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Multi-index evaluation of fish habitat in a cascaded hydropower reservoir of the Yangtze River, China

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ABSTRACT: Cascaded hydropower development in rivers has a greater negative impact on native fish than a single hydropower station. The effectiveness of commonly used measures to restore fish resources, such as ecological discharges, depends largely on reliable assessments of habitat quality. In this study, we developed a synthesized habitat quality index (SHQI) by combining the habitat suitability index (HSI) and habitat fragmentation indices to evaluate the fish habitat in the Longkaikou (LKK) reservoir between the Jinanqiao (JAQ) and LKK dams in the upper Yangtze River. We coupled a 2-dimensional physical habitat model and a fuzzy-logic habitat suitability model for spawning and juvenile *Coreius guichenoti*, an Endangered fish endemic to the Jinsha River basin. The impact of the JAQ reservoir flow and the impoundment level of the LKK reservoir were considered to analyze variation in habitat quality. The results revealed that habitat suitability and fragment conditions were, to some extent, spatially inconsistent. The SHQI suggested lentic areas could benefit juvenile fish more than lotic zones with higher quality but less connectivity. A higher impounded level of the LKK reservoir may be more favorable for juvenile fish in the lentic area. Only the lotic area was suitable for fish spawning, and a lower discharge from the JAQ reservoir and lower impounded level of the LKK reservoir could be more beneficial, with optimal values of 560 $m^3 s^{-1}$ and 1294 m, respectively. This study proposes a comprehensive assessment method for habitat quality that could provide scientific support for the conservation of fish resources and populations in cascaded hydropower developments.

KEY WORDS: Cascaded dams · Habitat modeling · Fragmentation index · Fish conservation · *Coreius guichenoti*

1. INTRODUCTION

Dams have been widely constructed during the past century to provide humankind with flood prevention, water resources, and hydropower. However, dams, particularly larger ones, have a significant impact on the composition and abundance of both terrestrial and aquatic organisms (Li et al. 2013, Reid et al. 2019, Wu et al. 2019). They alter the water quality and the structure and distribution patterns of aquatic organisms in the drainage systems. Fish are one of the most vulnerable species during dam construction and operation, which can lead to local extinction of fish species, an increase in invasive species, and change in fish community composition due to habitat fragmentation and changes in flow. These effects also occur in over half of the longitudinally fragmented rivers in Europe and in many regions throughout the USA (Cooper et al. 2017, Rytwinski et al. 2017, Duarte et al. 2021, Wang et al. 2021). A dam has the potential

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to disturb the longitudinal connection of rivers and fragment watersheds, preventing fish from migrating and fragmenting their habitats (Tiemann et al. 2004, Rodeles et al. 2020). Dam operation can pose a major threat to fish habitats by changing hydrological, hydrodynamic, and hypolimnetic processes, and the altered habitat can increase the risk of invasive fish species, which may have a detrimental impact on aquatic ecosystems (Kibler & Tullos 2013, Caiola et al. 2014, Yi et al. 2014, Li et al. 2015, Wang et al. 2018).

Habitat fragmentation adversely affects fish populations. High-quality habitat connectivity facilitates the easy movement of fish to suitable areas, where they can find mating partners and successfully spawn (Kanno et al. 2014). This is particularly crucial for endangered species. Habitat fragmentation, characterized by a reduction in habitat quantity, an increase in patch number and decrease in patch size, and an increase in physical distance between patches, has direct and indirect negative effects on fish population. The presence of particular internal factors, exemplified by the susceptibility of large and medium-sized fish with complex life cycles, and external factors, such as small isolated habitat areas with impermeable barriers, increases the likelihood of adverse effects, and can influence the degree of isolation following fragmentation. Small populations are also more susceptible to the impacts of random disturbance events, and reduced genetic diversity lowers reproductive performance and the ability to adapt to changing conditions (Bonte et al. 2012, Gido et al. 2015, Legrand et al. 2017). Cascading hydropower dams may have a major impact on the riverine ecosystem and complicated biophysical repercussions, which are more severe compared to single dams in terms of fish and habitat, such as the homogenization of functional traits and a decrease in spawning quantity caused by rhythmic changes in operation (Naiman & Turner 2000, Zhai et al. 2010, Li et al. 2021, Zhang et al. 2021, Ticiani et al. 2023). Moreover, the effects of cascading dams on fish populations and diversity are more difficult to predict than those of a single dam, and few works have evaluated habitat quality in cascaded hydropower reservoirs (Draštík et al. 2008, Chen et al. 2018, Ticiani & Delariva 2020). As a result, the unexplored cumulative impacts of cascade dams on fish has led to constraints on the development of fish conservation strategies. In recent years, there have been increasing concerns regarding the ecological impacts of the extensive construction of cascade hydropower worldwide.

Cascaded dams for hydropower production, such as those along the Yangtze, Mekong, and Amazon river basins, are becoming more prevalent (Räsänen et al. 2012, Castello et al. 2013, Ali et al. 2019). In recent years, many integrated, large-scale, cascaded hydropower plants have been rapidly developed in the upper Yangtze River basin (UYRB), especially in the mainstream of the Jinsha River basin (JRB). In 2005, plans were put forward to build cascade hydroelectric dams on the Jinsha River, and since then, several large dams have been completed or are being constructed. So far, 10 high dams with heights of over 100 m have been built in the middle and lower Jinsha River (see Fig. 1). The tail part of each reservoir almost connects with its upstream dam, leaving only a limited lotic area below the upstream dam. These cascaded reservoirs pose a great threat to the survival of the indigenous species in the upper Yangtze River and have been increasingly linked to ecological impacts on fish habitat, population, and diversity (Li et al. 2013, Wang et al. 2018). The JRB has the highest fish diversity among the Yangtze River subbasins. The YRB has 126 indigenous fish species in total, and 45 of them, along with their spawning grounds have been recorded in the JRB. Adaptation to fast-flowing and turbulent currents is common in the fishes endemic to the JRB (Chen et al. 1998). Among them, the representative species *Coreius guichenoti* has experienced a gradual decline in population since the 1970s, and the Three Gorges Dam has caused the loss of nursery habitat (Park et al. 2003, Cheng et al. 2015a). The recent construction of large dams has blocked their migration route and altered habitat conditions. The spawning and living habitats of *C. guichenoti* have sharply decreased, and their resources and population have been significantly threatened. *C. guichenoti* urgently requires protection and has been included in the 'National Key Protected Wildlife List' as a national second-class protected species in China in 2021 according to https://www.gov.cn/xinwen/2021-02/09/content_5586227.htm. This designation indicates its status, signifying its inclusion in a list of fauna under the strictest protection by national legislation. Additionally, it has been listed as Endangered in the IUCN Red List (Chen & Zhang 2023). To alleviate the negative impact of the dams on fish, the Chinese government has requested hydropower projects to develop or reinforce countermeasures for protection and restoration, such as establishing natural reserves, maintaining ecological flow discharges, releasing artificially bred fishes, and constructing fish passage facilities (Zhang et al. 2020). However, the implementation of measures has often been ineffective due to insufficient understanding of their environmental needs and the environmental changes caused by dam operations, resulting in inadequate and inefficient protection of fish species.

