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Fish Assemblage Responses to a Low-head Dam Removal in the Lancang River

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Abstract: Dam removal is becoming an effective approach for aquatic biodiversity restoration in damming river in order to balance the aquatic ecosystem conservation with large-scale cascade damming. However, the effects of dam removal on fish communities in Asian mountainous rivers, which are dominated by Cypriniformes fishes, are still not well known. To determine whether dam removal on a mountainous river benefit restoration of fish diversity, we investigated the response of fish assemblage to dam removal using a before-after-control-impact design in two tributaries of the Lancang River (dam removal river: the Jidu River, and control river: the Fengdian River). Fish surveys were conducted one year prior to dam removal (2012) and three years (2013–2015) following dam removal. We observed rapidly and notably spatio-temporal changes in fish biodiversity metrics and assemblage structure, occurring in the Jidu River within the first year after dam removal. Overall, fish species richness, density and Shannon-Wiener diversity all increased immediately in above- and below-dam sites, and maintained a stable level in subsequent years, compared to unchanged situation in the control river. All sites in the Jidu River experienced shifts in fish composition after dam removal, with the greatest temporal changes occurred in sites below- and above- the former dam, resulting in a temporal homogenization tendency in the dam removed river. These findings suggest that dam removal can benefit the recovery of habitat conditions and fish community in Asian mountainous rivers, but the results should be further evaluated when apply to other dammed rivers since the dam age, fluvial geomorphology and situation of source populations could all affect the responses of fish assemblages.

Keywords: fish diversity; dam demolition; habitat recovery; Cypriniformes; international rivers

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1 Introduction

Dams have dramatically altered over half of the river systems in the world (Nilsson et al., 2005) by creating physical barriers (Watters, 1996), converting lotic habitat to lentic habitat (Martinez et al., 1994), and modifying temperature and hydrological regimes (Magilligan and Nislow, 2005; Olden and Naiman, 2010). Conse-

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quently, dams truncate the distributions of aquatic species (Watters, 1996; Catalano et al., 2007; Zhang et al., 2018), block fish migrations (Bulow et al., 1988; Sá-Oliveira et al., 2015), and significantly change the composition of fish communities (e.g., from predominantly lotic-adapted to lentic-adapted species) (Yan et al., 2013; Sá-Oliveira et al., 2015). Furthermore, changes in water temperature induced by impoundments can prompt a suite of biological responses, including fish behaviour and metabolic rates (Helms et al., 2011), and river system disconnectivity can also lead to the isolation of fish populations and reductions in genetic diversity (Dudley and Platania, 2007; Tsuboi et al., 2010).

In the past several decades, as old dams become functionally obsolete or structurally deficient, dam removal is becoming an economically feasible management action to enhance the structural integrity of river systems (Stanley and Doyle, 2003; O'Connor et al., 2015). Given that dam removal may restore geomorphic and increase connectivity in previously disturbed lotic ecosystems (Bednarek, 2001; Hart et al., 2002), many ecologists and environment protection agencies recommended it as a crucial choice of river restoration (Doyle et al., 2005). Despite the high expectation of dam removal in ecological restoration, inconsistent responses of fish communities have been observed in previous studies. Some studies showed remarked increases in fish species diversity and abundance in the upper reaches of removed dam (Burroughs et al., 2009; Gardner et al., 2013; Chang et al., 2017), whereas other studies indicated immediate declines in species richness and abundance in the down reaches of removed dam (Catalano et al., 2007; Gardner et al., 2013). Temporal patterns of fish assemblage responses to dam removal may range from several months to several decades (Hart et al., 2002; Doyle et al., 2005). In addition, differences in the composition of fish fauna may also result in different responses to dam removals. For example, studies show that dam removal resulted in decrease in abundance of lentic species (e.g., *Cyprinus carpio*) and increase in the abundance of lotic species (*Micropterus dolomieu*) (Kanehl et al., 1997).

Low-head dams and small hydropower developments are widely distributed in mountainous streams in China, and their construction rate is higher than that of the large- and middle-scale cascade dams (Huang and Yan, 2009). By the end of 2012, more than 45 000 low-head dams had been built to produce electricity to aid rural economic development in China (Tian, 2013), which indicates that large-scale small hydropower development has been a major driver of changes in river ecosystems. Low-head dam removal may be considered as one effort used to compensate for the negative effects of human-mediated activities (e.g., construction of large cascade dams) on river ecosystems in China. Despite the fact that many ecological studies involving dam removal have been undertaken in Europe and North American (Hart et al., 2002), there are rare studies examining the effects of dam removal on fish assemblages in Asian mainland. Fish fauna in Asian mainland are dominated by Cypriniformes fishes (Chen, 1998; Chu et al., 1999), quite different from the fish fauna in Europe and North America (Nelson, 2006). Such differences in fish composition may result in different outcomes following the dam removal and affect the application of European and North American dam removal strategy in Asian rivers (Doyle et al., 2005).

