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RESEARCH ARTICLE

Impacts of cascade run-of-river dams on benthic diatoms in the Xiangxi River, China

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Abstract The ecological effects of small run-of-river dams on aquatic ecosystems are poorly understood, especially on downstream benthic algal communities. We examined impacts of such dams on the benthic diatom community at a regional scale in the Xiangxi River, China. A total of 90 sites were visited, which were divided into five habitats (H1–H5) according to impact extent of each dam. Using partial least squares (PLS) modeling, we developed two predictive models (diatom species richness and total diatom density) based on environmental variables of an unregulated habitat (H1). These models were then used to predict species richness and total densities at impacted habitats (H2–H5) and residuals, i.e. the differences between observed and predicted values, were used to evaluate impact strength of flow regulation. Significant impacts of flow regulation on diatom species richness were detected at three impacted habitats (H3–H5), where observed species richness were significantly higher—70.6, 63.9 and 46.6%, respectively—than predicted values. Then, possible mechanisms for observed impacts were discussed. Further research is necessary to address the potential negative impacts of cascade run-of-river dams on other aquatic organisms in different seasons, and to explore more appropriate mechanisms for such impacts, which may lead to sustainable management strategies and help to determine the optimal ecological water requirement for the Xiangxi River.

Keywords Benthic diatoms · Cascade run-of-river dams · PLS models · Xiangxi River

Introduction

Damming is probably one of the greatest stressors affecting the integrity of running waters (Heinz Center 2002; Garcia de Leaniz 2008), because it can interfere or even stop the transport of sediment and nutrients along waterways and eventually disturb ecological connectivity, which underpins the transfer of materials and products of ecological functions and processes (Jenkins and Boulton 2003). Additionally, impounded waters can trigger important changes in the composition of stream fauna, favoring lentic over lotic species (Raymond 1979; Lewis 2001; Shao et al. 2007; Zhou et al. 2007). However, the effects of small run-of-river dams on aquatic ecosystems are poorly understood. Benthic assemblages and plankton communities in downstream habitats might be strongly influenced by such dams, but only a few studies have examined the responses of fish, macroinvertebrates, zooplankton, phytoplankton and stream chemistry to such small dams (Almodóvar and Nicola 1999; Stanley et al. 2002; Thomson et al. 2005; Velinsky et al. 2006; Wu et al. 2007; Fu et al. 2008; Zhou et al. 2008). To our knowledge, even fewer studies have evaluated the responses of benthic algae to the construction of small run-of-river dams (Wu et al. 2009).

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As important primary producers in stream ecosystems, benthic algae are ubiquitous and sensitive to a broad range of stressors (Hambrook 2002). It has been widely reported that distribution patterns of benthic algae are strongly correlated with environmental factors, including geomorphic characteristics (Leland and Porter 2000), eco-climate (Weckström and Korhola 2001), hydrological regime, land use in the watershed (Leland and Porter 2000), instream nutrients such as N and P (Millie et al. 2002; Tang et al. 2002), and prey pressure (Anderson et al. 1999). Therefore, diatoms, the algal division predominant within periphyton of the Xiangxi River system (Tang et al. 2002, 2004; Wu et al. 2009), are increasingly being used as bio-indicators for environmental monitoring in Europe, North America, and elsewhere (Stevenson and Smol 2002).

The Xiangxi River, with a length of 94 km and a catchment area of 3,099 km^2, is the largest tributary near the Three-Gorge Dam (TGD) in Hubei province. Nevertheless, over 47 run-of-river dams have been built within the watershed due to a high natural gradient ($\sim$1,540 m from the headwaters to its confluence with the Yangtze River; Tang et al. 2006), and a series of small cascade dams has become one of the main human disturbances. Former studies on the Xiangxi River suggested that the effect of the dams varied with time, but was more pronounced in dry seasons or during long periods of drought (Zhou et al. 2008). We investigated 23 dams during the dry season (October 2005) within the Xiangxi River watershed, and estimated impacts of cascade run-of-river dams on the benthic algae community. Our specific aim was to detect downstream effects of cascade run-of-river dams on benthic diatom communities and explain possible mechanisms.