In order to develop habitat restoration and propose appropriate measures, the influence of dam construction and operational processes on the surrounding habitat and environment must be analyzed, assessed, and quantified. Through the coupling of hydrodynamic models (for hydraulic process prediction) and local habitat suitability functions (to predict the physical habitat quality), physical habitat modeling is an effective tool that may link hydrogeomorphic changes to ecological predictions (Yi et al. 2017, Zhang et al. 2018a). These models are very helpful in assessing the effects of hydropower projects on river ecology and calculating the flow needs for populations of aquatic creatures (Parasiewicz 2001, Zhang et al. 2018b, Shim et al. 2020). Nevertheless, earlier research has overlooked the spatial distribution and fragmentation of high-quality habitat patches in favor of concentrating primarily on habitat suitability, notably weighted usable area (WUA).

This study considers a cascaded reservoir in the mid-stream of the Jinsha River to establish a 2-dimensional physical habitat model that considers the flow discharge from the upstream dam and reservoir impoundment of the downstream dam. Considering *C. guichenoti*, which is endemic and endangered in the JRB, as a target fish, the habitat quality impacted by the cascaded operation was simulated and evaluated by introducing habitat fragmentation indices from landscape ecology concepts. The objectives of this study were as follows: (1) to establish a synthesized habitat quality index (SHQI) that combines the habitat suitability index (HSI) and habitat fragmentation indices, (2) to investigate habitat quality variations impacted by upstream and downstream operations in different regions of the reservoir, and (3) to propose suggestions that support scientific decision-making of fish habitat restoration engineering and population conservation.

2. MATERIALS AND METHODS

2.1. Study area

The JRB is part of the UYRB (upstream of Yichang, Fig. 1). Its length is around 3481 km and it can be divided into upper, middle, and lower reaches. It drops about 5100 m vertically and contains abundant fish species. Large dams on the JRB have been completed and are still being built (Fig. 1). There are 8 planned dams along the middle stretch of the Jinsha River: Longpan, Liangjiaren, Liyuan, Ahai, Jinanqiao, Longkaikou, Ludila, and Guanyinyan. Six hydropower stations have been built to date, Longpan and Liangjiaren are currently in the planning stages, with construction yet to commence. The Longkaikou (LKK) reservoir was chosen to simulate and evaluate the effects of cascade hydropower operation on fish habitat. It is located between the upstream Jinanqiao (JAQ) dam and the LKK dam, and spans from 26.805°N, 100.448° E to 26.527° N, 100.415° E. The height of the LKK and JAQ dams is 116 and 120 m, respectively. The length of LKK reservoir is 41.3 km, the surface area is 15.27 km^2, and its total storage capacity is 5.07×10^8 m^3. The normal and dead water levels for the LKK reservoir are 1298 and 1290 m, respectively.

2.2. Target fish species

The UYRB is one of the most biodiverse regions of China. It contains a diverse community of freshwater fishes, with over 180 species living in the river basin. The largemouth bronze gudgeon *Coreius guichenoti* (Sauvage & Dabry de Thiersant, 1874) is one of the unique and commercially significant fish species. It is a typical anadromous fish that migrates into the spawning areas in the JRB from the lower branch of the UYRB between May and July. The spawning grounds for *C. guichenoti* were widely distributed in the middle and lower mainstream of the Jinsha River. Construction of the cascaded reservoirs is gradually destroying the spawning grounds, increasing their risk of extinction (Xia et al. 2016, Yang et al. 2017a). Because the cascaded dams in the Jinsha River are designed to retain a lotic area downstream of each dam, the fish are restricted to the tail of the cascaded reservoir. Thus, this lotic area is the last refuge for these fish to achieve natural spawning activities. However, there have been no monitoring reports of spawning activity of the affected fish occurring in the tail of the reservoir area or downstream of the dam, although a considerable number of *C. guichenoti* parent populations have been observed in the lotic area of the reservoir in the JRB (Jiang et al. 2007).

2.3. Hydraulic model

The 2-dimensional hydrodynamics of the research region were simulated using the River2D model (Steffler & Blackburn 2002). This model can simulate complex flow patterns by solving the 2-dimensional, depth-averaged St. Venant equations using finite ele-