In 2012, a low-head dam was removed from the Jidu River, a tributary of the Lancang River, providing a rare opportunity to gain insight into the responses of fish assemblages in Asian mountainous river to dam removal. The purpose of the present study is to address the following questions: 1) how quickly do changes in the fish species composition occur after dam removal? 2) how do fish species composition and spatial distribution vary? Since this is the first case of dam removal for ecological recovery and restoration in China, our results could provide useful information for dam management and dammed river restoration where fish communities are dominated by Cypriniformes fishes in China.

2 Materials and Methods

2.1 Site descriptions

The Jidu River (JDR) and the Fengdian River (FDR) are both tributaries of the Lancang River (LCR), located in southwestern China (Fig. 1a). JDR has a mainstream length of 41.5 km and a watershed area of 238.0 km^2 (Fig. 1b and Fig.1c). JDR is a high-gradient (with average gradient 46.2 m/km), cold-water stream with steep stone banks, high current velocity, and coarse substrates. The hydrology of this river was disturbed between 2008 and 2012 because a diversion dam and flume were built

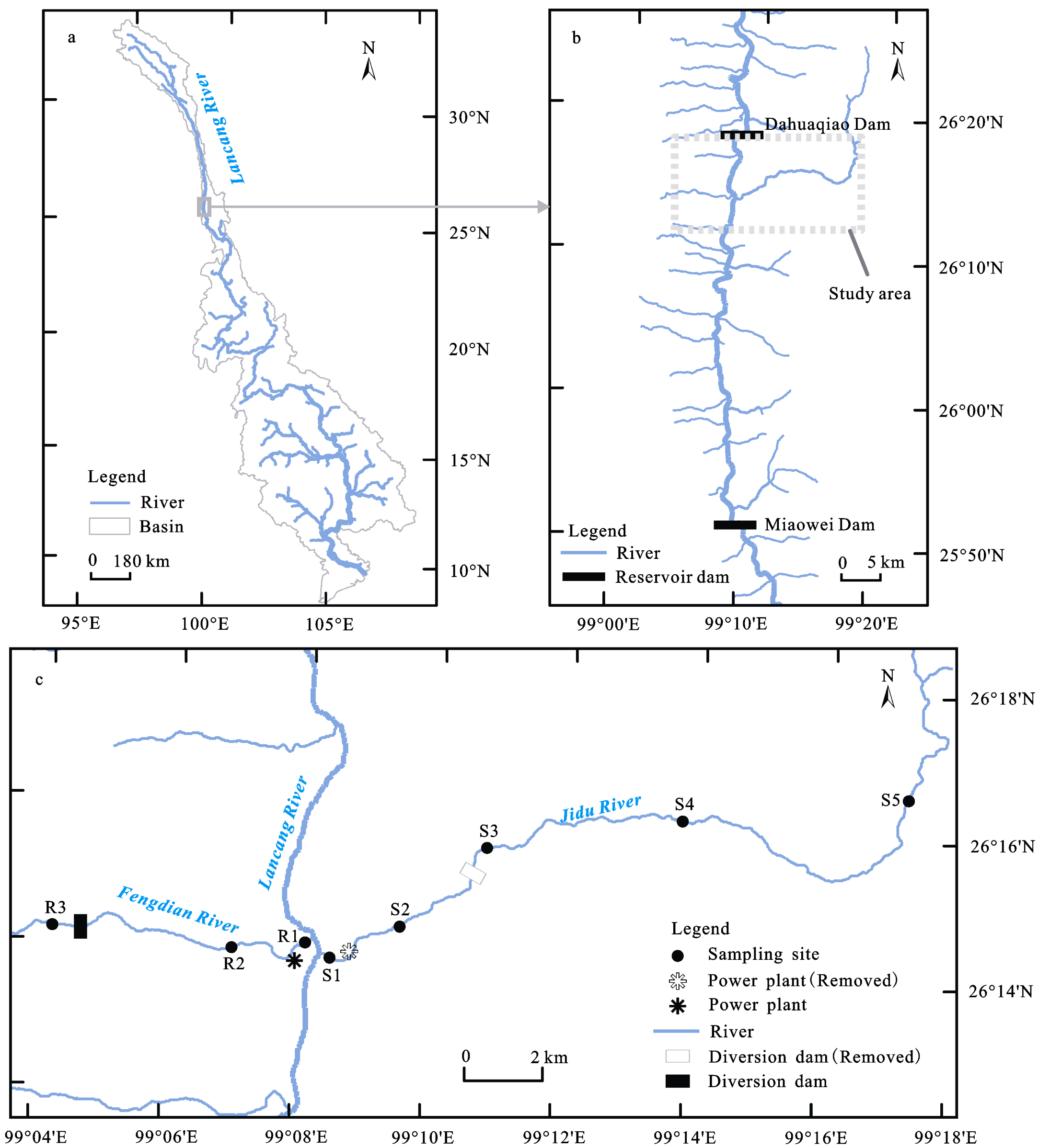

Fig. 1 The location of the study area and the distribution of sampling sites

less than 5.0 km upstream of the confluence, and they diverted most of the flow for the production of hydroelectric power. The 4.5-km reach directly below the dam received only seepage flow (< 0.1 m^3/s). The majority of flow was diverted through a flume to the Jidu power plant, and then all of water was returned to JDR and continued for 0.5 km to the confluence with LCR (Fig. 1c). The dam created a very small reservoir (<50 m in length), because the flow was immediately diverted through a flume and transported for hydroelectric power. Dam removal began in September 2012 with the removal of the diversion dam; its flume and power plant were removed in 2013. FDR, with two low-head dams on its mainstream, is near JDR. According to fish surveys before dam removal, FDR has a similar fish composition to JDR. Thus, it was designated as the control river in this study (Fig. 1c).

We compared fish assemblage response between a river experiencing dam removal (JDR) and a dammed river (FDR) using the before-after-control-impact (BACI) design (Stewart-Oaten, 1986). In our research system, JDR was divided into two reaches, one on either side of the Jidu dam, hereafter referred to as the 'downstream reach' and 'upstream reach' with respect to the dam site. The downstream reach has two sample sites (S1 and S2): S1 is between the outlet of the Jidu power plant and the confluence with LCR, and S2 is the 2.0-km reach directly below the dam. The upstream reach has three sample sites (S3–S5). S3 is the 1.0-km reach directly above the dam, and S4 and S5 are approximately 6.0 km and 13.0 km upstream from the dam, respectively. In FDR, there are three sample sites (R1, R2 and R3), which are symmetrical with S1–S3 in JDR (Fig. 1c)

