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Response of Fish Assemblages to Habitat Changes and Fishing Activity in a Tributary of the Jinsha River in Southwest China

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Abstract

Reservoir impoundment affects fish habitat condition, in turn likely influencing the spatial and temporal distribution patterns of fish assemblage structure in the impounded area. Fishing activity and instream gravel and sand mining are important anthropogenic factors, and flow discharge, water temperature, and precipitation are important natural environmental variables; both anthropogenic and natural factors likely have impacted fish assemblage structure in impounded and unimpounded waterbodies. We used multivariate analysis to evaluate the combined effects of two adjacent reservoir impoundments in the main stem of a large river (Jinsha River; the upper segments of the Yangtze River), overfishing, instream gravel and sand mining, the natural flow regime, and other environmental variables (water temperature and precipitation) on fish assemblage structure in the Heishui River, a small, free-flowing tributary upstream of the mainstream reservoirs. Fish assemblage data and abiotic data collected over 10 years (2008, 2010, and 2011–2017) were analyzed. The results showed that fish assemblages of the Heishui River temporally clustered into two groups that were strongly associated with the two downstream cascade reservoirs (Xiangjiaba and Xiluodu reservoirs) in the main-stem Jinsha River. The relationships between fish assemblage structure and abiotic factors were tested using a distance-based linear model and were visualized using distance-based redundancy analysis, showing that the main factors explaining the interannual and seasonal variation in fish assemblage structure were instream gravel and sand mining, mainstream reservoir impoundment, and seasonal flow regime. Among these, instream gravel and

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sand mining in this tributary played the most significant role in affecting the temporal variation of fish assemblage structure and explained 34.12% of the total variability. Mainstream reservoir impoundment and seasonal flow regime exerted secondary effects on the temporal variation of fish assemblage structure and together explained 13.39% (7.00% and 6.39%, respectively) of the total variability. This study suggests that the relevant administrative agencies should focus more on free-flowing habitat maintenance in this tributary and the control of instream gravel and sand mining.

Understanding how obvious changes to the external environment affect fish assemblage structure has been a key issue in aquatic ecology in recent decades (Quinn and Kwak 2003; Gao et al. 2015; Sá-Oliveira et al. 2015; dos Santos et al. 2018). Fish assemblages in many rivers worldwide have been subjected to various human-induced disturbances (dos Santos et al. 2018). In particular, river damming is one of the most widespread and drastic disturbances that can affect fish assemblages (Quinn and Kwak 2003; dos Santos et al. 2018; Loures and Pompeu 2019). River damming plays an important role in altering hydrological and hydrodynamic processes and is considered to be the greatest global threat to the biodiversity and integrity of fish species (Gao et al. 2010; Sá-Oliveira et al. 2015). The spatial distribution of lotic fish species in impounded areas is easily affected by flow regulation of the reservoir (Daufresne et al. 2015). Many lotic fish species have been forced to migrate immediately from the lacustrine zone to the riverine and transitional zones in a reservoir (Gao et al. 2010) or to the free-flowing segments of river tributaries (Hugo et al. 2018) upon the filling of the reservoir. Due to the shrinkage of running-water habitats in the main stem, the fish community structure of tributaries that are naturally connected to the main stem is important for contributing to the maintenance of diversity in areas that have already been impacted by damming (Hugo et al. 2018).

As important components of river networks, tributaries function as conduits for the flow of organic material and energy entering the river main stem (Koster et al. 2014). Tributary streams with hierarchical structures not only act as corridors for the movement and migration of aquatic fauna by linking geographically distinct populations across the river network but also directly provide important spawning and feeding grounds for fish in the river main stem through main-stem–tributary connections (Koster et al. 2014; Hugo et al. 2018). Due to the close links between the tributaries and river main stem, pronounced seasonal variation in fish assemblages is observed in many tributaries (Koster et al. 2014; Yang et al. 2018a). This may imply the close relationship between fish assemblages in the main stem and those in the tributaries. A previous study found remarkable variation in fish assemblage structure in the impounded reaches of tributaries after the filling of main-stem reservoirs (Guenther and Spacie 2006). However, less attention has been paid to the effects of

river damming in the main stem on the unimpounded reaches of tributaries or on natural tributaries (Falke and Gido 2006; Hugo et al. 2018).

In addition to dam construction, other anthropogenic activities—mainly including overharvest, instream sand and gravel mining, and water pollution—have led to destructive effects on fish assemblages by altering the hydrological, thermodynamic, and geomorphic regimes of freshwater systems (Gao et al. 2015; dos Santos et al. 2018). Generally, taken together, these stressors exert combined effects on the variation in fish assemblages (Gao et al. 2015). Hence, identifying the relative importance of different stressors on variation in fish assemblages is highly important for the targeted implementation of fish protection measures. However, studies evaluating the combined effects of different anthropogenic activities on fish assemblages often consider the effects of the different factors in isolation (Marshall et al. 2008; Gao et al. 2010; Mims and Olden 2013; Pelicice et al. 2015); consider the joint effect of two factors, such as river damming and water pollution (Barrella and Petrere 2003); or focus on either overfishing (Yang et al. 2018b) or climate change (Zhang et al. 2019). Meanwhile, the effects of multiple stressors (particularly including sand and gravel mining) have received less investigation in quantitative study (dos Santos et al. 2018).

Instream sand and gravel mining is relatively common in streams and rivers worldwide. Through head cutting, streambed degradation, and channel widening, instream sand and gravel mining can alter or destroy the natural physical habitat and in turn can affect benthic conditions (Haley and Johnston 2014). To date, the ecological effects of instream mining on fish assemblages have been considered to be mixed (Paukert et al. 2008). However, studies estimating the consequences of instream mining have focused on species richness and diversity while paying little attention to the variation in assemblage structure (Paukert et al. 2008; Hwang et al. 2014). The lack of information on the relationship between the variation in fish assemblage structure and instream mining is likely to hamper optimal decision making for the protection of fish resources.

The goal of the present study was to investigate the combined effects of cascade dams (a series of dams constructed immediately downstream of each other along a river) in the main stem of a large river, along with

overfishing, instream gravel and sand mining, the natural flow regime, and other environmental variables (water temperature and precipitation), on the variation in fish assemblages in an upstream, free-flowing tributary. We hypothesized that (1) the fish assemblage in the upstream, free-flowing tributary (which is naturally connected to the main stem) is strongly affected by the impoundment of downstream cascade reservoirs in the main stem; and (2) local variables, including fishing activity, instream gravel and sand mining, the natural flow regime, water temperature, and precipitation, also can significantly affect fish assemblage structure in the free-flowing tributary.