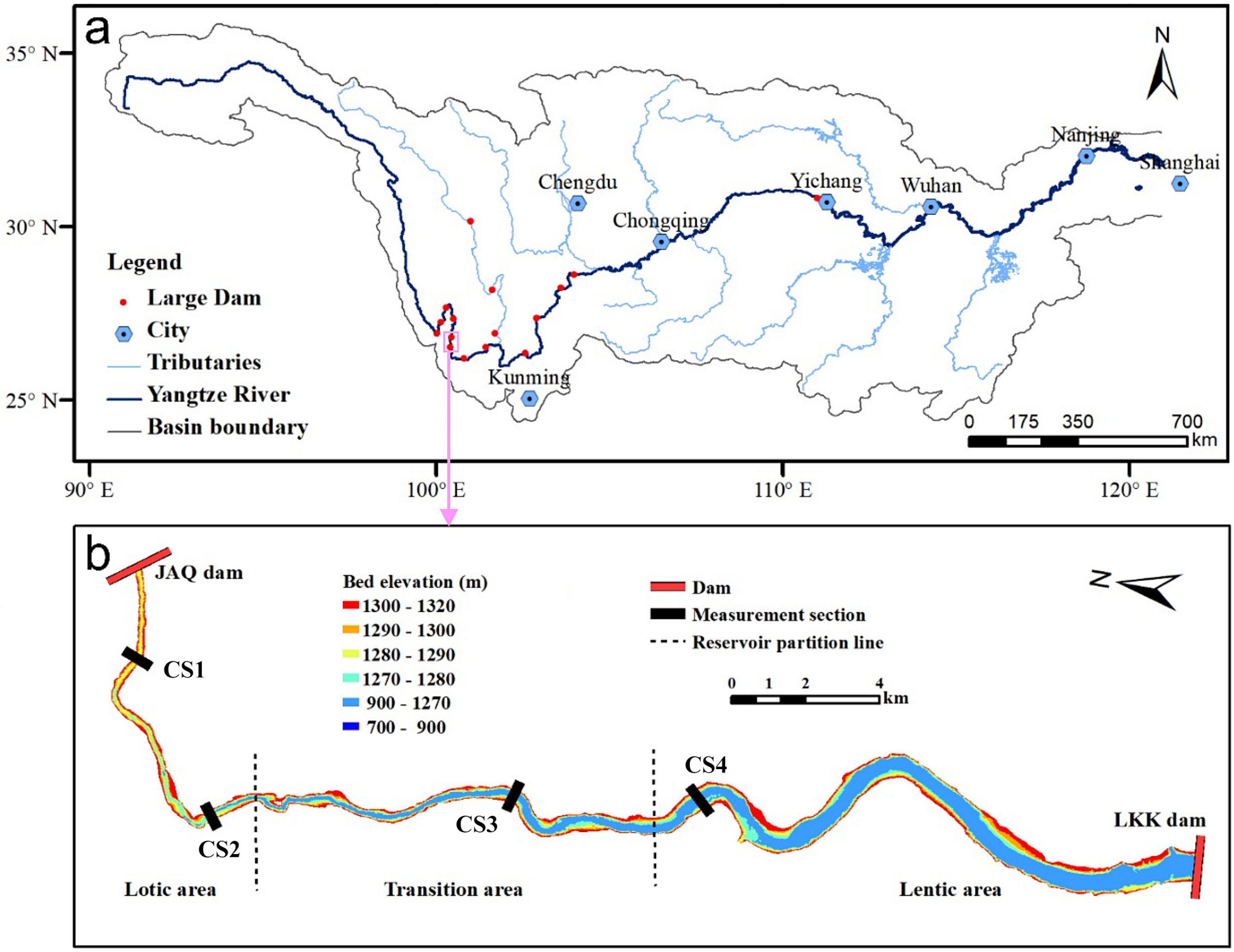

Fig. 1. The (a) upper Yangtze River and (b) study area. CS: cross-section

ment schemes and triangular irregular meshes. The water depth and velocity fields in the study area can be simulated with a steady flow model. The flow discharge from the JAQ reservoir was used as the upstream boundary condition, while the impounded water level of the LKK reservoir was used as the downstream boundary condition. Three typical impounded scenarios were selected for the downstream boundary conditions: a 1298 m normal water level, a 1290 m dead water level, and a 1294 m median level. For the upstream boundary conditions, we set an incremental flow sequence of 280 m^3 s^{-1}, from 280 to 7000 m^3 s^{-1} using 24 scenarios. Consequently, a total of 72 model scenarios were used to cover all possible hydrological change scenarios to model the hydrodynamics of the research region. We divided the study area (whole area [WA]) into 3 parts: the lotic area (LoA) close to the JAQ dam, the lentic area (LeA) close to the LKK dam, and the transitional area (TA), based on the simulated flow velocity (Fig. 1). The boundary between the LoA and TA was selected as the river section where the average velocity is >0.3 m s^{-1} when modeling with the minimum water discharge of 280 m^3 s^{-1}. The boundary between the TA and LeA was determined as the section where the average velocity is <0.3 m s^{-1} when modeling with the maximum water discharge of 7000 m^3 s^{-1}.

2.4. Fuzzy logic-based habitat model

To determine habitat suitability for *C. guichenoti* in the study area, a fuzzy logic-based habitat model was used to simulate for spawning and juvenile fish.

Unlike the preference function technique, fuzzy sets are employed to characterize habitat circumstances in the fuzzy logic approach. The input variables are defined verbally in categories such as 'low', 'medium', and 'high' based on existing habitat data and ecological specialists' knowledge, and the data is processed using mathematical methods (Mocq et al. 2013). Membership functions are used to define fuzzy collections with non-independent boundaries, where an element belonging to one collection can be partially owned by another collection at the same time, and where the membership function represents the degree of membership of each variable value in the collection represented by 0 to 1. Fuzzy rules establish the relationship between the variables of input and habitat suitability of a specific fish at different life stages. Fuzzy rules have antecedent and consequent parts using if — then rules. The antecedent part covers particular habitat circumstances, while the consequent part assesses the habitat conditions required by organisms for survival, growth, and reproduction. For instance, in the rule 'If high water depth, high flow rate, Then HSI is low,' the 'If' is antecedent and the 'Then' is consequent. Evaluation of the habitat is performed following the establishment of the fuzzy input variable set and rules. This method and the Mamdani-Assilian program are comparable (Mamdani 1974). In this case, the fuzzy output is transformed to clear values of the HSI (ranges from 0 to 1) based on fuzzy sets of output variables using the center of gravity method (Ouellet et al. 2021). Mocq et al. (2013) provide detailed methodologies and processes for fuzzy logic systems for habitat modeling.

The habitat suitability of the target fish was assessed and quantified utilizing the habitat model CASiMiR-GIS (Schneider et al. 2012), considering velocity and depth. This model for evaluating habitat can be used in rivers of various sizes, flow patterns, and bed structures (Noack et al. 2013). It is based on fuzzy logic and can be applied in a GIS environment, where parameters are defined and habitat suitability maps are visualized and further simulation results are available. The fuzzy sets (Fig. 2) and rules (Table 1) applied to the juvenile and spawning *C. guichenoti* were based on those used in our previous studies (Yang et al. 2017b,