Methods

Study area and site locations

Originating from Shennongjia Mountain (at 3,150 m, the highest mountain in central China), the Xiangxi River has three main tributaries—Jiuchong, Gufu, and Gaolan Rivers (Fig. 1b) (Tang et al. 2006). Many small, run-of-river dams have been constructed along this river, and in dry seasons much of the flow is abstracted and diverted through a special penstock to power plants, leaving the main channel with only a small part of the original flow.

We investigated 23 dams in October 2005, and at most, five sites (S1–S5) were established at each river segment (Fig. 1c). S1 was located approximately 50–100 m upstream of the dam where river channels were in a completely natural state, free of impacts from the dam. S2 was just upstream from the dam and slightly influenced by the intake dam. S3 was in a pool below the dam, which was formed by overflow erosion in rainy seasons, and no velocity was detected during the sampling period. S4 was upriver from the outlet of the small hydropower station (SHP), and flow was recovered after water gathering downstream from S3. S5 was at the outlet of the SHP, where powerful currents discharging from the outlet have formed a deep pool. We sampled mainly in this area, despite its small size. Due to cascade construction of dams, sampling sites at upstream SHPs usually overlapped with the site of an adjacent dam, meaning a total of 90 sites were finally visited, which were divided into five habitats (H1–H5) according to impact extent of each dam. H1 (20 sites) comprised unregulated sites including all of S1; S2–S5 were made up of H2–H5 (19, 21, 15 and 15 sites, respectively), separately.

Field sampling and identification

Algae were collected from all available substrates and habitats. The objective was to collect a single composite sample that represented the benthic algae community in the reach. Three to five representative stones (diameter < 25 cm) were collected from each section, and the surface area within a 2.7-cm diameter corer was brushed thoroughly and then rinsed with 350-ml distilled water. The sample was divided into two parts: one was preserved with 4% formalin for identification and the other was filtered through a Whatman GF/C filter for chlorophyll *a* (Chl *a*) measurement. In the laboratory, Chl *a* was determined spectrophotometrically following acetone extraction according to APHA (1992).

Identification of benthic algae involved two steps. First, we analyzed non-diatom algae with a 0.1-mL counting chamber and a microscope at 400× magnification. Second, we prepared permanent diatom slides after oxidizing the organic material with acid. We counted a minimum of 300 valves at 1,000× magnification under oil immersion. We identified algae to the lowest taxonomic level possible with keys in Anonymous (1992); Hu et al. (1980); Zhang and Huang (1991); and Zhu and Chen (2000). The densities of benthic algae were expressed as ind m^{-2}.

Measurement of physicochemical factors

Values of pH, dissolved oxygen (DO), conductivity (COND), Chloride (Cl), total dissolved solid (TDS), water temperature (WT), oxidation reduction potential (ORP) and turbidity (TURB) were measured in situ with a Horiba W-23XD (multiprobe sonde). Water depth, channel width and current velocity (LJD-10 water current meter; Chongqing hydrological machines manufactory, Chongqing, China) were also measured at each site.

