Influences of local habitat, tributary position, and dam characteristics on fish assemblages within impoundments of low-head dams in the tributaries of the Qingyi River, China

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ABSTRACT

Low-head dam impoundments modify local habitat and alter fish assemblages; however, to our knowledge, the pattern of how fish assemblages in the impoundments relate to local habitat, tributary position, and dam characteristics is still unclear. We used data collected in 62 impoundments created by low-head dams in headwater streams of the Qingyi River, China, to examine relationships between fish assemblages and local habitat, tributary position, and dam characteristics. We also assessed the relative importance of the three groups of factors in determining fish species richness and composition. Linear regression models showed that fish species richness was related to substrate heterogeneity, confluence link, and dam number upstream. Redundancy analysis showed that fish species compositions were influenced by substrate heterogeneity, confluence link, dam height, dam numbers upstream and downstream. Overall, dam characteristics were more important in affecting fish species richness but less important in determining fish species composition than local habitat (i.e., substrate heterogeneity) and tributary position. Our results suggest that low-head dam may affect fish species richness in impoundments by modifying local habitat and constraining fish movement, and the relative abundances of those fish species may depend more on species habitat presences and stream size than on impoundment size and number.

Keywords: Substrate coarseness and heterogeneity; Confluence link; Dam number and area

INTRODUCTION

Distribution and abundance of stream fishes are influenced jointly by historical processes, abiotic and biotic factors and ecological processes (Dauwalter et al., 2008; Gilliam et al., 1993; Hoeinghaus et al., 2007). At local scale, because of interspecific differences in physiology, behavior, and habitat preference (Jackson et al., 2001), local fish assemblages relate to stream segment habitat features, including flow regime (Yan et al., 2011), water temperature (Wang et al., 2003), dissolved oxygen (Ostrand & Wilde, 2001), and substrate size (Wang et al., 2013). Also, some stream size descriptors, such as water depth (Harvey & Stewart, 1991), stream width (Yan et al., 2010), and discharge (Chu et al., 2015a) are important factors in determining local fish diversity. At a river network scale, the nature of the continuities between mainstems and tributaries, and among tributaries, may result in spatial auto-correlation of abiotic and biotic factors and ecological processes within a watershed (Grant et al., 2007). Local fish assemblages are also determined by the tributary position within the drainage network, which determines fish immigration and extinction rates (Grenouillet et al., 2004; Taylor & Warren, 2001; Yan et al., 2011). Some descriptors of tributary position, such as link magnitude, downstream link, and confluence link, also have been reported to influence local species richness and compositions of stream fishes (Grenouillet et al., 2004; Li et al., 2014; Osborne & Wiley, 1992; Smith & Kraft, 2005; Yan et al., 2011). In addition, such spatial pattern of fish assemblages and their relationship with natural environmental factors are modified by anthropogenic

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activities in the stream channel or in their watersheds, such as land use, dam construction and water pollution (Chu et al., 2015a; Harding et al., 1998; Vila-Gispert et al., 2002).

Dams are widely recognized as one of the primary means by which humans alter or modify fluvial ecosystems (Poff & Hart, 2002; Rosenberg et al., 1997). Numerous investigations have revealed that dams affect stream fish in diverse ways, including blocking fish passage, altering flow and thermal regimes, modifying local habitat condition, and altering the prey base (e.g., Murchie et al., 2008; Nilsson et al., 2005; Poff & Zimmerman, 2010; Rosenberg et al., 2000; Wang et al., 2011). However, most of our knowledge on how dams affect lotic systems and fish assemblages is derived from investigations on large dams, while small low-head dams have been given less attention (Singer & Gangloff, 2011; Thoni et al., 2014; Yan et al., 2013). Although some researchers have found that fish species richness (Tiemann et al., 2004) and assemblage structure (Raborn & Schramm, 2003) in the dammed segments did not differ from free-flowing segments, others observed that low-head dams may substantially reduce local fish species richness (Dodd et al., 2003) and alter fish assemblage structure (Gillette et al., 2005; Poulet, 2007). These differences in results may be associated with dam size and location. Substantial modifications in fish assemblages may occur only in the impoundments immediately upstream, but not downstream of the dams (Yan et al., 2013). Compared with free-flowing stream segments, impoundments created by low-head dams are characterized with slower flows, deeper and wider water bodies, and smaller substrates (Gillette et al., 2005; Tiemann et al., 2004). Such local habitat modifications may alter fish assemblages by decreasing the numbers of lotic species and increasing the numbers of lentic species (Gillette et al., 2005; Tiemann et al., 2004; Yan et al., 2013). Moreover, multiple low-head dams upstream and/or downstream may cumulatively affect local habitat and fish assemblages (Cumming, 2004; Helfrich et al., 1999; Wang et al., 2011). Effects of impoundment are likely to increase with downstream flow past consecutive dams because river transport is largely unidirectional (Santucci et al., 2005).