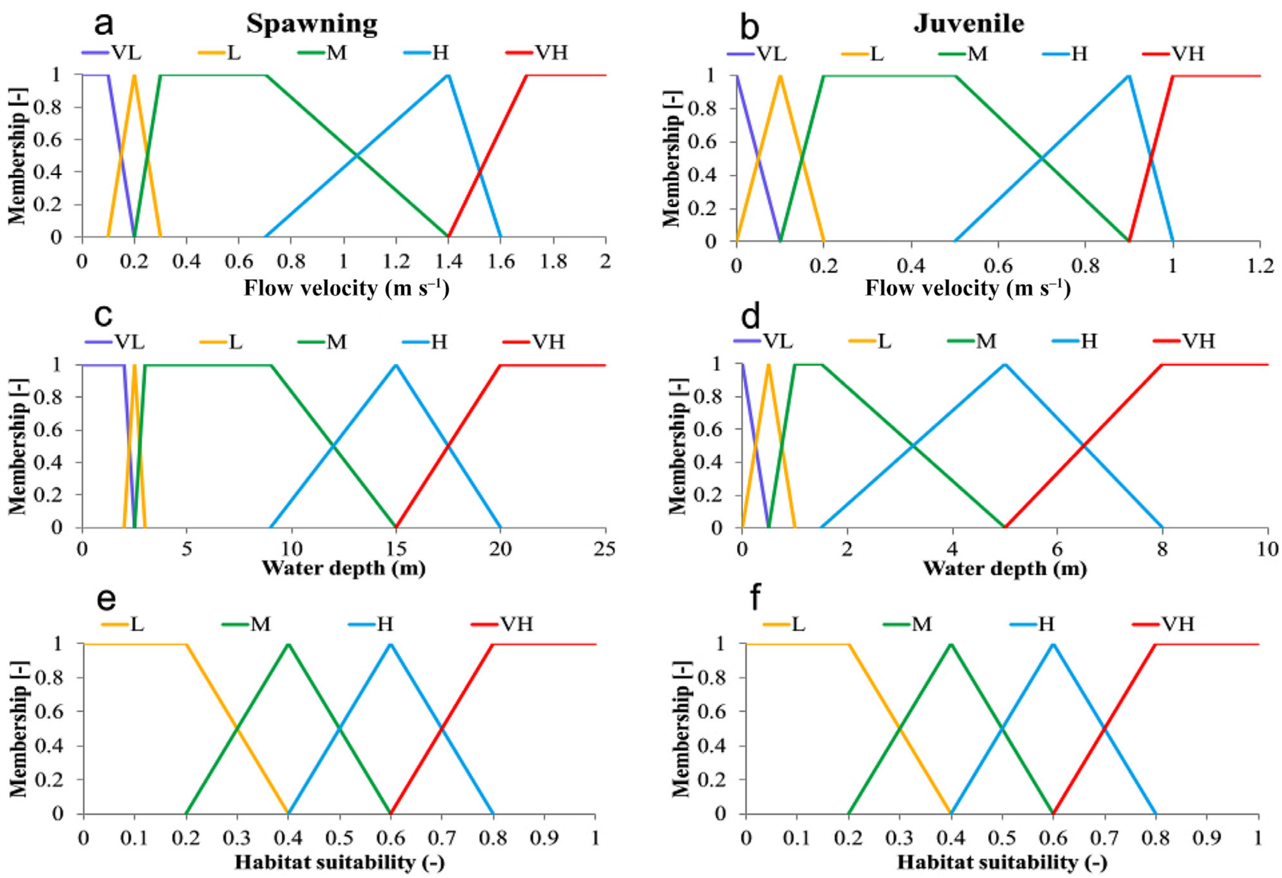

Fig. 2. Membership functions for (a,b) velocity, (c,d) water depth, and (e,f) output HSI using the CASiMiR-GIS model, which quantifies the gradation and uncertainty of environmental variables in determining habitat suitability for fish. VL: very low; L: low; M: medium; H: high; VH: very high

Table 1. Fuzzy rules for spawning and juvenile *Coreius guichenoti* for habitat modeling. SI: suitability index; VL: very low; L: low; M: medium; H: high; VH: very high

Velocity	Depth	SI_spawning	SI_juvenile
VL	VL	L	L
VL	L	L	M
VL	M	L	M
VL	H	L	M
VL	VH	L	L
L	VL	L	L
L	L	M	M
L	M	H	H
L	H	M	M
L	VH	L	L
M	VL	L	L
M	L	H	H
M	M	VH	VH
M	H	H	H
M	VH	L	L
H	VL	L	L
H	L	M	M
H	M	H	M
H	H	M	L
H	VH	L	L
VH	VL	L	L
VH	L	L	L
VH	M	L	L
VH	H	L	L
VH	VH	L	L

Zhang et al. 2019). The linguistic categories of very low (VL), low (L), medium (M), high (H), and very high (VH) were used to express 2 input habitat factors, and 4 groups were generated from the output HSI values (L, M, H, and VH). Therefore, the 25 fuzzy rules that emerged were built on the expertise and judgment of experts.

WUAs, which were generated from habitat models, were used to quantitatively evaluate the river habitat state at a specific river discharge. By dividing the WUA by the wetted area, the hydraulic habitat suitability index (HHSI), which has values ranging from 0 to 1, was calculated. This index allows comparisons of simulations between sites by eliminating the impact of the wetted area.

$$\mathrm{WUA} = \sum_{i=0}^{n} A_i \mathrm{HSI}_i \quad (1)$$

$$\mathrm{HHSI} = \frac{\mathrm{WUA}}{\text{Wetted area}} \quad (2)$$

where A_i is the area of the ith cell of the model grid, HSI_i is the suitability index for the ith cell, and n is the number of cells. To compare the effect of cascaded reservoir operation on the different parts of the LKK reservoir, the WUA and HHSI for the LoA, TA, and LeA were calculated separately.

2.5. Habitat fragmentation indices

Another important factor influencing habitat quality is habitat fragmentation, i.e. the suitable habitat area is divided into several habitat patches. Habitat patches can be formed by clumps of high-quality habitats, which is important for organisms to aggregate and migrate. As fish in imminent danger require a broad habitat patch in order to survive (Schuler et al. 2017), 2 patch-based habitat fragmentation indices, the habitat patch connectivity index (HPCI) and habitat patch aggregation index (HPAI), were used to quantify the habitat fragmentation status. A HSI threshold of 0.6 was used to obtain habitat patches from the habitat model results before computing the HPCI and HPAI.

The HPCI reflects the degree to which different patches relate to each other. The degree of connectivity can be defined as the probability of any 2 fish being located in the same high-quality patch. As the HPCI value decreases, the degree of habitat fragmentation becomes more severe, indicating a reduction in connectivity. The HPCI can be calculated using the following formula:

$$\mathrm{HPCI} = \sum_{i=1}^{n} \left(\frac{Ap_i}{A_t} \right) \quad (3)$$

where n is the number of habitat patches, Ap_i is the area of the ith habitat patch and A_t is the total area of all the patches. It ranges from 0, when connectivity between habitat patches is lowest, to 1, when habitat patches are fully connected.

The HPAI presumes that the class with the highest level of aggregation consists of patches that share the greatest number of potential edges. The class with the lowest amount of aggregation is the one in which the patches have no edges in common (totally disaggregated). The ratio of the actual number of comparable adjacencies between patches of the same kind to the maximum number of conceivable similar adjacencies on the map is used in the calculation. Based on this method, the HPAI can be calculated as:

$$\mathrm{HPAI} = \frac{e}{\mathrm{Max}_e} \quad (4)$$

where e is the number of similar adjacencies of habitat patches based on the single-count method and Max_e is the maximum possible number of similar adjacencies that can be determined using the method of He et al. (2000). The index ranges from 0 when there are no similar adjacencies (i.e. when the patch is maximally disaggregated) to 1 when e reaches its maximum (i.e. when the class is maximally aggregated). In this study, the HPCI and HPAI were calculated using landscapemetrics, an open-source R package in the R v.4.0.2 (R Core Team 2020).

2.6. Synthesized habitat quality indices

The habitat quality index characterizes size and suitability of a region for the home range of a species. Prior research has tended to concentrate on habitat quantity, such as WUA. However, high WUA values do not always indicate excellent condition. Thus, we quantified the habitat quality by considering both habitat suitability and fragmentation status, and propose a synthesized habitat quality index (SHQI). The SHQI was calculated as the HHSI multiplied by the mean of the HPCI and HPAI. We used the mean of the HPCI and HPAI because these 2 indices are highly correlated but reflect different properties of the habitat patches. The SHQI is calculated as:

$$\text{SHQI} = \frac{(\text{HPCI} + \text{HPAI})}{2} \times \text{HHSI} \quad (5)$$

3. RESULTS

3.1. Hydraulic model evaluation

Based on a simple trial-and-error method by manually refining the parameters to match the model results with the measured data, it was determined that 0.04 was the appropriate roughness coefficient for the hydraulic simulation models. The flow velocity and depth of the 4 measurement sections (Fig. 1) were compared between the observed and predicted values (Fig. 3). The results revealed that the simulated and measured values were in good agreement. The mean absolute errors of simulated water depth and velocity were 0.51 m and 0.18 m s^{-1}, respectively. Their root mean square errors were 0.55 m and 0.22 m s^{-1}, respectively. The results showed that the model can reliably simulate the hydrodynamic characteristics of the study area.