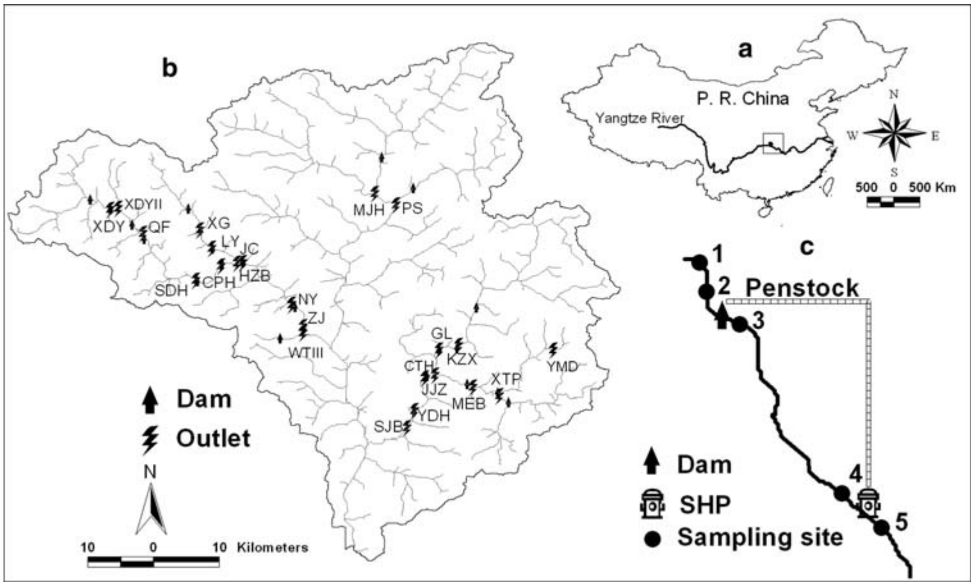

Fig. 1 Small run-of-river dams within the Xiangxi River watershed (**b**) in the People's Republic (P. R.) of China (**a**) and sketch map of sampling sites (**c**). *SHP* Small hydropower station; *letters* in **b** are names of SHPs

We collected ~1 L of water in pre-cleaned plastic containers to measure chemical variables, including total phosphorus (T-P) and PO_4–P, in the laboratory, according to standard methods, soon after sampling (Chinese Environmental Protection Bureau 1989).

Modeling and statistical analysis

According to Wang et al. (2005) and van Dam et al. (1994), we first calculated as many diatom indices as possible (pollution-tolerance index, species richness, total density, Margalef diversity, Pielou evenness, Shannon–Wiener diversity and five growth forms) based on diatom abundances at each site. Together with Chl *a*, 12 indices were calculated in total.

Partial least squares regression (PLS) was used to build predictive models for these indices. PLS modeling combines ordination and regression, and its detailed introduction has been described by ter Braak and Juggins (1993); Eriksson et al. (1995); Wold (1995); Englund et al. (1997) and Zhang et al. (1998).

In our study, PLS modeling was performed using the software SIMCA-P 11.5 for Windows. We began by building PLS models to describe how diatom indices at unregulated sites were related to environmental variables. Cross validation was used to assess the significance of each PLS model. Squared predictive residuals called PRESS (predicted residual sum of squares) were first summed, and this procedure was repeated until each group had been left out once. Second, all partial PRESS values were summed to form a total PRESS, which is a measure of the predictive capability of a component of the PLS model. This total PRESS was then compared to the residual sum of squares (SS). A component (model dimension) was considered significant if the ratio (PRESS/SS) was statistically smaller than 1.0. Lastly, Q^2 (the cross-validated variance) was calculated (1 − PRESS/SS) and for a significant model or a component, Q^2 should be larger than a critical value (in our study, $Q^2_{\mathrm{limit}} = 0.05$, corresponding to $P < 0.05$).

We then, modified the models by excluding variables directly affected by flow regulation. From these new models, we predicted diatom indices at impacted sites. The residuals, i.e. the difference between values observed and those predicted from the models, were used to estimate the impacts of flow regulation. Effects were calculated using [(observed value − predicted value)/predicted value] × 100. In accordance with Englund et al. (1997) and Zhang et al. (1998), an impact of flow regulation was regarded as significant if 95% confidence intervals for the means of effects did not include zero, corresponding to $P < 0.05$.

Results

Algal species richness and environmental variables

Benthic algae sampling yielded 146 taxa (mostly at species levels), belonging to Bacillariophyta, Chlorophyta and Cyanophyta. Main genera of non-diatom algae, whose average density in all sites was 1.45×10^9 ind m^{-2}, were *Oscillatoria*, *Phormidium*, *Stigonema*, *Ulothrix* and *Uronema*. In all samples, the largest number of species belonged to Bacillariophyta (79.4% of the total taxa), as was similarly the case in other studies of benthic algae in the Xiangxi River (Tang et al. 2002, 2004; Wu et al. 2009). We therefore focused on diatoms in subsequent analyses. *Rossithidium linearis* and *Cocconeis placentula* were the most abundant species; their relative abundances were 48.5

and 8.1%, respectively. The average diatom density at all sites taken together was 5.57×10^9 ind m^{-2} and mean species richness at all 90 sites was 18.3, ranging from 4 to 41 (Table 1).

The 15 environmental variables from all 90 sites and 5 habitat groups are summarized in Table 2. Of all physicochemical variables, current velocity differed most significantly among the five groups (ANOVA, $P < 0.05$). From H1 to H3, flow velocity declined from 0.74 to 0 m s^{-1} while remaining constant at H4 and H5 (0.58 and 0.46 m s^{-1}, respectively).