METHODS

Study area and fish collection.—The Jinsha River, located in the upper Yangtze River basin (Figure 1), is the most biodiverse region of China and is an important hydropower development area. Since 2005, many cascade hydropower dams have been constructed on the Jinsha River. The effects of cascade hydropower stations on fish assemblages have attracted increasing attention in recent years (Cheng et al. 2015). Currently, there are four large hydropower stations in the lower reaches of the Jinsha River: Wudongde and Baihetan dams are under construction, and impoundment of Xiangjiaba Reservoir (XJBR) and Xiluodu Reservoir (XLDR) by Xiangjiaba and Xiluodu dams began in October 2012 and May 2013, respectively.

This study was performed in the lower reaches of the Heishui River, a typical mountainous tributary situated in the lower reach of the Jinsha River (Figure 1). The Heishui River mouth has a distance of about 50 km from the backwater tail of XLDR when that reservoir operates at its highest water level. The Heishui River has a total length of 173.3 km, with a natural fall in elevation of 1,931 m and a total drainage area of 3,653 km² (Yang et al. 2018a). The average annual discharge at the Heishui River mouth is 80.0 m³/s (Fu et al. 2016). The Heishui River has a conductivity of 125.2–245.0 μ S/cm, and its riverbed is mainly covered by gravel, rock, and sand (Fu et al. 2016). This river is wadeable. Due to diversified habitats, more than 20 fish species inhabit the Heishui River, including 13 endemic fish species (Yang et al. 2018a). Some segments of the river are important spawning grounds for many endemic fishes (Yang et al. 2018a).

Electrofishing was conducted in the whole river segments (1) between Laomuhe Station and the town of Hulukou and (2) between the town of Shili and the village of Xiejiaba from 2006 to 2017 (i.e., 2006, 2008, and 2010–2017). Fish collections were performed twice (in July and December) in each sampling year. Each sampling event lasted 4–5 d until all river segments were sampled, and sampling was carried out for approximately 6 h/d. A

battery-supplied backpack electrofishing machine with a nominal power of 3,000 W was used for fish collection. The sampling crew comprised three persons: one person operated the electrofishing machine, while the other two used handheld nets to catch the fish. Because the sampling reach was wadeable, fish collection was performed by walking along the riverbanks. All captured individuals were first identified at the species level in the field.

Habitat data acquisition.—Daily water temperature and daily flow discharge data during the two sampling months in the Heishui River (Ningnan hydrologic station) were collected from the Hydrological Almanac of the Yangtze River (unpublished data). The precipitation data for July and December of each year were collected from the Sichuan statistical yearbook (2006–2017) and the Meteorological Bureau of Ningnan County (Statistical Bureau of Sichuan and National Bureau of Statistics Survey Office in Sichuan 2013–2017).

Fishing intensity and mining indicators.—It is difficult to estimate the fishing intensity of the surveyed area due to the considerable level of illegal fishing. However, due to the dietary habits of the local population, the fishermen prefer to catch the fish species with a large size (e.g., *Schizothorax prenanti*); thus, the fishing intensity for a fish species with large sizes likely can indirectly reflect the fishing intensity in the entire study area. The fishing intensity during each sampling season in each year was estimated using the variable exploitation rates of *Schizothorax prenanti* (*Ers*). The *Ers* data were obtained via population dynamic analysis for this important and dominant fish species. First, the asymptotic length and growth coefficient of *Schizothorax prenanti* during the whole sampling period were estimated by the von Bertalanffy growth function. The von Bertalanffy growth function was established by fitting to the data on individual age and body length (Pauly et al. 1992). We used the Pauly (1980) equation to estimate the instantaneous natural mortality coefficient (*M*) for each year based on the data for asymptotic length, growth coefficient, and average annual water temperature. In this study, we assumed that *M* was a constant among different sampling seasons and years. The catch curve method (Pauly 1990) was then used to estimate the instantaneous total mortality coefficient (*Z*) of the population in different sampling seasons. Finally, the fishing mortality coefficient (*F*) for each sampling season was calculated as the difference between *Z* and *M*, and the exploitation rate (*E*) in each sampling season was calculated as $E = F/Z$.

Likewise, it was difficult to obtain data on the intensity of instream gravel and sand mining in the sampling area due to the lack of standardized and timely reporting for the amount of gravel and sand extracted from the river. Therefore, we chose an alternative variable to represent this intensity—namely the annual fixed asset investment (*Afsi*) in Ningnan County. Liu and Sun (2008) found that there was a double