3.2. Habitat model results

Based on the hydrodynamic modeling results from the combination scenarios of 24 flow discharges and 3 impounded water level boundaries, habitat modeling was conducted for spawning and juvenile *Coreius guichenoti*. We compared the WUAs and HHSIs for the WA, LoA, TA, and LeA that were calculated based on the habitat modeling results (Fig. 4).

For the juvenile fish habitat in the WA (Fig. 4a), the WUAs show a clear unimodal trend as the flow discharge increases from 280 to 7000 m^3 s^{-1}. However, there is no noticeable change for the HHSI and it remains around 0.6 as the discharge increases. As the impounded water level of the LKK reservoir increases, the WUAs increase when the discharge is >1400 m^3 s^{-1}, while a higher impounded level results in a lower HHSI (Fig. 4a). The variation characteristics of the WUA and HHSI in the LoA, TA, and LeA are notably different (Fig. 4b–d). Generally, they exhibit

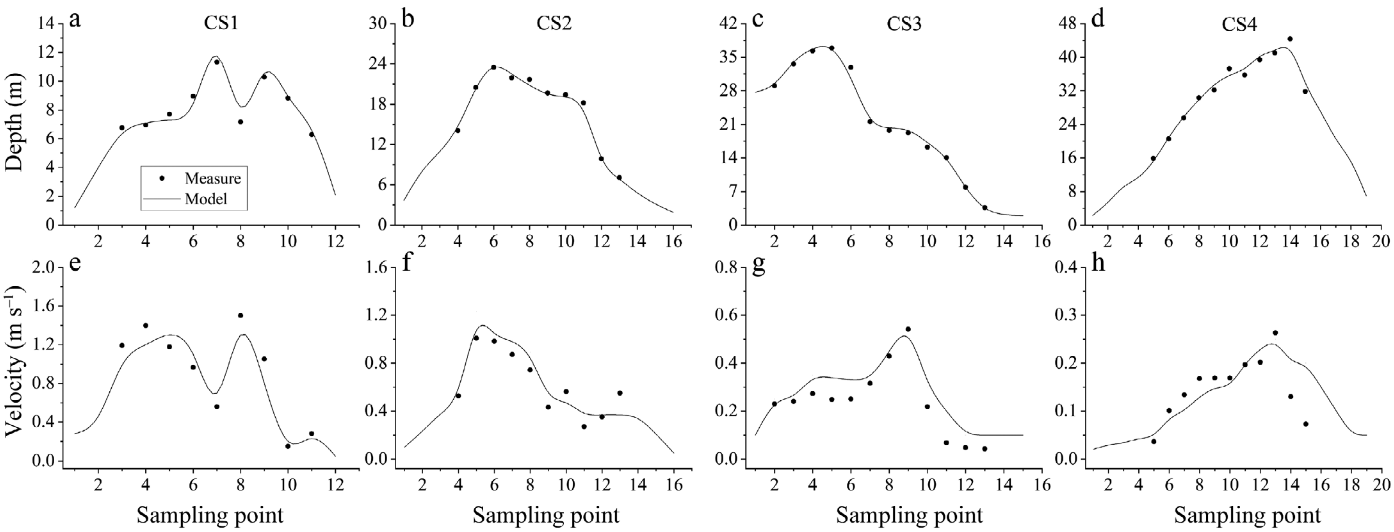

Fig. 3. Comparison of the simulated and measured (a–d) water depth and (e–h) velocity at 4 measurement cross-sections (CS1 to CS4)