2.2 Fish surveys

Fish surveys were conducted once prior to dam removal (September 2012) and three times (September 2013, 2014 and 2015) after dam removal. All eight sites were sampled in river reaches of 300 m to 400 m in length, which included both pool and riffle habitats. Collections were made using a backpack electrofishing unit (LR-24Electrofisher, Smith-Root, Inc., Vancouver, WA, USA). The fish sampling crew consisted of three persons. One operated the backpack electrofishing unit, and two were equipped with dip nets and followed the operator and netted fish. At each site, the sampling area was measured to calculate fish abundance and biomass per unit area. Individual fishes were identified to species, and the total weight of each species was measured using an electronic balance. All fish were held in a water basin after being sampled and released back in the river following identification and measurement. Feeding guilds were assigned to each species based on Chu et al. (1999) and FishBase (Froese and Pauly, 2016).

2.3 Habitat characterization

Water temperature and water depth are two important factors that influence fish communities affected by dam building. In the downstream reach of JDR and FDR, water temperature was logged at two-hour intervals from April 2013 to April 2014 and water depth were logged from March to June 2014. As major components in stream food webs (Cummins and Klug, 1979), benthic macroinvertebrates may play an important role in the distribution patterns of fish. Therefore, the biomass of benthic macroinvertebrates was surveyed at all sites in summer 2015 (Fig. 1). At each site, three quantitative bottom samples were taken with a Surber net (30 cm × 30 cm in area, with a mesh size of 500 μm) and sieved with a 500-μm sieve in the field. Specimens were manually sorted out from sediment on a white porcelain plate in the field laboratory and preserved in 70% ethyl alcohol. The wet biomass of macroinvertebrates was obtained with an electronic balance after samples were blotted. Each habitat (e.g., riffle, pool, edge) was sampled proportionally based on its representation at each site. At each sampling site, altitude was registered using a Garmin GPS-76 system. The channel width and water depth were averaged from several equal transects. Distance from source was obtained from a digital map with a 1 : 50 000 scale. Dissolved oxygen (DO) and pH were measured in the field with a Bante 900 Pmulti-parameter water quality meter (Bante Instruments Limited, Shanghai, China). Total nitrogen (TN), total phosphorus (TP), and chemical oxygen demand (COD) were measured according to the standard methods for observation and analysis in China (Huang et al., 1999).