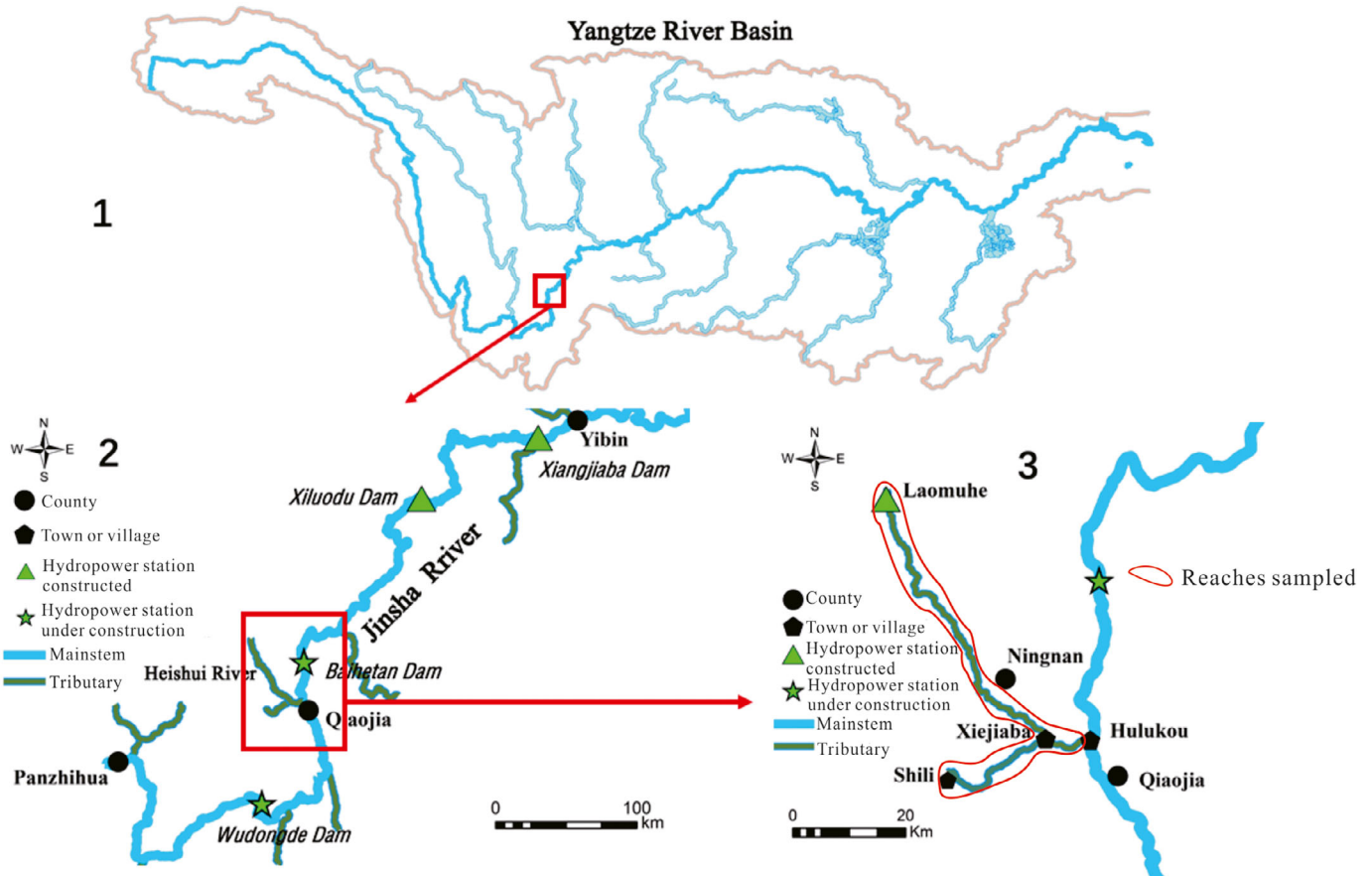


FIGURE 1. Map of the study area, including the Yangtze River basin (1), the lower reaches of the Jinsha River (2), and the lower reaches of the Heishui River (3), China. Impoundment of the Xiangjiaba and Xiluodu reservoirs began in October 2012 and May 2013, respectively. Sampling was carried out in the whole river segments between the Laomuhe hydropower station and the town of Hulukou and between the town of Shili and the village of Xiejiaba (3).

logarithmic relationship between cement consumption and fixed asset investment, and Xu et al. (2016) found that the quantity of sand dredging was proportional to cement production. Hence, investment of fixed assets is positively related to sand dredging quantity. If we can confirm that the fixed asset investment in the survey area is mainly in the construction industry and that the gravel and sand required by the construction industry are obtained mainly from the Heishui River, then the *Afsi* can indirectly reflect the amount of instream gravel and sand mining in the Heishui River. Based on the statistical bulletin of the national economic and social development of Ningnan County (http://www.ningnan.gov.cn/zfxgk_31568/zfxgknr/tjsj_31356/202003/t20200307_1492159.html), more than 95% of the fixed asset investment in the survey area is in the construction industry. According to the field survey, there are only two main rivers in the survey area: the Heishui River and the Jinsha River. There are some sand mining areas in the Jinsha River, whereas a larger quantity of sand mining areas can be observed in the Heishui River. However, the gravel and sand required by the

construction industry in Ningnan County are obtained mainly from the Heishui River, considering that the city is near the river, thus providing an advantage in terms of lower costs for gravel and sand transportation. The *Afsi* data for 2008–2017 were collected from the statistical bulletin of the national economic and social development of Ningnan County (2015–2017), while the *Afsi* data for 2006 were acquired from the Statistics Bureau of Ningnan County. The statistics describing all variables are presented in Table 1.

Statistical analysis.— All scientific names of the fish collected in the field were checked against FishBase (Froese and Pauly 2018), and the ecotypes of all fish species were identified using the relevant literature (Ding 1994; Froese and Pauly 2018) based on the feeding habits and flow preferences of each species. The percentage of the number of individuals for each fish species in the entire sampling period was calculated. Sampling effort was measured in days, and CPUE was standardized to the number of fish captured in a single day (Majewski et al. 2013). Each fish species' CPUE in each sampling month (July and

TABLE 1. Statistics describing the variables used in this study during the different sampling months (*Mat* = monthly average water temperature; *Maf* = monthly average flow discharge; *Mp* = monthly precipitation; *Afsi* = annual fixed asset investment in Ningnan County; *Ers* = exploitation rate for *Schizothorax prenanti*; *Ismr* = impoundment stage of the main-stem reservoirs in the Jinsha River).

Variable	Summer (Jul)		Winter (Dec)		Summer (Jul) + winter (Dec)	
	Range	Mean	Range	Mean	Range	Mean
<i>Mat</i> (°C)	21.1–24.2	23.1	11.7–13.6	12.9		
<i>Maf</i> (m ³ /s)	53.1–279.1	147.9	28.9–52.0	41.0		
<i>Mp</i> (mm)	83.4–431.5	190.7	0–31.4	6.9		
<i>Afsi</i> (100 million yuan)					3.51–110.01	52.11
<i>Ers</i>	0.54–0.75	0.65	0.55–0.75	0.65		
<i>Ismr</i>	1.0–3.0		1.0–3.0			

December) during each year was calculated. A $\log_{10}(x + 1)$ transformation was applied to all CPUE data to decrease the influence of highly abundant species on the subsequent analyses (Yang et al. 2012).