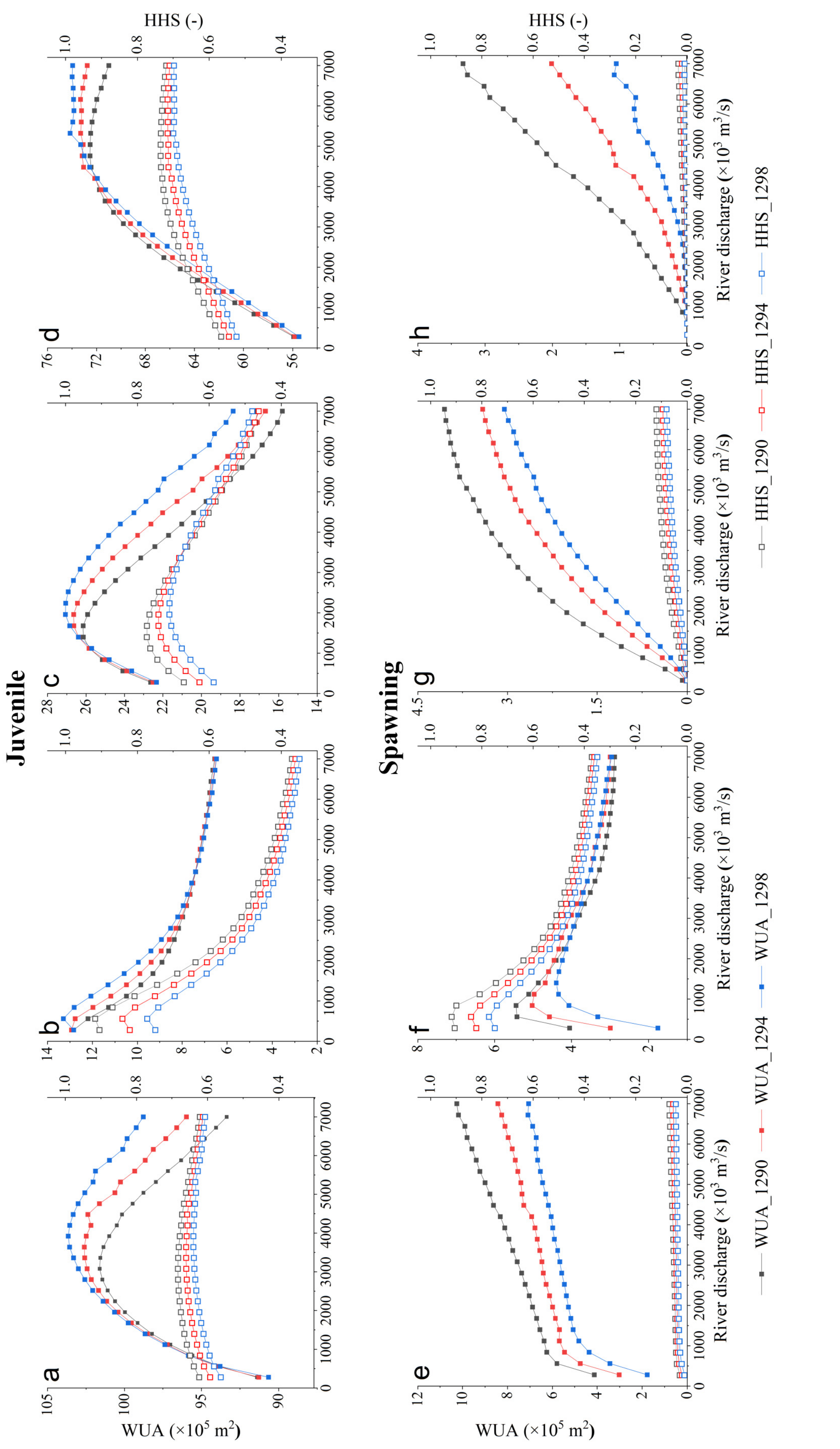

Fig. 4. Weighted usable area (WUA) and hydraulic habitat suitability index (HHSI) of (a–d) juvenile and (e–h) spawning *Coreius guichenoti* for the (a,e) whole area (WA), (b,f) lotic area (LoA), (c,g) transitional area (TA), and (d,h) lentic area (LeA) at different flow discharges and reservoir impounded water levels

decreasing, unimodal, and increasing trends in the LoA, TA, and LeA, respectively. Low discharge (<1960 $m^3 s^{-1}$) in the LoA, medium discharge (560 to 4480 $m^3 s^{-1}$) in the TA, and high discharge (>1960 $m^3 s^{-1}$) in the LeA could be suitable for juvenile *C. guichenoti* (HHSI > 0.6). The comparison shows that the suitable area in the LeA is 3 to 6 times greater than that in the LoA and TA at any flow discharge from the JAQ reservoir. A higher impounded level of the LKK reservoir may be more favorable for juvenile *C. guichenoti.*

For the spawning fish habitat in the WA, although the WUA and HHSI increase with discharge, they are much lower (HHSI < 0.1) than those of the juvenile fish habitat (Fig. 4a,e). Comparisons show that the TA and LeA are not suitable for fish spawning (HHSI < 0.15; Fig. 4g,h). For the LoA, lower discharge from the JAQ reservoir and a lower impounded level of the LKK reservoir could be more beneficial to the spawning of *C. guichenoti*. The optimal discharge and impounded water levels are 560 $m^3 s^{-1}$ and 1290 m, respectively. The comparisons show that the increase in WUA with an increase in discharge in the WA do not represent suitable habitat for fish spawning in the LoA.

3.3. Habitat quality indices

The distribution of suitable habitat patches (SHPs) for spawning fish in the LoA and juvenile fish in the WA at different flow discharges were compared (Fig. 5). For the spawning fish, the area of SHPs and their connectivity decrease significantly as the flow discharge increases. For juvenile fish, there are hardly any SHPs in the LeA and they mainly appear in the TA and LoA when the flow discharge is low. As the discharge increases, highly connected SHPs appear in the LeA and TA. Using the SHP data, the habitat fragmentation indices and the SHQI were calculated and compared for juvenile and spawning fish (Fig. 6).

For juvenile fish, the HPCI and HPAI demonstrate similar trends in the WA and in the separate regions. The habitat fragmentation status of the whole reservoir decreases as the flow discharge increases (Fig. 6a,b). Similar to the changing trend of HHSI in the separate regions, low-flow discharges in the LoA, medium-flow discharges in the TA, and high-flow discharges in the LeA result in higher HPCI and HPAI. The comparison shows that the HHSI is higher, whereas the HPAI and HPCI are lower, in the LoA at low-flow discharges. Higher-flow discharges produce lower HHSI but higher HPAI and HPCI in the LeA. However, the SHQI resulted in better habitat quality in the LeA at high-flow discharge than that in the LoA at low-flow discharge. Compared to Fig. 4(b–d), while the HHSI did not reach its peak for juvenile fish in LeA, this scenario underscores the SHQI's ability to correct observed discrepancies when relying solely on habitat suitability or area for habitat quality assessment. The SHQI can also reduce the vast difference in the WUA between the LoA and LeA by introducing fragmentation factors.

For spawning fish, modeling results showed that HPCI and HPAI are very low in the TA and LeA, indicating high fragmentation of the suitable habitat (Figs. 6e,f). Only the LoA is suitable for spawning, as

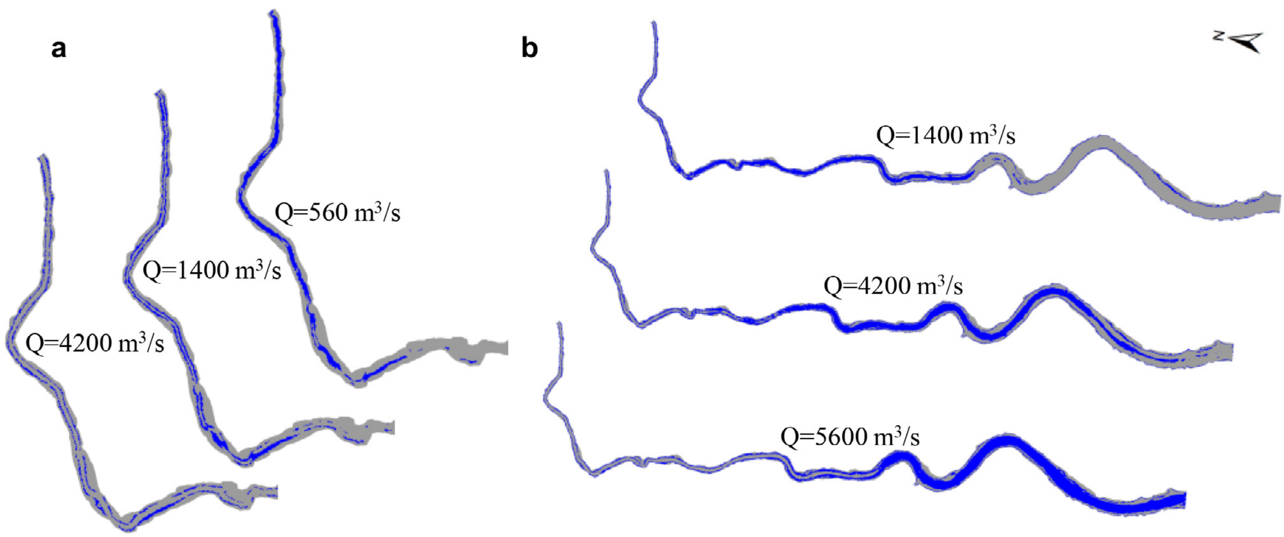

Fig. 5. Suitable (HSI > 0.6, blue) and unsuitable (HSI ≤ 0.6, grey) habitat distribution for (a) spawning *Coreius guichenoti* in the lotic area (LoA) (LKK reservoir level 1290 m), and (b) juvenile *C. guichenoti* in the whole area (WA) (LKK reservoir level 1298 m) at typical flow discharges (Q) from the JAQ dam