2.4 Statistical analysis

Permutational analysis of multivariate dispersions (PERMDISP, Anderson, 2006) was separately used to test whether the heterogeneity of fish composition varied between different years in the two rivers. PERMDISP is similar to the Levene's test of homogeneity of variances, and it further uses the ANOVA F-statistic to compare among-group differences based on the distance each observation is from its group centroid. Significance of among-group differences was tested through permutation of least-squares residuals. The null hypothesis that there were no differences among the four years was tested using a permutations test with 9999 iterations.

3 Results

3.1 Habitat

After the dam removal (April 2013 to April 2014), the average daily water temperature in the downstream reach of JDR was 14.9℃, but in the downstream reach of FDR, it was 12.1℃, indicating that the water in JDR was significantly warmer after the dam removal (Fig. 2a). In the downstream reach of JDR in summer (March to June 2014), the average water depth (± SD) was

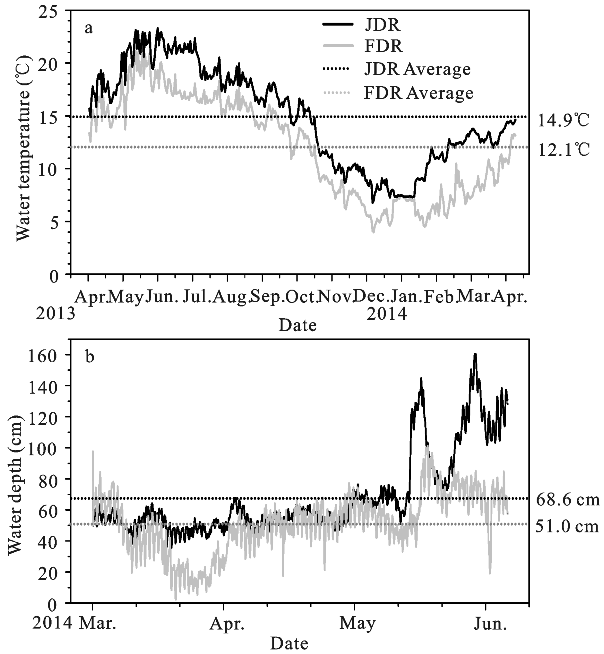

Fig. 2 Water temperature (a) and water depth (b) in the Jidu River after dam removal and the control river (Fengdian River)

(68.6 ± 20.5) cm and its daily variation amplitude (± SD) was (12.3 ± 4.8) cm. In the downstream reach of the control river, the summer average water depth ((51.0 ± 13.6) cm) was lower than that in JDR, and its daily variation amplitude ((22.0 ± 5.9) cm) was higher than that in JDR (Fig. 2b).

Both rivers have similar biophysical backgrounds characterized by alkalescence, high level of dissolved oxygen and low levels of nutrient salts (Table 1), indicating that the dam removal did not significant change the water quality in JDR.

Based on the survey in summer 2015, the invertebrate biomass in JDR was higher than that in FDR (Fig. 3), particularly in the sites above the dam (S3 vs. R3).

3.2 Changes in fish species composition

We collected 1955 fish individuals, representing 17 species in 16 genera and 6 families, in both rivers across sampling years. Of them, 16 species were endemic to China, and 13 species were endemic to LCR. Cypriniformes were the dominant order, comprising four families (Cyprinidae, Nemacheilidae, Cobitidae and Balitoridae), 12 genera and 12 species, followed by Siluriformes (3 species) and Perciformes (2 species) (Fig. 4). Fish species composition significantly changed in JDR after dam removal. The fish richness in JDR increased from 9 to 17 after dam removal, indicating notable responses of fish assemblage to dam removal. In contrast, there was no significant change in fish composition (from 8 to 7) in FDR during this period.

3.3 Changes in fish distributions

Pre-removal distribution patterns varied among these nine species in JDR. Four species (*Pseudorasbora parva*,

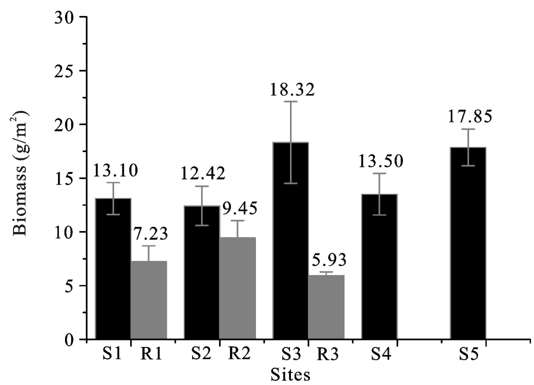

Fig. 3 Macroinvertebrate biomass in the Jidu River after dam removal and in the control river (Fengdian River). Numbers show the mean biomass, and error bars represent ±1 standard error from the mean.