Hierarchical cluster analyses using group-average linking based upon the Bray–Curtis similarity matrix were employed to identify the potential temporal groupings of fish assemblages (Clarke and Gorley 2006; Majewski et al. 2013). The Bray–Curtis similarity matrix was created by using the $\log_{10}(x + 1)$ -transformed CPUE data for each species in each sampling month during each year. The permutation-based analysis of similarity (ANOSIM) was simultaneously applied to test for statistically significant groupings (Clarke and Gorley 2006). Similarity percentage analysis was then applied to identify the species that provided the greatest discrimination amongst the statistical groupings, and all of the species cumulatively contributing over 70% of the dissimilarity were listed in one table (Clarke and Gorley 2006). Canonical analysis of principal coordinates (CAP) was chosen to identify the fish species distribution along seasonal gradients (summer [July] and winter [December]; Anderson et al. 2008). Detrended correspondence analysis (DCA) was first used to select the model analyzing the biotic–abiotic relationships, considering that the species that are controlled by environmental factors tend to have unimodal distributions. If the maximum value of axis lengths in the first four axes of the DCA is more than 4, then it is more suitable to select the unimodal model (canonical correspondence analysis); if the maximum value is less than 3, it is better to select the linear model (redundancy analysis); and if the maximum value is between 3 and 4, both unimodal and linear models are feasible. In our study, the maximum value of axis lengths in the first four axes of the DCA was 2.1924 (Appendix Table A.1). Hence, a distance-based linear model (DistLM; Anderson et al. 2008) was used to examine the relationships between CPUE and the six abiotic variables (Table 1). In this model, each species' CPUE in each sampling month for each year was

defined as the response variable, whereas the six abiotic variables were defined as the explanatory variables. Prior to this analysis, the six abiotic variables were estimated for linear dependencies by calculating their variance inflation factors (VIFs); abiotic variables with VIFs greater than 10 (i.e., indicating collinearity) were excluded from DistLM analysis (Borcard et al. 2011).

In the DistLM analysis, Akaike's information criterion and 9,999 permutations based on the similarity matrices were used to identify the model with optimal fitness of prediction. The Bray–Curtis index was used to determine the distances between relative species abundance and the abiotic variables (Sangil et al. 2013). During this process, the data describing CPUE and abiotic variables were normalized to reduce the influence of the outliers and extreme values. Meanwhile, to identify the potential interaction effects among the biotic–abiotic relationships, both marginal and sequential tests were used separately to examine the responses of the CPUE data to the changes in each variable and in the entire set of abiotic variables, thereby leading to the identification of significant abiotic variables for the subsequent distance-based redundancy analysis (dbRDA). Finally, dbRDA was used to visualize the effects of the abiotic variables on temporal changes in the fish assemblage according to the multivariate regression model generated by DistLM analysis (Anderson et al. 2008).

Statistical analyses were performed with PRIMER-E version 6 and PERMANOVA+ (Anderson et al. 2008). The significance level in this work was set to $P < 0.05$.

RESULTS

Fish Species Composition

Overall, 20,054 specimens belonging to 3 orders, 8 families, and 44 species were collected during the sampling periods (Table 2). Cyprinidae was the dominant family (18

species), followed by Bagridae (8 species), Cobitidae (6 species), Homalopteridae (4 species), Amblycipitidae (3 species), Siluridae (2 species), Sisoridae (2 species), and Gobiidae (1 species). Among all of the captured fish species, 65.91% of fish species fed mainly on periphytic algae (phytobenthivorous) and/or zoobenthos (zoobenthivorous), and 77.27% of fish species preferred to inhabit running water (lotic). The most abundant fish species were *Homatula variegata* (accounting for 24.17% of the total number of collected fish individuals; CPUE = 118.22 individuals/d), followed by *Homatula potanini* (19.38%; 94.78 individuals/d), *Triplophysa anterodorsalis* (13.30%; 65.07 individuals/d), *Glyptothorax sinensis* (5.92%; individuals/d), and *Schizothorax prenanti* (5.90%; 28.88 individuals/d).

Temporal Changes in the Fish Assemblage

Cluster analysis of species abundance in summer and winter over 10 years identified two major cluster groupings at a similarity level of 67.42% (Figure 2; ANOSIM: global $R = 0.672$, $P = 0.001$, $n = 999$ permutations). Group 1 consisted of fish assemblages sampled in the 4 years prior to the impoundment of XJBR and XLDR (2006, 2008, 2010, and 2011) and the fish assemblages sampled in the summers of 2012 and 2013, while group 2 was comprised of fish assemblages sampled during the 4 years after impoundment of XJBR and XLDR (from 2014 to 2017) and the fish assemblages sampled in the winters of 2012 and 2013 (Figure 2). Prior to impoundment of XJBR and XLDR, the fish assemblage structures between different seasons in the same year tended to cluster together; however, after impoundment of those reservoirs, the fish assemblage structures in the same season across years tended to cluster together (Figure 2).

The similarity percentage analysis showed that 19 fish species (mainly the phytobenthivores and/or zoobenthivores) contributed 71.91% of the dissimilarity in fish assemblages between groups 1 and 2 (Table 3). *Schizothorax wangchiachii* accounted for the highest proportion of the average dissimilarity between groups 1 and 2 at 5.80%. *Schizothorax wangchiachii*, together with *Homatula variegata* (5.26%), *T. anterodorsalis* (5.03%), *Euchiloglanis kishinouyei* (4.19%), Freshwater Minnow *Zacco platypus* (4.15%), *Spinibarbus sinensis* (3.98%), *Lepturichthys fimbriata* (3.85%), *Gobiobotia filifer* (3.82%), *Jinshaia sinensis* (3.79%), *Gobiobotia sinensis* (3.78%), *Jinshaia abbreviata* (3.70%), and *Schizothorax grahami* (3.61%), accounted for over half of the average dissimilarity between the groups. The abundances of 14 lotic fish species and 1 eurytopic fish species decreased from group 1 to group 2, whereas four lotic fish species increased their abundances from group 1 to group 2 (Table 3). Canonical analysis of principal coordinates indicated a separation between the summer fish assemblage and the winter fish assemblage for each year (Figure 3). The CAP axis 1 (CAP1) separated

the fish assemblages between groups 1 and 2, while CAP2 almost separated the fish assemblages between summer and winter. The ANOSIM demonstrated significant differences in the fish assemblages between summer and winter in group 1 ($R = 0.787$, $P = 0.002$) and in group 2 ($R = 0.682$, $P = 0.008$); the summer ($R = 0.718$, $P = 0.005$) and winter ($R = 0.671$, $P = 0.010$) fish assemblages were significantly different between groups 1 and 2. Figure 3 also shows that there was a higher dissimilarity in fish assemblage structure between the two seasons (winter and summer) in group 2 than in group 1.

