the negative impacts of TGD operation on FMDC spawning.

We found that negative impacts on Chinese sturgeon spawning would be triggered by the combined impact of climate warming and TGD operation, as the spawning window narrowes under the combined impact of TGD operation and climate-induced water warming but barely changes when impacted only by climate-induced water warming. It is surprising that climate cooling in isolation originally has negative impacts by decreasing the spawning window; however, its power to weaken the negative impacts of TGD operation are revealed by this study. This is because the spawning window increased (especially for the OSP, Fig. 8b) and the spawning time returned to that observed under natural conditions under the combined impacts of climate cooling and TGD operation. In short, future climate warming will aggravate the negative impacts of hydropower operation, while climate cooling is likely to mitigate the negative impacts on the spawning of the Chinese sturgeon.

4.2. Implications and recommendations

Cascading hydropower development and climatic extremes represent typical factors that can impact fish habitat, reproductive activity, and population dynamics. Hydropower operation influences thermal habitat and fish spawning through a hysteresis effect on the thermal regime (Fig. 2). A previous study and monitoring demonstrated that a delay in the water temperature course could be further strengthened by the cumulative impacts of cascading hydropower operation (Deng et al. 2008), which then had an extensive impact on aquatic ecology. Through physical modeling and prediction of the Yangtze River Basin with consideration of the TGD and other constructed and under-construction dams in the upper Yangtze River, a recent study showed that if more reservoirs are put into operation, the water temperature below the TGD will further increase in the spawning months of the Chinese sturgeon and further decrease in the spawning month of the FMDCs (Wang et al. 2020). As we simulated climate warming and cooling scenarios by progressively increasing or decreasing the water temperature in the TGD operation periods to analyze their combined impacts, it is reasonable to take the scenarios of water cooling in the FMDC spawning period and water warming in the Chinese sturgeon spawning period as a result of a further lag in the water temperature caused by the cumulative impacts of cascading hydropower operation. From this perspective, we speculate that water temperature decreases of 1 °C and 2 °C resulting from cascaded hydropower operation would lead to further spawning postponement of the FMDCs by 7 and 12 days, respectively, and that water temperature increases of 1 °C and 2 °C resulting from cascaded hydropower operation would lead to a further delay of FMCC spawning by 9 and 20 days, respectively (Fig. 7). Moreover, increasing water temperatures induced by cascading hydropower operation would expand the spawning window of the FMDCs, and this positive impact would cease when the water temperature decreased by more than 1.6 °C (Fig. 8a). A greater water temperature increase induced by cascading hydropower operation would result in a greater narrowing of the spawning window of the Chinese sturgeon, especially the optimal spawning window, which would no longer exist if the water temperature increased by more than 1.6 °C (Fig. 8b). As indicated by Huang and Wang (2018), cascade dams have led to an ongoing decline in the abundances of the Chinese sturgeon, and therefore, the cumulative effects of cascading hydropower operation and future climate warming would cause the natural population of the Chinese sturgeon to go extinct in a few years.

Climatic extremes, such as heatwaves, heavy rainfall, and droughts, are typical events of future climate change, and the rate and magnitude of these events are likely to increase in the future (IPCC 2014). There is growing recognition of the importance of extreme climatic events in determining changes in freshwater biotic populations and ecosystem functions (Parker et al. 2008, Leigh et al. 2015). Extreme heatwaves and cold weather are expected to impose intense shifts in thermal regimes, which are likely to severely disturb fish spawning activities. As the timing, frequency, and magnitude of future climate extremes are hard to determine, the responses of fish thermal habitat and spawning activity to climatic extremes could be difficult to accurately predict. However, our research provides basic data and schemes for evaluating the impact of extreme climate conditions on the spawning of the FMDCs and Chinese sturgeon.

Our study investigated the impacts of thermal regime variation on habitat quality and spawning activity, considering the pivotal role of water temperature in the spawning of the FMDCs and Chinese sturgeon, while the possible effects of hydroenvironmental and meteorological factors associated with climate change and hydropower operation were not considered. Specific flow characteristics are often required for the effective spawning of many fish species. Numerous studies have explored constructed physical habitat models considering spawning preferences for hydrological (e.g., flooding extent and frequency) and hydraulic (e.g., depth and velocity) factors of the studied fish species to determine the eco-environmental flow that is beneficial to fish spawning (Yi et al. 2016). The indirect influences of meteorological factors can be correlated with the initiation of spawning. Studies have suggested that the spawning activities of the FMDCs tend to occur after consecutive rainy days (Wang et al. 2010) and that the spawning activities of the Chinese sturgeon are positively correlated with rainy days but negatively correlated with cloudy days (Zhang et al. 2008). Nevertheless, suitable water temperature is the basic controlling factor that induces spawning activities in the two kinds of fish species, and other factors during the spawning periods most likely influence the duration and scale of spawning. To acquire a comprehensive understanding of all possible ecological factors impacted by climate change and hydropower operation that affect fish spawning, the use of complex mathematical modeling coupling environmental and ecological processes could be implemented in further studies.

To facilitate the spawning of the FMDCs in the middle Yangtze River, the TGD has implemented ecological regulation experiments to regenerate the natural flooding process when the water temperature rises to 18 °C. As a suitable temperature must occur for reproduction, water temperature is the key factor for determining the timing, duration, and intensity of ecological operation that should be implemented for the Chinese sturgeon and FMDCs. Our study revealed that both climate warming (which decreases the spawning window) and cascaded hydropower operation (which delays spawning as indicated by the climate-induced warming scenario) would have negative impacts on FMDC spawning, and the effect of the ecological regulation experiment would be limited or completely lost under their combined impacts. Therefore, operational rules for water temperature compensation, e.g., elevating the water temperature from the early spawning period to expand the spawning window, must be formulated. For conservation of the Chinese sturgeon population, the release of artificially bred juvenile fish is the main adopted measure. However, we suggest that conservation measures should focus on protecting natural spawning habitat to restore the natural population. Our study indicated that climate-induced water cooling by at least 1.2 °C can advance spawning and expand the spawning window of the Chinese sturgeon to match those observed in the natural state (Fig. 7b). Reducing the temperature of the discharged water by adjusting the cascading hydropower operation scheme during the spawning period is thus essential for maintaining natural spawning. In addition, the availability of an appropriate quantity of spawning habitat is also one of the most important factors in the conservation and survival of wild freshwater fish species, especially those under threat of extinction, such as the Chinese sturgeon. Increasing spawning activity by finding and constructing new suitable habitats can be suggested as a potential mitigation measure in addition to controlling water temperature.

Our study mainly focused on the thermal requirements for fish spawning. However, the gonad development cycle is also highly dependent on water temperature, and the thermal regime variation induced by TGD operation has a critical impact on the gonad development cycle and could be highly correlated with spawning delays and population degradation (Wang et al. 2014, Huang & Wang 2018). Future research efforts could fully explore the thermal regime requirements for the gonad development cycle and determine their responses to future climate change and cascading hydropower operation. At any rate, as the FMDCs and the Chinese sturgeon are representative warm-water and cool-water fish species, respectively, in the Yangtze River Basin, our research provides insights into the management and conservation of fish species in other hotspot areas.

CRediT authorship contribution statement

Peng Zhang: Writing - original draft, Methodology. **Ye Qiao:** Data curation. **Gaël Grenouillet:** Writing - review & editing. **Sovan Lek:** Conceptualization. **Lu Cai:** Visualization. **Jianbo Chang:** Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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