Table 1 Mean value ± SD of environmental variables at the 8 studied sites in the Jidu River and the Fengdian River in April 2014

Sites	Distance from the dam (km)	Elevation (m)	pH	DO (mg/L)	TN (mg/L)	TP (mg/L)	COD (mg/L)
S1	4.5	1408	7.60±0.34	8.93±0.61	1.03±0.47	0.120±0.090	2.01±0.93
S2	2.0	1503	7.23±0.22	8.74±0.73	0.72±0.34	0.053±0.270	1.11±0.36
S3	1.0	1628	7.19±0.19	8.54±0.77	0.85±0.42	0.071±0.063	0.98±0.52
S4	6.0	1922	7.12±0.25	8.61±0.63	0.80±0.61	0.049±0.031	1.88±0.54
S5	13.0	2213	6.96±0.08	8.47±0.86	0.85±0.52	0.071±0.023	1.37±0.61
R1	6.0	1407	7.20±0.16	9.21±0.79	0.79±0.49	0.044±0.015	1.26±0.79
R2	4.0	1506	7.11±0.21	8.56±0.69	0.73±0.23	0.087±0.043	1.36±0.34
R3	1.0	1779	7.01±0.27	8.40±0.47	0.82±0.45	0.092±0.024	0.89±0.57

Tinca tinca, *Hemimyzon tchangi*, and *Rhinogobius giurinus*) occurred below, but never above the dam, whereas one species (*Triplophysa brevicauda*) was found above, but never below the dam. The remaining four species (*Schizothorax lissolabiatus*, *Carassius auratus*, *Homatula anguillioides*, and *Misgurnus anguillicaudatus*) were collected both in the upstream and downstream reaches in JDR. After the dam removal, each of the five species with truncated pre-removal distributions colonized new upstream sites or downstream sites. Furthermore, eight new species (including three Cyprinidae fishes: *Cyprinus carpio*, *Percocypris retrodorslis*, and *Garra mirofrontis*; three Sisoridae fishes: *Oreoglanis setiger*, *Creteuchiloglanis longipectoralis*, *Glyptothorax zanaensis*; and finally, *Sinibotia longiventralis* and *Rhinogobius cliffordpopei*) colonized in the JDR (Fig. 4). In FDR, eight species were captured in 2012 and nine species between 2013–2015 (Fig. 4).

3.4 Changes in fish species richness, density, biomass and diversity

Before the dam removal, fish species richness was highest at S1 and R1 (8 species for both sites). After the dam removal, species richness at sites below the dam (S1 and S2) and above the dam (S3) increased quickly (ranging from 5 to 10 species) within one year after dam removal, and richness maintained a stable level in subsequent years (Fig. 5a). During the same period, the species richness was relatively consistent at the sites R1–R3 in the control river.

The fish density increased sharply at S1–S3 after dam removal (Fig. 5b), largely due to the abundant increase of two species, *S. lissolabiatus* and *H. anguillioides* (Fig. 4). However, fish density changed little at the upper sites (S4 and S5) of JDR and in the control river (R1–R3) (Fig. 5b). Similarly, fish biomass at sites S1 and S2 increased sharply over the next 2 years after the dam removal, but biomass at sites above the dam were consistently low and essentially flat from 2012 to 2015 (Fig. 5c). After the dam removal, the Shannon-Wiener diversity index broadly increased at S2–S5 of JDR, but it remained at a stable level in other sites (Fig. 5d).

3.5 Changes in fish assemblage structure

The PERMDISP analysis indicated a temporal homogenization trend that appeared as a pattern of greatest dispersion among sites in JDR during 2012, followed by a trend towards similarity between sites in subsequent