Relationship between the Fish Assemblage and Abiotic Variables

The VIF analysis detected no collinearity among the six abiotic variables (monthly average water temperature [*Mat*], monthly average flow discharge [*Maf*], monthly precipitation [*Mp*], *Afsi*, *Ers*, and impoundment stage of the main-stem Jinsha River reservoirs [*Ismr*]), thus enabling the use of all six selected variables in the DistLM analysis. In the marginal tests of the DistLM analysis, four habitat variables (*Mat*, *Afsi*, *Ers*, and *Ismr*) were significantly associated with the abundances of species within the fish assemblages (all $P < 0.05$). The above-described variables explained 32.47, 0.34, 0.15, and 0.33% of the variation, respectively. In the sequential test of the DistLM analysis, five variables (excluding *Ers*) explained 47.10% of the total variation (adjusted $R^2 = 0.471$) and were identified as the final predictor variables for the dbRDA. Three variables were significantly associated with the species abundances and identified as significant variables. The *Afsi* variable had a greater explanatory ability (30.47%) than *Ismr* (7.00%) and *Maf* (6.39%; Table 4).

Based on the DistLM analysis results, five predictor variables were selected and employed in the dbRDA to visualize the effect of changes in the abiotic variables on the temporal variations of the fish assemblages in the lower reaches of the Heishui River. The two dbRDA axes (dbRDA1 and dbRDA2) together explained 46.6% of the total variation. The order of importance of the five abiotic variables for affecting the temporal variation in the fish assemblage was as follows: $Afsi > Ismr > Maf > Mp > Mat$. The fish assemblages in group 1 (except for summer 2012 and summer 2013) were positively associated with dbRDA1, while all of the fish assemblages in group 2 were negatively associated with dbRDA1. With the exception of winter 2010, the winter fish assemblages were positively associated with dbRDA2, while all of the summer fish assemblages were negatively associated with dbRDA2. The variable *Afsi* was positively correlated with the winter and summer fish assemblages in group 2, whereas it was negatively related to the winter and summer fish assemblages in group 1. The variable *Ismr* was

TABLE 2. Species composition, ecotype, and abundance of fishes collected from the lower reaches of the Heishui River, 2006–2017 (ZB = zoobenthivorous; PB = phytobenthivorous; Z = zooplanktivorous; C = carnivorous; O = omnivorous; EU = eurytopic; L = lotic).

Order	Family	Species	Feeding habits	Flow preference	Percentage of individual number (%)	CPUE (individuals/d)
Cypriniformes	Cobitidae	<i>Homatula potanini</i>	HP	L	19.38	94.78
		<i>Homatula variegata</i>	HV	L	24.17	118.22
		<i>Sinibotia supercilialis</i>	SSUP	L	0.42	2.07
		<i>Leptobotia taeniops</i>	LT	L	0.11	0.56
		<i>Paramisgurnus dabryanus</i>	PD	L	0.97	4.76
		<i>Triplophysa anterodorsalis</i>	TA	L	13.30	65.07
	Cyprinidae	Freshwater Minnow	ZP	L	2.31	11.32
		<i>Zacco platypus</i>				
		<i>Gobiobotia filifer</i>	GF	L	0.45	2.20
		<i>Anabarilius liui liui</i>	ALL	L	0.00	0.02
		Chinese Lizard	SD	EU	0.97	4.76
		<i>Gudgeon Saurogobio dabryi</i>				
		Chinese False	AR	EU	0.19	0.93
		<i>Gudgeon Abbottina rivularis</i>				
		<i>Abbottina obtusirostris</i>	AO	L	0.46	2.24
		<i>Onychostoma simum</i>	OS	L	0.05	0.24
		<i>Garra imberba</i>	GI	L	0.29	1.44
		<i>Pseudogyrinocheilus prochilus</i>	PPRO	L	0.10	0.49
		<i>Spinibarbus sinensis</i>	SSIN	EU	0.70	3.44
		<i>Percocypris pingi</i>	PPIN	L	0.06	0.29
		<i>Schizothorax prenanti</i>	SP	L	5.90	28.88
		<i>Schizothorax wangchiachii</i>	SW	L	4.14	20.27
		<i>Schizothorax chongi</i>	SC	L	0.24	1.20
		<i>Schizothorax grahami</i>	SG	L	0.80	3.93
		<i>Schizothorax kozlovi</i>	SK	L	0.20	1.00
		Common Carp	CC	EU	0.48	2.34
		<i>Cyprinus carpio</i>				
		Goldfish <i>Carassius auratus</i>	CA	EU	0.42	2.07
	Homalopteridae	<i>Lepturichthys fimbriata</i>	LF	L	2.58	12.63
		<i>Jinshaia sinensis</i>	JS	L	4.98	24.37
		<i>Jinshaia abbreviata</i>	JA	L	1.59	7.78
		<i>Sinogastromyzon sichangensis</i>	SSIC	L	0.10	0.51
Siluriformes	Siluridae	Amur Catfish <i>Silurus asotus</i>	SA	EU	0.69	3.39
		Chinese Large-mouth Catfish <i>Silurus meridionalis</i>	SM	L	0.07	0.34

TABLE 2. Continued.

Order	Family	Species	Feeding habits	Flow preference	Percentage of individual number (%)	CPUE (individuals/d)
	Bagridae	Yellow Catfish <i>Tachysurus fulvidraco</i>	TF	EU	0.05	0.27
		<i>Tachysurus nitidus</i>	TN	EU	0.11	0.56
		<i>Pseudobagrus vachellii</i>	PV	EU	0.30	1.46
		<i>Pseudobagrus crassilabris</i>	PC	L	0.34	1.66
		<i>Pseudobagrus emarginatus</i>	PPEM	L	2.64	12.90
		<i>Pseudobagrus pratti</i>	PPRA	L	0.30	1.49
		<i>Pseudobagrus truncatus</i>	PT	L	0.07	0.37
		<i>Hemibagrus macropterus</i>	HM	L	0.21	1.02
	Amblycipitidae	<i>Liobagrus marginatus</i>	LMUS	L	3.04	14.88
		<i>Liobagrus nigricauda</i>	LN	L	0.00	0.02
		<i>Liobagrus marginatoides</i>	LMES	L	0.03	0.17
	Sisoridae	<i>Glyptothorax sinensis</i>	GS	L	5.92	28.95
		<i>Euchiloglanis kishinouyei</i>	EK	L	0.64	3.15
Perciformes	Gobiidae	<i>Rhinogobius giurinus</i>	RG	EU	0.14	0.68

largely positively correlated with the winter fish assemblages in group 2 and was largely negatively correlated with the winter assemblages in group 1, while the variables *Maf*, *Mp*, and *Mat* were positively associated with

the summer fish assemblages in groups 1 and 2 and displayed a negative relationship with the winter fish assemblages in groups 1 and 2 (Figure 4).