We hypothesize that the fish assemblages in the impoundments of low-head dams are influenced by size of dams, number of dams upstream and/or downstream, local habitat conditions, and tributary position in the stream network. However, to our knowledge, the combined influences of local habitat, tributary position, and low-head dam characteristics on fish assemblages have not been thoroughly examined. Chu et al. (2015b) collected fishes from 62 impoundments created by low-head dams in headwater streams of the Qingyi River, China. After classifying the 25 fish species collected into 12 indigenous (naturally inhabiting in lotic headwater streams) and 13 native-invading species (naturally preferring lentic or slow-flowing waters of mid to lower reaches of a river network), the authors assessed the influence of abiotic (local habitat) and biotic (native invader) factors on the indigenous fish assemblages. However, they did not examine how the entire fish assemblages, indigenous and native-invasive fishes together, related to abiotic factors. In this study, we used the data of Chu et al. (2015b) to examine relationships between abiotic factors and fish assemblages in the 62 impoundments. Our aims were: (1) to determine the pure and combined effects of three groups of environmental factors (i.e., local habitat, tributary position, and dam characteristic) on fish species richness; (2) to determine the pure and combined effects of these environmental factors on fish species composition; (3) and to assess the relative importance of the three groups of environmental factors influencing local species richness and species composition.

MATERIALS AND METHODS

Study area

The Qingyi River originates in the northern portion of Huangshan Mountain and flows northeast toward its confluence with the lower Yangtze River, China. As a result of a subtropical monsoon climate, this basin is characterized by asymmetric seasonal temperature and precipitation distributions. Monthly mean temperature ranges from -2.1 ºC in January to 27.5 ºC in July and approximately 79% of the annual rainfall occurs from April to September. Approximately 1 000 low-head dams have been built on the tributaries of this basin for agricultural irrigation, resident water consumption, and recreational fishing (Chu et al., 2015b; Yan et al., 2011, 2013).

Fish sampling

A total of 62 impoundments created by low-head dams within the first-order (defined from the Anhui Province topographic maps of 1: 300 000 scales using the method of Strahler (1957)) headwater streams were sampled once during October and November 2011. Each sampled impoundment was selected in the field based on criteria that dam height was less than 4 m and impoundment water depth was less than 1 m. Only one site of 50 m long was sampled within each impoundment; however, when impoundments were less than 50 m long, the entire impoundments were sampled. Fish were collected using a backpack electrofishing gear (CWB-2000 P, China; 12 V import and 250 V export) by wading in two passes without blocking nest. Each electrofishing pass was operated with a uniform sampling effort (approximately 30 min sampling time for each 50 m sampling segment) by the same three persons, one operating the gear and the other two capturing fishes. Fish were identified in the field to species, counted, and returned to the sampling sites alive.

Environmental survey

We characterized local habitat conditions of each sampled impoundment by eight habitat variables, including wetted width (m), water depth (m), water temperature (ºC), dissolved oxygen (mg/L), conductivity (mS/s), current velocity (m/s), and substrate coarseness and heterogeneity. Wetted width was measured along five transects equally spacing across the stream channel. Water depth, water temperature, dissolved oxygen, and conductivity were measured at four equal interval points along each transect (JENCO 6350, 9010, USA). Current velocity was taken at 60% of water depth at each point (FP111, USA). Substrate was quantified with a 1 m lead core divided into 10 cm sections, using the frequency size class method of Bain (1999). Mean and standard deviation of dominant substrate values were regarded as indices of substrate coarseness and heterogeneity, respectively.