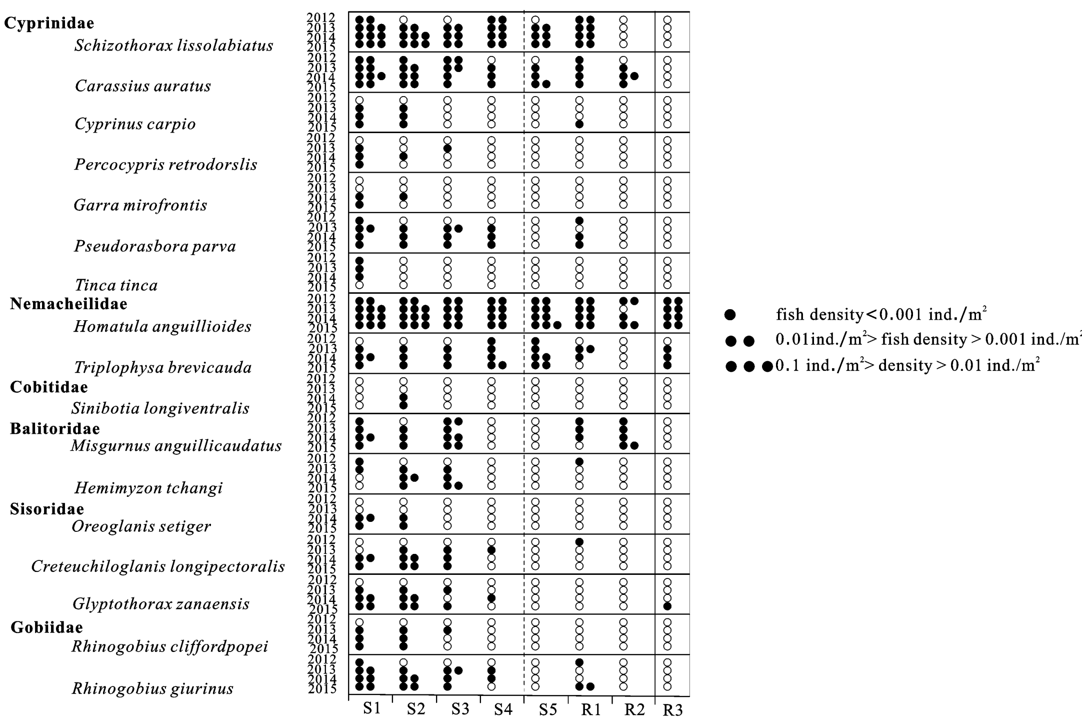

Fig. 4 Fish distributions change in the Jidu River (S1–S5) and the Fengdian River (R1–R3) at all sampling sites, showing the presence (solid circles) or absence (open circles) of 18 fish species before (2012) and after (2013–2015) the dam removal. The location of the former dam on the Jidu River is indicated by the vertical dashed line.

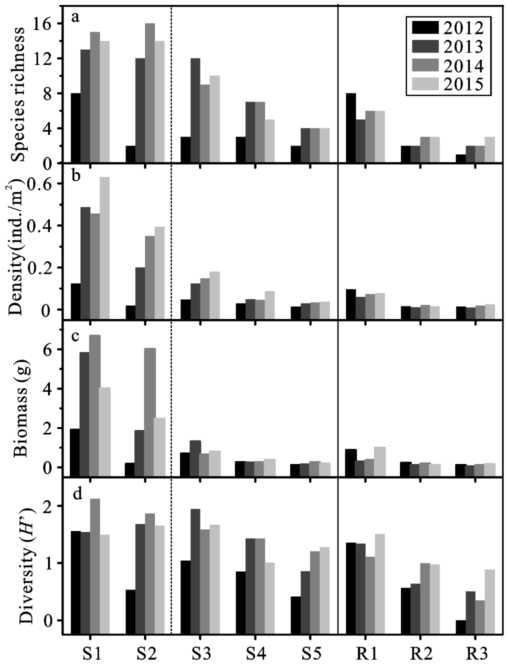

Fig. 5 Species richness (a), density (b), biomass (c) and diversity (H') (d) of fish assemblage before (2012) and after (2013–2015) the dam removal at eight sites (S1–S5 in the Jidu River, and R1–R3 in the Fengdian River). The former dam site is indicated by the vertical dashed line.

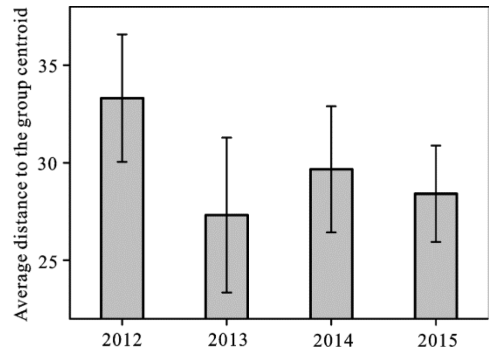

Fig. 6 Permutational analysis of multivariate dispersions (PERMDISP) showing the mean ± SE distances to the group centroid based on fish dissimilarity in the Jidu River sites in 2012–2015

years (Fig. 6). However, this homogenous trend was not significant (P = 0.602)

3.6 Changes in feeding guilds

Changes in fish assemblage composition in JDR were accompanied by shifts in relative abundance of different feeding guilds (Fig. 7). Before the dam was removed, the omnivorous fishes dominated almost all sites in JDR. After the dam removal, the relative abundance of insectivores increased at sites S1–S3; this was mainly influenced by the increase of the three Sisoridae fishes of *O. setiger*, *C. longipectoralis*, and *G. zanaensis*. Moreover, some piscivorous fishes were also observed in S3. In sites R1, R2, R3, S4, and S5, the fish feeding guilds were constant and only omnivorous (with the exception of an insectivore *G. zanaensis* individual in site R3).