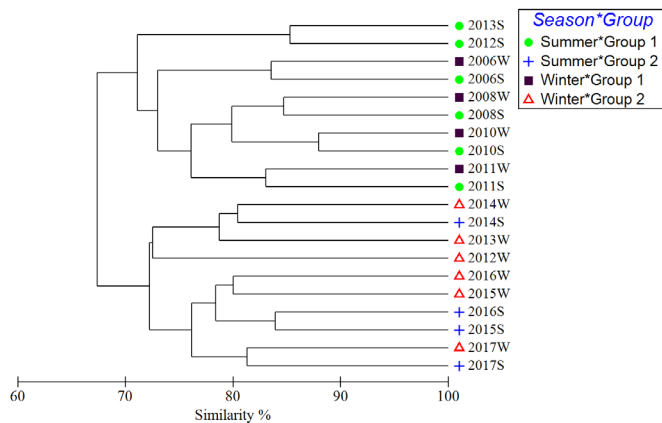


FIGURE 2. Dendrogram of hierarchical cluster analysis results for Heishui River fish assemblages in the summer (S) and winter (W), 2006–2017. Different marks (green circles, blue plus signs, black squares, and red triangles) indicate different seasons and groupings.

DISCUSSION

Temporal Distribution Pattern of Fish Assemblages

Hugo et al. (2018) found that the preservation of dam-free tributaries is of utmost importance because these tributaries contribute to diversity maintenance in the areas that are already impacted by damming in the main-stem river. Fluvial specialists have dominated the fish assemblages of the free-flowing segments in tributaries, even if the tributaries are directly connected to a mainstream reservoir (Guenther and Spacie 2006; Hugo et al. 2018). Although our study has reached an analogous conclusion, the shifts in abundances of the fluvial specialist species were clearly observed from 2006 to 2017. Abundances of many lotic species clearly decreased, while abundances increased slightly only for very few lotic species, highlighting the dramatic temporal variation in the fish assemblage of the Heishui River (Ding 1994).

TABLE 3. Fish species that contributed to the dissimilarity in the fish assemblages between groups 1 and 2 and their feeding habits and flow preferences (ZB = zoobenthivorous; PB = phytobenthivorous; Z = zooplanktivorous; C = carnivorous; O = omnivorous; EU = eurytopic; L = lotic).

Species	Average abundance		Contribution to dissimilarity		Feeding habits	Flow preference
	Group 1 (individuals/d)	Group 2 (individuals/d)	Contribution (%)	Cumulative (%)		
<i>Schizothorax wangchiachii</i>	1.77	1.00	5.80	5.80	PB	L
<i>Homatula variegata</i>	3.11	3.61	5.26	11.06	ZB, PB	L
<i>Triplophysa anterodorsalis</i>	3.36	2.52	5.03	16.09	ZB, PB	L
<i>Euchiloglanis kishinouyei</i>	1.11	0.13	4.19	20.28	ZB, PB	L
Freshwater Minnow <i>Zacco platypus</i>	1.33	0.67	4.15	24.43	Z, ZB	L
<i>Spinibarbus sinensis</i>	1.01	0.15	3.98	28.41	O	EU
<i>Lepturichthys fimbriata</i>	1.90	1.25	3.85	32.26	PB	L
<i>Gobiobotia filifer</i>	0.95	0.03	3.82	36.08	ZB	L
<i>Jinshaia sinensis</i>	2.01	2.03	3.79	39.87	PB	L
<i>Gobiobotia sinensis</i>	2.49	2.09	3.78	43.66	ZB, PB	L
<i>Jinshaia abbreviata</i>	1.64	0.78	3.70	47.36	PB	L
<i>Schizothorax grahami</i>	1.19	0.34	3.61	50.97	PB	L
<i>Liobagrus marginatus</i>	2.13	1.43	3.49	54.46	ZB	L
<i>Homatula potanini</i>	3.33	3.46	3.42	57.88	ZB, PB	L
<i>Sinibotia superciliaris</i>	0.88	0.09	3.36	61.24	ZB	L
<i>Pseudobagrus emarginatus</i>	1.52	1.80	3.08	64.33	C, ZB	L
<i>Schizothorax prenanti</i>	2.50	2.23	3.01	67.34	PB	L
Chinese Lizard Gudgeon <i>Saurogobio dabryi</i>	1.12	0.82	2.47	69.81	ZB	L
<i>Paramisgurnus dabryanus</i>	1.06	0.94	2.11	71.91	ZB, PB	L

Fish assemblages sampled in different months of different years were separated into two distinct groupings that were mainly related to the pre- and postimpoundment periods for XJBR and XLDR. With the exception of the summer 2013 fish assemblage, impoundment of XJBR and XLDR clearly separated the fish assemblages of the different seasons for all sampling years into two groups reflecting the periods before and after impoundment of these reservoirs. The fish assemblage for summer 2013 (after impoundment of XJBR and XLDR) belonged to group 1 and the fish assemblage for winter 2012 (after impoundment of XJBR) belonged to group 2, which may be attributed to the seasonal spawning migration of the fish. Yang et al. (2018a) found that fish spawning migrations have significant impacts on the fish assemblage variation in the sampling area of this tributary. Some fish species migrating to this tributary in the summer (the main reproduction season) likely gave rise to the stability of the fish assemblage in summer 2013 during a short period after mainstream reservoir impoundment, whereas an immediate change was observed in the fish assemblage for winter 2012 after the completion of the XJBR impoundment. This change may

be due to the lesser migration into the Heishui River in the winter. The CAP and ANOSIM also showed the clear seasonal variation in the Heishui River fish assemblage, in agreement with the results obtained by Yang et al. (2018a).

Although the fish assemblage in summer 2013 was highly similar to that before the impoundment of XJBR, the significant change in the fish assemblages for both summer and winter after the summer of 2013 presumably indicates the effects of the time of river damming on the upstream natural tributaries. It is likely that the ecological effects of reservoir impoundment in the mainstream on the tributary fish assemblage appear gradually over time. Quinn and Kwak (2003) found that reservoir impoundment exerted long-term effects on the downstream riverine fishes, and they concluded that short-term monitoring after impoundment is inadequate for determining the impact of dams on lotic fish assemblages. Furthermore, Loures and Pompeu (2019) found that even after two decades of monitoring, important changes in the fish assemblages within both lotic and lentic environments of the Araguari reservoir cascade system (Paraná River basin, Brazil) were still observed.