We quantified the dam characteristics of each sampled impoundment by two groups of dam variables, including dam size and dam numbers. Dam size consisted of the height (m), length (m) and area (m^2) of each low-head dam surveyed. Dam height was estimated as the vertical distance from the natural streambed at the downstream toe of the dam to the lowest point on the dam crest. Dam length was measured as the horizontal distance across channel at the dam crest. Then, dam area was calculated from its height and length, by approximation to a half ellipse. Dam number involved the numbers of upstream and downstream dams for each impoundment surveyed. Because each surveyed impoundment was located at the first-order headwater stream, dam number upstream was counted as the number of all dams (including low-head dams and hydropower stations) upstream of each sampling site along each surveyed headwater stream. Dam number downstream was counted in terms of all dams downstream of each surveyed low-head dam along the mainstem of the Qingyi River before it flows into the Yangtze River.

The impoundments sampled were all located in the first-order streams, suggesting that both stream order (Strahler, 1957) and stream link magnitude (Shreve, 1966) of all tributaries surveyed amounted to one. So, according to Yan et al. (2011), we quantified other two variables (confluence link and downstream link) to describe the tributary position of each impoundment within the Qingyi basin network. Confluence link is the number of confluences downstream from each segment (Fairchild et al., 1998), and downstream link is the linkage number of the stream segment that the sampling stream segment immediately flowing into (Osborne & Wiley, 1992). The two variables were assigned to each segment sampled using Anhui Province topographic maps (1: 300 000 scales).

Data analysis

We used stepwise regression to evaluate the effects of environmental variables on fish species richness (Legendre & Legendre, 1998). First, we built three regression models to determine the effects of local habitat alone, tributary position alone, and dam characteristics alone on fish species richness. We entered 10 habitat variables, two tributary variables, and five dam variables into the three regression models, respectively. Second, we entered all the 17 explanatory variables measured into one regression model to identify the combined effects of the three groups of environmental factors on fish species richness. Because only one significant predictor variable was screened out for all the four models, we did not use Akaike's Information Criterion (AIC) to select the optimal model for explaining the variance in fish species richness any more. Prior to analysis, fish and environment data were log-transformed to meet the assumptions of normality and homogeneity of variances. We used the SPSS 13.0 statistics package to perform statistical analysis, and statistical significance was accepted at $P<0.05$.

Using CANOCO 4.5 software package (ter Braak & Verdonschot 1995), we performed a redundancy analysis (RDA) to evaluate the variations in species composition in relation to environmental variables. We used RDA instead of CCA in the relationship analysis because detrended correspondence analyses indicated that our fish data set had a short gradient length (a measure of species turnover) for which the linear model of RDA was more appropriate than CCA (ter Braak & Verdonschot 1995). Similar to our regression analysis, we performed three RDAs to assess the correlations between fish species composition and local habitat alone, tributary position alone, and dam variables alone, respectively; then, we performed one RDA to determine how the three groups of environmental factors affected jointly fish species composition. These analyses included the relative abundances of all fish species except that occurring at two sites or fewer to avoid biased weighting. All the variables entered the analysis after a forward selection procedure, showing their importance in explaining the total variability in species composition. The significance ($P<0.05$) of the RDA gradient was assessed by Monte Carlo permutation tests and their importance measured by the eigenvalues of the first two axes (ter Braak & Verdonschot 1995). All fish and environment data were $\log_{10}(X+1)$ transformed to meet assumptions of multivariate normality and to moderate the influence of extreme data.

RESULTS

Species richness

When the three groups of environmental variables were considered separately, our results showed that fish species richness was related negatively to substrate heterogeneity (local habitat), and confluence link (tributary position), and positively related to number of upstream dams (dam characteristic) ($P<0.05$). The number of dams upstream explained the most variability (55%) and substrate heterogeneity explained the least variability (30%) in species richness (Table 1). However, when the combined effects of the three groups of factors on fish species richness were considered, only the number of upstream dams explained species richness ($P<0.05$), whereas local habitat and tributary position variables were less important ($P>0.05$) (Table 1).

Table 1 Linear regression models of fish species richness versus local habitat, tributary position, and dam characteristic

Variables	Independent variables	*R*	*t*	*P*
Local habitat	Substrate heterogeneity	0.30	–2.20	<0.05
Tributary position	Confluence link	0.50	–3.99	<0.01
Dam characteristic	Dam number upstream	0.55	4.64	<0.01
Combined	Dam number upstream	0.55	4.64	<0.01

Species composition

When the three groups of environmental variables were considered separately, substrate heterogeneity (local habitat) (Figure 1A), confluence link (tributary position) (Figure 1B), and dam height and numbers of dams upstream and downstream (dam characteristic) (Figure 1C) were significantly related to species composition (*P*<0.05). These variables explained 55.6% (substrate heterogeneity), 57.0% (confluence link) and 32.0% (dam characteristics) of the variance of species composition, respectively. When combining local habitat, tributary position, and dam characteristic together, the key factors influencing species composition included substrate coarseness and heterogeneity, confluence link, and dam area (*P*<0.05) (Figure 1D).