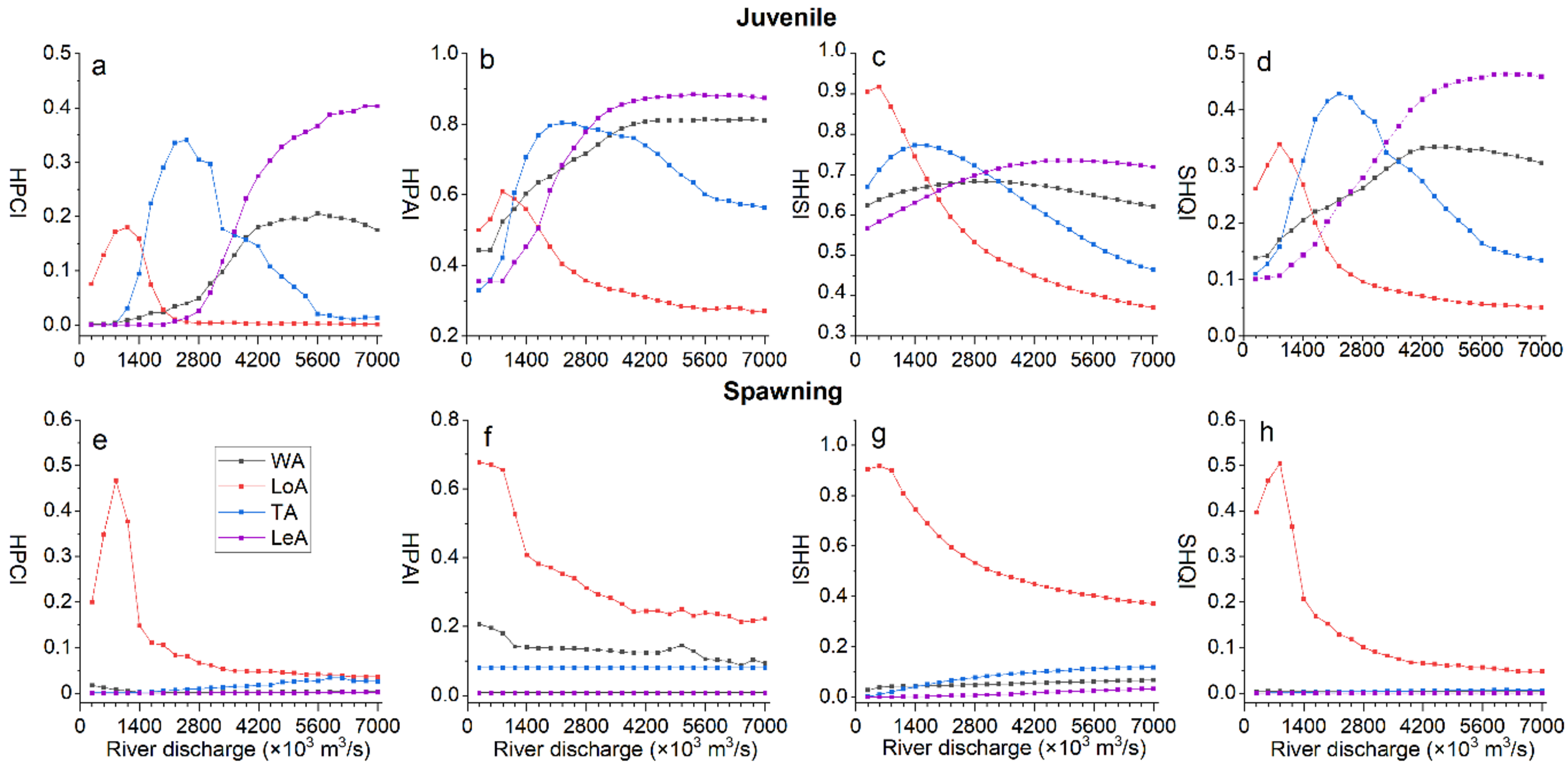

Fig. 6. Comparison of the habitat patch connectivity index (HPCI), habitat patch aggregation index (HPAI), synthesized habitat quality index (SHQI), and hydraulic habitat suitability index (HHSI) in different areas for (a–d) juvenile and (e–h) spawning *Coreius guichenoti* at different flow discharge. WA: whole area; LoA: lotic area; TA: transitional area; LeA: lentic area

the HPCI, HPAI, and HHSI are relatively high when the flow discharges are low. The comparison shows that both the HPAI (>0.6) and HHSI (>0.8) are high for flow discharges less than 840 $m^3 s^{-1}$, whereas the HPCI is highest (0.48) at 840 $m^3 s^{-1}$. By combining these 3 indices, the resulting SHQI shows that the optimal flow discharge is 840 $m^3 s^{-1}$, which is greater than that indicated by the HHSI (540 $m^3 s^{-1}$). This shows that the difference in the HHSI from 280 to 840 $m^3 s^{-1}$ is low, but there is a clear difference between the HPCI and HPAI at low-flow discharges. Therefore, the new index can effectively identify the optimal flow discharge for spawning *C. guichenoti.* Generally, the SHQI can better reveal habitat quality than the WUA and HHSI for both juvenile and spawning fish.

4. DISCUSSION

4.1. Implications for spawning habitat restoration

In this study, the results of the spawning habitat fragmentation status of *Coreius guichenoti* revealed that low fragmentation only appeared in the lotic area of the reservoir, and low river discharge could produce higher habitat connectivity and aggregation in this area. The habitat modeling results showed that suitable river discharge for spawning in the lotic area could be <1400 $m^3 s^{-1}$, with an optimal discharge of 560 $m^3 s^{-1}$. However, the ideal river discharge was increased to 840 $m^3 s^{-1}$ to reduce the impact of spawning habitat fragmentation. According to the operational rules of the LKK reservoir, the impounded water level should be 1290 m in July. This impounded reservoir level is optimal for spawning habitat and July is the spawning month for *C. guichenoti*. Therefore, we suggest that ecological operation should be conducted in July, and flow discharge from the JAQ reservoir should be at 840 $m^3 s^{-1}$ to trigger the spawning activity of *C. guichenoti*. However, successful spawning also depends on the presence of sexually mature adults. Releasing captive-bred sexually mature individuals to suitable river segments could be an effective method to replenish the number of breeding colonies. Future research should also explore the impact of environmental changes, especially the complex water temperature dynamics in the reservoir, on the gonadal development of adult fish.