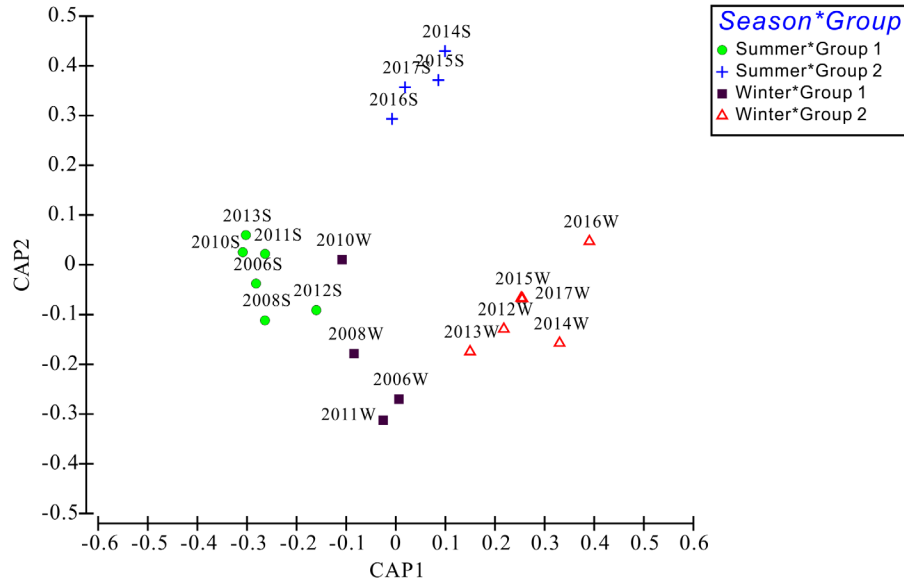


FIGURE 3. Canonical analysis of principal coordinates (CAP) for Heishui River fish assemblages in the summer (S) and winter (W), 2006–2017. Different marks (green circles, blue plus signs, black squares, and red triangles) indicate different seasons and groupings.

TABLE 4. Results of a distance-based linear model routine considering the Heishui River fish assemblages during 2006–2017. Marginal tests examined the relationships between each abiotic variable and biological data. Sequential tests examined the relationships between all of the abiotic variables and biological data. Bold italic type indicates significance ($P < 0.05$). Percent variation is the percentage of the total variation explained by the variable (*Mat* = monthly average water temperature; *Maf* = monthly average flow discharge; *Mp* = monthly precipitation; *Afsi* = annual fixed asset investment in Ningnan County; *Ersp* = exploitation rate of *Schizothorax prenanti*; *Ismr* = impoundment stage of the main-stem reservoirs of the Jinsha River).

Variable	Marginal tests			Sequential tests			
	Pseudo- <i>F</i>	<i>P</i>	Percent variation	Pseudo- <i>F</i>	<i>P</i>	Percent variation	Adjusted R^2
<i>Mat</i>	8.656	<i>0.001</i>	32.47	1.212	0.324	3.37	0.74
<i>Maf</i>	1.877	0.082	9.44	2.823	<i>0.003</i>	9.38	6.39
<i>Mp</i>	1.407	0.175	7.25	1.744	0.059	4.92	2.50
<i>Afsi</i>	9.326	<i>0.001</i>	0.34	9.326	<i>0.001</i>	34.12	30.47
<i>Ersp</i>	3.225	<i>0.007</i>	0.15				
<i>Ismr</i>	8.953	<i>0.001</i>	0.33	3.119	<i>0.001</i>	9.21	7.00

Relationship between the Fish Assemblage and Habitat Variables

Consistent with our first hypothesis and partly consistent with our second hypothesis, our results indicated that *Maf*, *Afsi*, and *Ismr* significantly influenced the annual and seasonal variation in the Heishui River fish assemblage. The variable *Maf* reflects variation in the flow regime, *Afsi* indicates variation in the intensity of instream gravel and sand mining, and *Ismr* highlights the upstream effects of the reservoir cascade in the main-stream. Among these, *Afsi* played the most important role in determining the temporal variation in the fish assemblage of the Heishui River. Previous studies have found that sand mining induces drastic physical changes that in turn give rise to severe declines in species richness

and diversity and fish abundance (Dudgeon et al. 2006; Hwang et al. 2014) and production (Mingist and Gebremedhin 2016). By strongly altering the substrate composition, sand mining likely destroys the feeding, resting/refuge, and spawning habitats of some fish species (Paukert et al. 2008; Boucher et al. 2014; Ramezani et al. 2014; Smith et al. 2016). In this study, the spawning grounds of many endemic fish species (particularly species belonging to the subfamily Schizothoracinae, which spawn demersal eggs between sand and gravel) were distributed in the sampling area (Yang et al. 2018a). It is likely that the gravel and sand mining in the Heishui River affected the availability of spawning grounds; therefore, the gravel and sand mining activities in this tributary should be strictly controlled in the future.

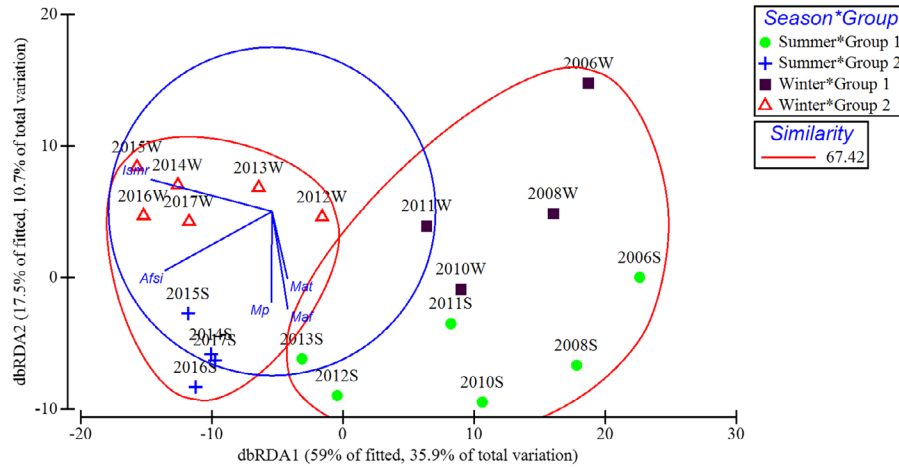


FIGURE 4. Visualization of the effect of abiotic changes on temporal variation in Heishui River fish assemblages during summer (S) and winter (W) for two clustered groups by using the distance-based redundancy analysis (dbRDA) method. Different symbols (green circles, blue plus signs, black squares, and red triangles) indicate different seasons and groupings. Variables are monthly average water temperature (*Mat*), monthly average flow discharge (*Maf*), monthly precipitation (*Mp*), annual fixed asset investments in Ningnan County (*Afsi*), and impoundment stage of the main-stem reservoirs in the Jinsha River (*Ismr*).