Different species responded differently to environmental variables. As substrate heterogeneity increased, abundances of *Vanmanenia stenosoma*, *Cobitis rarus* and *Acrossocheilus fasciatus* increased and *Carassius auratus*, *Opsarrichthys bidens* and *Odontobutis obscura* decreased (Figure 1A). When confluence link increased, *C. rarus* and *A. fasciatus* became more abundant and *Abbottina rivularis*, *Pseudorasbora parva*, *Rhodeus ocellatus*, *Hemiculter leucisculus* and *O. obscura* became less abundant (Figure 1B). As the number of upstream and downstream dams declined, the number of *O. bidens*, *A. rivularis*, *R. ocellatus* and *P. parva* increased whereas *V. stenosoma*, *A. fasciatus* and *Pseudogobio vaillanti* decreased. As dam height increased, *Zacco platypus*, *Cobitis sinensis* and *C. rarus* increased, whereas *P. vaillanti* and *Ctenogobius* spp. decreased (Figure 1C). When the combined effects of the three groups of factors on fish species composition were considered, substrate heterogeneity and confluence link showed positive correlations with the first RDA axis, and substrate coarseness and dam area negatively related to the second RDA axis (Figure 1D).

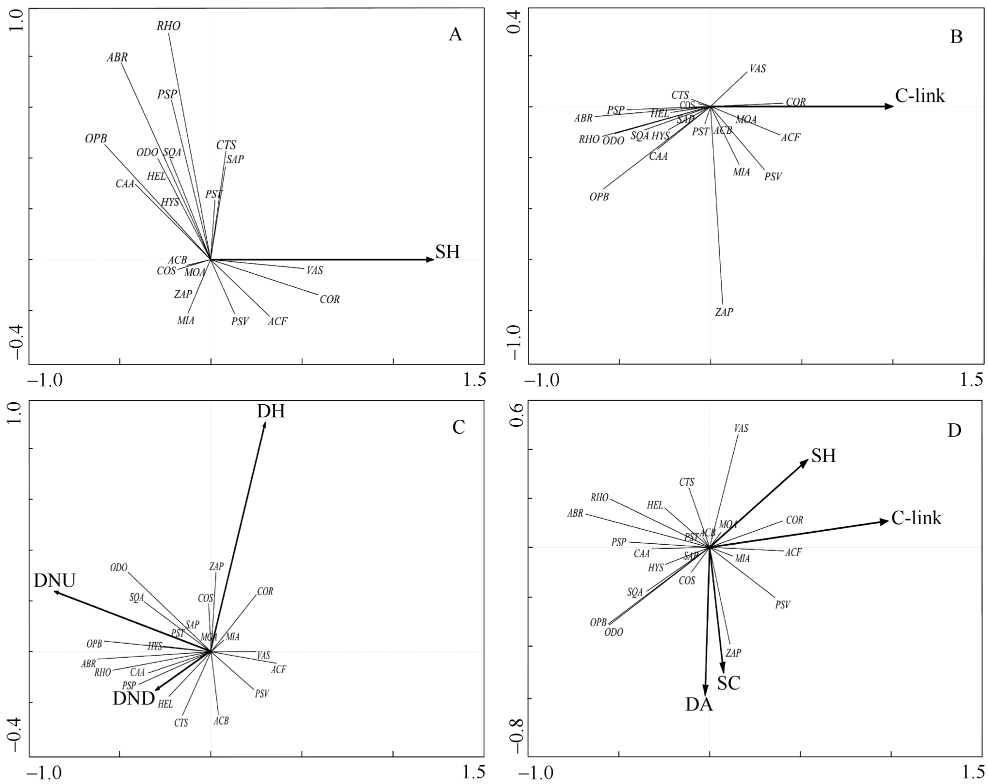

Figure 1 Redundancy analysis (RDA) diagrams for fish species composition and local habitat (A), tributary position (B), dam characteristic (C) and their combinations (D) in the impoundments created by low-head dams

Italic codes represent fish species (Appendix I), and bold abbreviations represent environmental variables (Appendix II).