4 Discussion

JDR experienced notable spatiotemporal changes in fish

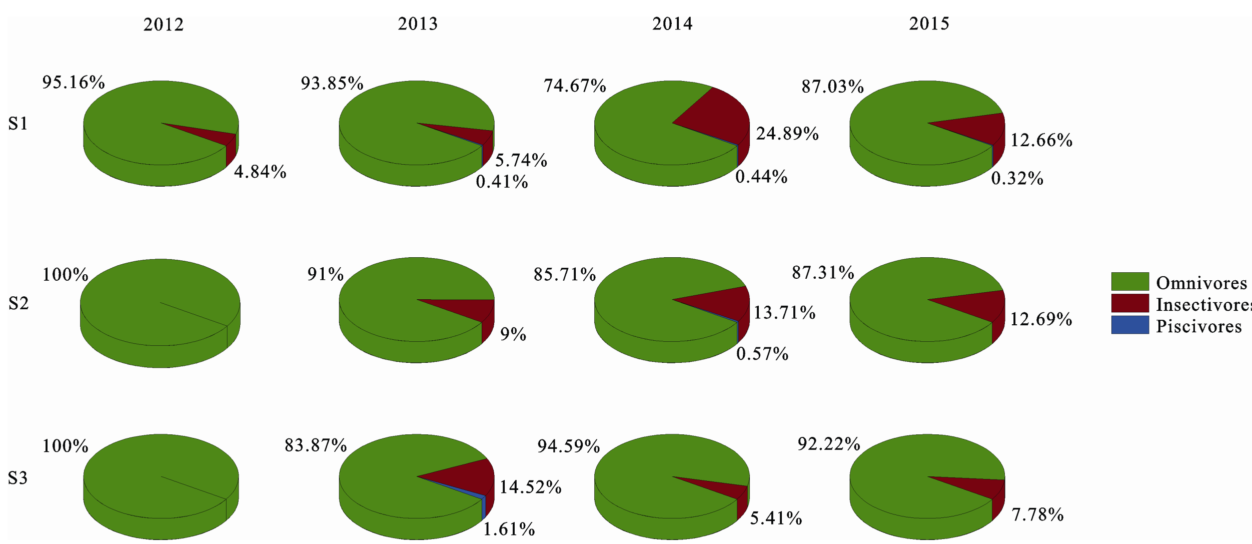

Fig. 7 Proportion of fish assemblage by representative feeding guilds at sites S1–S3 in the Jidu River before (2012) and after (2013–2015) the dam removal

assemblage structure after dam removal, with rapidly increases in fish species richness, density and diversity index in above- and below-dam sites. There have been many ecological studies on dam removal carried out in Europe and North America (Doyle et al., 2005; Dorobek et al., 2015). However, no such studies involving the effects of dam removal on fish fauna in Asian mainland rivers, especially in those ones dominated by Cypriniformes fishes. To our knowledge, the current work is the first study examining the recovery process of fish assemblages after dam removal in Asian mainland river. The promising results in this study may provide major benefits to the restoration of fish communities that are severely disturbed by pervasive low-head dams in China (Tian, 2013) and enhance the understanding of Cypriniformes fish restoration in this area.

The mechanisms driving the spatio-temporal recovery of fish assemblages after dam removal are not well understood (Doyle et al., 2005). A variety of factors can influence the responses of fish assemblages following a dam removal; thus, it is difficult to predict the restoration of fish assemblages across a range of temporal or spatial dimensions. In our study, fish composition and spatial distribution in JDR experienced dramatic changes after dam removal. Five species with truncated pre-removal distributions colonized new upstream or downstream sites, which demonstrates the importance of dam removal for restoring river connectivity and promoting gene flow at the catchment scale (Fagan, 2002). Although the need for river connectivity is mainly reported for salmonid fishes (Stanley and Doyle, 2003; Mchenry and Pess, 2008), removing dams may also release restrictions on movement of other non-salmonid fishes (Fullerton et al., 2010). The observed re-colonization after the removal of the dam in our study suggests that dams also blocked the movement of Cypriniformes fishes from source populations into sites above or below the former dam.