Dam-induced habitat fragmentation often causes a decrease in population size, leading to an increased probability of local extinctions (Morita et al. 2019, Marshall et al. 2021). Such fragmentation not only physically prevents aquatic animals from reaching upstream habitats, but also hinders mobility between suitable habitats for certain life stages (Sindt 2021, Sethi et al. 2022). Moreover, fragmented habitats can also decrease mate availability and mating success rates. The rapid hydropower development, especially the 10 large cascaded dams constructed in the UYRB, has induced a dramatic disappearance of vital lotic habitats for endemic fishes to complete their life stages. The loss of lotic habitats would result in a partial or perhaps complete loss of fish spawning sites, particularly for the 45 species that spawn only in the Jinsha River (e.g. *C. guichenoti*, *Leptobotia elongata*, *Rhinogobio ventralis*, *Liobagrus kingi*, and *Semilabeo notabilis*) (Cheng et al. 2015b). Unsuitable hydrodynamic conditions for spawning could be the primary reason why *C. guichenoti* and other fishes fail to spawn successfully in the reservoir area. Maintaining ecological flow and restoring natural flow regimes are considered effective ways to remediate the damage to the spawning habitats (Freeman et al. 2001, Kiernan et al. 2012, Stuart & Sharpe 2021). These measures have been employed with the goal of fish protection below dams in many river systems (Richter & Thomas 2007, Kondolf et al. 2013, Grantham et al. 2014, Barfoot et al. 2018). Ecological reservoir operation has been tested in the Jinsha River to stimulate spawning activity for the endemic fish (e.g. *C. guichenoti* and *L. elongata*) that prefer spawning in flowing waters. However, the effects of such engineering measures have not yet been scientifically assessed. To effectively restore the habitat of fish spawning grounds, we must have an accurate understanding of the hydraulic habitat conditions in the reservoir area based on fish spawning requirements, especially in the reservoir area of cascade hydropower stations that are affected by the dispatch of upstream and downstream dams simultaneously.

4.2. Suggestions for population conservation

Artificial propagation and release are major measures for restoring resources and conserving populations of endangered fish species. In China, mostly along the Yangtze River, this method has been used as a significant conservation measure for over 20 endangered fishes, such as *Acipenser sinensis* (Liu et al. 2020, Wang et al. 2020). An artificial breeding station was constructed for each of the 6 hydropower stations in the middle JRB. Large-scale artificial reproduction has been achieved for over 20 endemic fishes with continuous breakthroughs in fish breeding technology. Although fish releasing might pose genetic and ecological hazards, there is no other way to save some fish species in the JRB, especially those whose spawning habitats have been severely damaged (such as *Acipenser dabryanus* and *C. guichenoti*) (Dudgeon 2011). A critical issue in the releasing method is the selection of release timing and location, which determines whether the released fish can survive normally (Baker & Sammons 2021, Markham & Robinson 2021). However, habitat conditions at the release sites have not been comprehensively assessed for almost any releasing activities.

Generally, the fish bred at the breeding stations belonging to a certain hydropower station can be released either into its reservoir or downstream of the hydropower dam. Our simulation results show that the high-quality habitat for juvenile *C. guichenoti* fish is downstream of the JAQ dam (LoA and part of TA) and that habitat fragmentation is low when the flow discharge from the JAQ reservoir is small. When the flow discharge is large, the high-quality fish habitat is mainly in the reservoir area (LeA and part of TA) close to the LKK dam. Therefore, it is recommended that the release of fish from the JAQ proliferation station should be at a time when the discharge is <1400 m^3 s^{-1} and occur close to the JAQ dam. The fish-releasing campaign of the LKK proliferation station was conducted during the period when the flow discharge into the reservoir was >4200 m^3 s^{-1}. Selecting the right time to release fish into the area close to the breeding station can not only improve their survival rate in the reservoir area but also reduce the cost of fish transportation and the maintenance of fish survival during transport. However, to develop artificial reproduction and fingerling-rearing methods for significant endemic fishes, further research needs to be done. To prevent the possibility of lowering the fitness of wild populations, it is essential to create adequate management guidelines for conserving hatcheries (Naish et al. 2007, Holsman et al. 2012).

4.3. Application to protect endangered fish species

To protect *C. guichenoti*, as well as other endangered fish species, building fish passage facilities, releasing artificially bred fish, and adjusting operation schemes to discharge ecological-friendly flow are required to restore affected fish for each hydropower project. However, the JAQ hydropower station, which operates under a weekly regulation mode, is constrained by the limitations imposed by natural inflow. It is challenging to achieve the optimal flow rate due to these constraints. This emphasizes the critical need for coordinated ecological scheduling among the cascade reservoirs to meet the water requirements of fish species. Currently, upstream hydropower stations at JAQ have commenced ecological scheduling experiments, targeting fish species like *C. guichenoti* in 2020 and 2021. Habitat suitability modeling is an effective scientific approach to guide the implementation of these measures. The habitat modeling and evaluation approach proposed in this study helps to reasonably model habitat quality by incorporating habitat fragmentation indices and represents a useful tool that can be used to predict cascaded hydropower impacts on fish habitat. The approach can be used for other cascaded reservoirs and it is not limited to 1 reservoir. It can also be used to model large river networks if sufficient data are available. Additional variables can be included in the model framework, including water level fluctuation, which may help to predict hydrological effects on fish habitat. The established model can be used to evaluate the habitat suitability of other endangered fish species in the studied reservoir. It is worth noting that the spatial variation trends of the WUA and HHSI were not completely synchronized under the combined control of the upstream and downstream hydropower dam. The WUA could not necessarily represent the habitat quality of the reservoir, especially from the perspective of regions with different hydrodynamic characteristics. This asynchrony requires a comprehensive assessment based on the specific research objectives. In further studies, it will be important to prioritize the conservation needs of highly threatened fish species while also considering the survival requirements of other local fish species, which can be achieved by incorporating multiple species, especially multiple endangered species, in habitat modeling frameworks to further optimize the resolution of this issue. Meanwhile, in order to achieve restoration of the population, the habitat requirements at whole life stages should be considered in the habitat model to evaluate the habitat integrity that allows endangered fish species to complete their life histories.

5. CONCLUSIONS

In this study, we found significant spatial differences in habitat suitability in the lotic, transitional, and lentic zones of the reservoir. Habitat suitability and habitat fragment conditions showed spatial inconsistencies to some extent. Notably, we observed substantial differences in the habitat requirements between juvenile and spawning fish. This finding underscores the necessity of considering the needs of fish at different life stages when formulating conservation measures. A comprehensive understanding of their adaptability and survival requirements across various habitats is crucial. This study systematically evaluated the habitats in a cascaded hydropower reservoir in terms of habitat suitability and habitat fragmentation, providing recommendations for the conservation and restoration of *Coreius guichenoti*. Although this study provides an important tool and method to quantify habitat quality under complex hydrodynamic variation, the habitat factors that affect fish populations vary, especially in reservoirs. Other considerations include water temperature, water quality, and biological factors like food resources and predators that could be considered in future studies. Moreover, a large-scale fish habitat evaluation for whole life stages in all species' ranges should be conducted to provide robust schemes for effective fish population restoration and sustainable river management.

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