DISCUSSION

In this study, we found that fish species richness in impoundments behind low-head dams of the Qingyi River was related to substrate heterogeneity, confluence link, and dam number upstream, and fish species composition was influenced by substrate heterogeneity, confluence link, dam height, dam numbers upstream and downstream. Dam characteristics like number of dam upstream were more important in affecting species richness but less important in determining fish species composition than local habitat like substrate heterogeneity and tributary position like confluence link.

Substrate provides the prerequisite micro-conditions for many stream fishes and can be viewed as an indicator of stream habitat quality (Bain, 1999). Substrate coarseness and heterogeneity, representing substrate size and microhabitat diversity, may substantially influence stream fish assemblages (Matthews, 1998). The positive relationship between substrate heterogeneity and fish species richness in the free-flowing segments of streams have been observed by many researchers (e.g., Gorman & Karr, 1978; Gratwicke & Sperght, 2005; Li et al., 2014; Wang et al., 2013). However, we found that fish species richness in the impoundments behind low-head dams was negatively related to substrate heterogeneity. This discrepancy may be associated with the difference in environmental conditions and fish species compositions between impoundments and free-flowing segments. Compared with free-flowing segments, impoundments behind low-head dams are characterized by slower flows, deeper water and finer substrate, and by less endemic lotic fishes and more widespread lentic fishes (Gillette et al., 2005; Tiemann et al., 2004; Yan et al, 2013). The total of 25 fish species collected in this study included 12 indigenous specialist species naturally inhabiting upland streams, and 13 invasive generalist species naturally preferring lowland waters (Chu et al., 2015b). Although species richness of indigenous species is positively related to substrate heterogeneity (Chu et al., 2015b), our redundancy analysis showed that the abundances of most invasive species, such as *C. auratus*, *P. parva*, *A. rivularis*, *M. anguillicaudatus*, *R. ocellatus* and *O. obscura*, were negatively related to substrate heterogeneity. Therefore, the habitat-generalist characteristics of invasive fishes in impoundments could lessen the positive correlation between substrate heterogeneity and fish species richness observed elsewhere.

Fluvial systems have interconnected network architectures with complex but definable 'network geometry' (Fausch et al., 2002; Wiens, 2002) or “dendritic ecosystem network” (Grant et al., 2007). At a river network scale, local fish assemblages are determined by tributary position within a watershed network (Grenouillet et al., 2004; Yan et al., 2011), because the rates of fish immigration and emigration influence local fish assemblages in streams and depend on tributary position (Robinson & Rand, 2005; Taylor & Warren, 2001). This may explain why some adventitious streams, defined as streams at least three stream orders smaller than that into which they flow, often hold more diverse fish assemblages than headwater streams with similar size to adventitious streams (Hitt & Angermeier, 2008; Osborne & Wiley, 1992). We found that both species richness and fish assemblages were significantly related to confluence link, suggesting that fish movements may influence fish assemblages within the impoundments by low-head dams. Others have revealed that some variables on tributary position, such as downstream link (Grenouillet et al., 2004; Osborne & Wiley, 1992;) and confluence link (Li et al., 2014; Smith & Kraft, 2005) influence local fish assemblages in free-flowing segments.

We found that both fish species richness and composition in impoundments were related to the number of dams upstream and/or downstream, suggesting of cumulative effects of multiple dams on fish assemblages. These cumulative effects have been also observed by other researchers such as Helfrich et al. (1999), Cumming (2004), and Wang et al. (2011). Because river transport is largely unidirectional, effects of impoundment often increase with downstream flow past consecutive dams (Santucci et al., 2005). Our redundancy analysis showed that the abundances of most indigenous species were negatively related to the number of dams upstream, but the opposite was observed for invasive species. Similarly, in the same study area, Chu et al. (2015b) found that local species richness of indigenous fishes correlated negatively with the number of dams upstream, while the richness of invasive fishes correlated positively with the number of upstream dams. Therefore, multiple impoundments behind low-head dams may cumulate effects on local fish assemblages, negatively impacting indigenous fishes but benefiting invasive species. In addition, we also found that fish species composition in impoundments was related to dam height and dam area. This is consistent with the opinion that the magnitude of dam effects and the degree to which local habitat conditions and fish assemblages are impacted depend on dam size, because dam size influences the size of their impoundments (March et al., 2003; Poff & Hart, 2002).