Compared to *Maf*, *Ismr* displayed greater explanatory ability (Table 4). The significance of *Ismr* indicated the obvious upstream effects of mainstream reservoir impoundment on the fish assemblage in this tributary. Due to the shrinkage of running-water habitats in the main stem resulting from impoundment of XJBR and XLDR, the abundances of some lotic fish species in the main stem inevitably decreased (Cheng et al. 2015), likely reducing the individual quantities of some fish migrating into this tributary during the spawning seasons. The upstream effects of a reservoir on fish assemblages were also observed in other studies (Falke and Guido 2006; Gao et al. 2010; Franssen and Tobler 2013). However, the degree of impact of mainstream reservoir impoundment on fish assemblage variation in a natural tributary likely depends on (1) the proportion of fish migrating between the mainstream and the tributary, (2) the size of suitable habitat area for endemic fish species in the tributary, and (3) the tributary's spatial proximity to the reservoirs (Falke and Guido 2006; dos Santos et al. 2018). The higher proportion of resident fish species in the tributary indicates that the lower impact results from the immigration and emigration of individual fish, while a sufficiently suitable habitat area for the endemic fish species in the tributary is beneficial for the stability of their populations (Falke and Guido 2006; Zhang et al. 2019). In addition, the distance from a reservoir likely influences the interspecies relationships among fishes in the tributary over the long run because the reservoir is a source of diffusion of various exotic or eurytopic species (Gao et al. 2010; Franchi et al. 2014; Casimiro et al. 2017).

Our results also showed that *Maf* played an important role in constructing the temporal variation in the fish

assemblage over all periods of observation, indicating the significance of the natural flow regime (Table 4). Many studies have found that the natural flow regime reflects long-term, historical patterns of flow variability that have shaped riverine species' adaptations and continue to shape community and ecosystem structure and function by structuring the physical habitat template, providing connectivity and framing biotic interactions (Marchetti and Moyle 2001; Mims and Olden 2013; Poff 2017; dos Santos et al. 2018). Moreover, *Maf* peaked in summer and declined in winter (Figure 4), indicating that the seasonal variation in flow discharge has a profound impact on the changes in fish assemblage structure. Previous studies have found that yearly and seasonal variation in the flow regime has a large effect on fish assemblages (Marchetti and Moyle 2001; Jowett et al. 2005). Furthermore, Kennard et al. (2007) found that characteristics of long-term flow regime (e.g., predictable seasonal flow variation) were more important predictors of fish assemblages than the variables describing the short-term history of hydrological events.

The variable *Ersp* had a significant effect on the temporal variation in fish assemblages in the marginal tests but was excluded from being used as the final predictor variable for the sequential tests (Table 4), indicating that some of the variables were interrelated (Yang et al. 2018b). Compared to the other five variables, *Ersp* showed a weaker interpretive ability for the temporal variation in fish assemblages when all variables were used together in the DistLM. However, during the sampling period, the *Ersp* value for each sampling month was greater than 0.5, meaning that at least half of *Schizothorax prenanti* deaths were attributable to fishery capture and indicating strong

fishing pressure throughout the entire sampling period (Raghavan et al. 2011). This may also suggest that in the river section with continuous high fishing intensity, the river damming, seasonal flow changes, and instream sand mining play more important roles in shaping fish assemblage structure relative to fishing activity (dos Santos et al. 2018; Yang et al. 2018b).

Recommendations for Fish Resource Management

Identification of important anthropogenic factors that affect the temporal variation in fish assemblages has important implications for the conservation and management of fish resources (Quinn and Kwak 2003). The present study showed that three significant factors (mainstream reservoir impoundment, instream gravel and sand mining, and natural seasonal flow variability) were closely correlated with fish assemblage structure in the unimpounded segments of a tributary. Therefore, considering that the lower reaches of the main-stem Jinsha River will host the reservoir cascade, the relevant government agencies should devote more attention to (1) the maintenance of free-flowing habitat in this tributary and (2) the control of instream gravel and sand mining. Removal of all dams upstream of the study area and minimization of instream gravel and sand mining in the Heishui River are likely to be the optimal solutions for the conservation of endemic fish resources considering that the suitable running-water habitat area in the main-stem Jinsha River and its tributaries is quite small (Zhang et al. 2014; Cheng et al. 2015; Zhang et al. 2019).

Conclusions

In this study, biotic–abiotic relationships were developed to predict and analyze the impacts of mainstream reservoir impoundment, instream gravel and sand mining, fishing activity, and natural seasonal flow regime on the temporal variation in fish assemblage structure within unimpounded segments of a tributary (the Heishui River). The instream gravel and sand mining strongly disrupts the suitable habitats of many fish species in this tributary, significantly affecting the temporal variation pattern of fish assemblages. Meanwhile, a significant upstream effect of mainstream impoundment (XLDR and XJBR) on interannual and seasonal variation in the Heishui River fish assemblage was observed. In addition, the seasonal flow regimes also significantly and vigorously shaped the patterns of temporal variation in the Heishui River fish assemblage. However, the implications of this study may be limited because abiotic changes occurring in the years since this study was conducted, as well as other factors (e.g., water quality and interspecies relationships), may affect fish assemblages. An improvement to identify the true relationship between the biotic and abiotic factors should rely on a more long-term approach and specifically on ecological monitoring in the future.

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Appendix: Additional Data

TABLE A.1. Summary of detrended correspondence analysis (DCA) showing the first four axes (DCA1–DCA4).

Axes	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.2066	0.1088	0.0872	0.0569
Axis lengths	1.9083	1.4173	2.1924	1.14867