In addition to river connectivity, the habitat changes associated with dam removal may also influence the spatial distribution of fish assemblages. In the present study, the downstream portion of the experimental river experienced obvious environmental changes, *i.e.*, warmer water and more stable water depths (Fig. 2); providing more appropriate habitat for fishes (Baltz et al., 1987; King and Warburton, 2007). Furthermore, we found changes in the composition of fish feeding guilds, with an increase of insectivores after dam removal (Fig. 7). Such increases in above- and below-dam sites were accompanied by an increase in macroinvertebrates at these sites (Fig. 3), which indicates that benthic invertebrates, as important components of stream food webs (Cummins and Klug, 1979), could potentially drive changes in fish assemblages. For example, Kanehl et al. (1997) found that invertebrate recovery was slightly faster due to their short lifespan and, they supported the recovery of smallmouth bass in the Milwaukee River. Given that the improvement of biotic-abiotic conditions were accompanied by the recovery of river connectivity and their comprehensive interaction on fish assemblages, further studies are required to better understand the mechanisms of fish assemblage restoration in rivers where dams have been removed.

The changes in fish assemblages in JDR occurred within the first year following the dam removal, suggesting that rapid geomorphic recovery and habitat changes occurred at the former dam sites, because the recovery rate of fish assemblages is determined by the habitat recovery rate (Doyle et al., 2005). For JDR, impoundments had little accumulated sediment due to its young age (< 5 years). Removing this dam could rapidly progress geomorphic recovery at the dam site and have minimal effects on downstream fish habitats after dam removal. In addition, JDR is located along a mountainous area that creates a high slope (average gradient = 46.2 m/km), and it has high-energy systems that erode sediment and recover habitats more efficiently (Catalano et al., 2007). The rapid recovery of fish assemblages after dam removal may also be induced by the re-colonization of individuals that previously resided in LCR, because the river reach of LCR that is connected to JDR is still without dam influences, and it supports natural fish assemblages (Liu et al., 2011; Zhang et al., 2018). The recovery rate of fish assemblages in this study is consistent with other studies that have reported annual-scale recoveries after dam removals (Catalano et al., 2007; Poulos et al., 2014), indicating that fish assemblages mainly composed of Cypriniformes fish can also recover quickly after a dam is removed.

A homogenized trend of fish assemblages was observed in JDR after dam removal, with an increase in the similarity among sites. This means that the circumstance changes after dam removal, fish species no longer experienced dispersal limitation caused by the dam, and the pronounced differences in composition between dam-impacted (below- and above-dam) sites and other sites were eliminated. It is well known that fragmentation induced by damming could cause local extirpations of sensitive species in dam-impacted river reaches (Olden and Poff, 2003). Thus, great community dissimilarities are often observed for fishes between river reaches both adjacent to dams and those far from dams (Katano et al., 2006; McLaughlin et al., 2006; Perkin and Gido, 2012; Kornis et al., 2015), as was the case in JDR prior to dam removal. Similar to other rivers in Europe and North America, this study indicated that dam removal in Asian mountainous rivers can also enhance the recovery of habitat fragmentation and lead to community homogenization overtime by facilitating species re-colonization (Rahel, 2002; Kornis et al., 2015).

Our study indicates that dam removal can improve habitat quality and provide major benefits to fish restoration in a tributary of LCR. Hence, these promising results provide useful implications for conservation biologists and environmental management agencies. However, there are several caveats to applying our results to other dammed rivers. First, the dam in JDR is very young, with a relatively small quantity of sediment stored in the reservoir, which is beneficial to the rapid recovery of habitat (Doyle et al., 2005). In addition, the recovery of the eight fish species in JDR was attributed to the well-protected source populations in LCR. Such variables could lead to uncertainty in regard to the responses of fish assemblages to dam removal. Therefore, to verify this conclusion, more studies should be implemented on a broader range of dams removed from rivers.

5 Conclusions

In this study, we observed rapid and notable spatio-temporal changes in fish biodiversity metrics and assemblage structure, which occurred in JDR within the first year following the removal of the dam. The fish species richness, density and Shannon-Wiener diversity increased immediately for all fish in both the above- and below-dam sites after dam removal. Restoration of fish assemblages in JDR after dam removal should be driven by improved habitat traits, such as river connectivity, water temperature, water depth and fish food sources. These results provide practical information for aquatic ecosystem conservation in dammed mountainous rivers.

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