The relative importance of different environmental variables in determining fish assemblages may depend on many factors, such as spatial scale at which an investigation is conducted (Jackson et al., 2001; Wang et al., 2006), features of environmental conditions in a particular region (Hughes et al., 2015; Wang et al., 2006), and indicator used to describe fish assemblages (species richness *v.s.* species composition) (Li et al., 2014; Yan et al., 2011). We demonstrated that dam characteristics (i.e., dam number upstream) were more important in affecting fish species richness in impoundments than local habitat (i.e., substrate heterogeneity) and tributary position (i.e., confluence link). By modifying local habitat features, low-head dams and other co-occurring anthropogenic activities (e.g., land use and water pollution) decrease local species richness, alter the longitudinal pattern of fish species richness along upstream-downstream gradient, and lessen the effects of habitat factors on local species richness (Chu et al., 2015a). In addition, by blocking fish passage, dams also constrain fish movements among stream segments and lower the effects of tributary position on fish species richness (Yan et al., 2011). However, we also demonstrated that dam characteristic was less important in influencing fish species composition than habitat and tributary position. This suggests that the relative abundances of those fish species may depend more on species habitat preferences and stream size than on impoundment size and number (Yan et al., 2011).

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Appendix I Species composition, code, and classification (indigenous *v.s.* invasive) of fishes in 62 impoundments surveyed

Order/Family/Species	Code	Classification
CYPRINIFORMES		
Cyprinidae		
Acrossocheilus fasciatus	ACF	Indigenous
Zacco platypus	ZAP	Indigenous
Pseudogobio vaillanti	PSV	Indigenous
Phoxinus oxycephalus	PHO	Indigenous
Acheilognathus barbatulus	ACB	Indigenous
Opsarrichthys bidens	OPB	Indigenous
Squalidus argentatus	SQA	Invasive
Sarcocheilichthys parvus	SAP	Invasive
Gnathopogon imberbis	GNI	Invasive
Carassius auratus	CAA	Invasive
Pseudorasbora parva	PSP	Invasive
Abbottina rivularis	ABR	Invasive
Rhodeus ocellatus	PHO	Invasive
Hemiculter leucisculus	HEL	Invasive
Cobitidae		
Misgurnus anguillicaudatus	MIA	Invasive
Cobitis sinensis	COS	Indigenous
Cobitis rarus	COR	Indigenous
Homalopteridae		
Vanmanenia stenosoma	VAS	Indigenous

Continued

Order/Family/Species	Code	Classification
PERCIFORMES		
Gobiidae		
Ctenogobius sp	CTS	Indigenous
Mastacembelidae		
Mastacembelus aculeatus	MAA	Invasive
Electridae		
Hypseleotris swinhonis	HYS	Invasive
Odontobutis obscura	ODO	Invasive
SIURIFORMES		
Bagridae		
Pseudobagrus truncatus	PST	Indigenous
Amblycipitidae		
Liobagrus styani	LIS	Indigenous
SYNBRANCHIFORMES		
Synbranchidae		
Monopterus albus	MOA	Invasive

Appendix II Summary statistic for explanatory variables measured for local habitat, tributary position, and dam characteristics

Variables	Abbreviation	Range	Mean
Local habitat			
Wetted width (m)	WW	5.1-48.4	21.1±11.9
Water depth (m)	WD	0.13-0.93	0.47±0.20
Water temperature (ºC)	WT	15.9-29.0	19.8±2.5
Dissolved oxygen (mg/l)	DO	5.6-12.7	8.5±1.5
pH	pH		
Conductivity (mS/s)	Con	19.3-156	78.6±34.5
Current velocity (m/s)	CV	0.03-0.63	0.18±0.15
Canopy (%)	Can		
Substrate coarseness	SC	1.3-3.8	2.2±0.9
Substrate heterogeneity	SH	0-1.56	1.02±0.36
Tributary position			
Confluence link	C-link	16-26	20.9±2.6
Downstream link	D-link	2-17	4.28±4.01
Dam characteristics			
Dam height (m)	DH	0.6-3.8	2.5±1.8
Dam length (m)	DL	9.7-70.2	28.4±17.3
Dam area (m^2)	DA	6.4-500.5	87.8±52.3
Dam number upstream (ind.)	DNU	0-18	3.0±3.4
Dam number downstream (ind.)	DND	3-20	9.0±4.0