Effects of flow regulation on diatom indices

Significant models were developed for species richness and total density, out of 12 indices. An analysis of species richness at unregulated sites (H1), with respect to 15 environmental variables, yielded two significant components ($Q^2_{cum} = 0.38$). A similar analysis for total diatom density produced one significant component ($Q^2 = 0.12$) (Table 3). Two models indicated that channel width, flow velocity, pH, WT and SAL were important for both species richness and total density (Fig. 2).

To estimate the effects of flow regulation, we built new PLS models for diatom species richness and total diatom density based on H1, excluding flow velocity, which was assumed to be directly influenced by flow regulation. Two significant components were extracted for diatom species richness ($Q^2_{cum} = 0.26$) and one for total diatom density ($Q^2 = 0.06$) (Table 3). These models were then used to predict species richness and total density at four other habitats (H2–H5). At H3, H4 and H5, the respective, observed species richness values of 70.6, 63.9 and 46.6% were significantly higher than predicted values, while at H2, the effect did not differ significantly from zero (Figs. 3, 5a). Figure 4 shows the predicted versus observed values of total diatom density at four different habitat groups (H2–H5). We found that for H3, H4 and H5, but not H2, most observed total densities were higher than predicted values. Nevertheless, the effects observed at H2–H5

Table 1 Mean and range of diatom species richness and total diatom density at all sites and each habitat group

Sites	*n*	Richness (range)	Total density ($\times 10^9$ ind m^{-2}) (range)
All sites	90	18.3 (5 to 41)	5.57 (0.04 to 32.75)
H1	20	14.6 (9 to 30)	2.58 (0.04 to 14.73)
H2	19	15.7 (8 to 40)	3.30 (0.13 to 18.40)
H3	21	22.0 (11 to 41)	8.96 (0.77 to 32.75)
H4	15	18.3 (5 to 29)	5.23 (0.25 to 10.76)
H5	15	21.3 (13 to 33)	8.03 (0.30 to 18.38)

Table 2 Mean and range of 15 environmental variables at all sites and each habitat group

Variables	All sites	H1 (20)	H2 (19)	H3 (21)	H4 (15)	H5 (15)
PO_4–P (mg L^{-1})	0.0090 (0 to 0.04)	0.0110 (0 to 0.04)	0.0080 (0 to 0.02)	0.0104 (0 to 0.04)	0.0081 (0 to 0.02)	0.0067 (0 to 0.02)
T–P (mg L^{-1})	0.0262 (0.01 to 0.08)	0.0269 (0.01 to 0.08)	0.0263 (0.01 to 0.05)	0.0285 (0.01 to 0.07)	0.0241 (0.01 to 0.06)	0.0243 (0.01 to 0.05)
pH	7.87 (6.41 to 8.90)	7.93 (6.41 to 8.90)	7.9 (6.49 to 8.90)	7.89 (7.00 to 8.74)	7.79 (6.50 to 8.87)	7.83 (6.54 to 8.86)
COND (ms m^{-1})	27.13 (6.40 to 39.80)	28.03 (16.60 to 39.50)	27.56 (17.10 to 38.60)	27.24 (17.50 to 39.60)	27.45 (7.70 to 39.80)	24.89 (6.40 to 39.00)
TURB (NTU)	39.19 (6.10 to 61.20)	40.73 (12.60 to 56.90)	42.75 (13.80 to 61.20)	37.88 (13.10 to 57.30)	35.88 (8.50 to 50.50)	37.81 (6.10 to 59.90)
DO (mg L^{-1})	10.05 (7.53 to 16.31)	10.07 (9.09 to 11.64)	10.06 (9.22 to 11.58)	9.78 (7.53 to 16.31)	10.1 (9.36 to 11.43)	10.34 (9.28 to 11.80)
WT (°C)	14.15 (10.58 to 19.77)	14.08 (10.58 to 17.26)	13.62 (10.63 to 16.76)	14.4 (10.67 to 17.62)	15.09 (12.09 to 19.77)	13.63 (12.14 to 15.01)
SAL	0.01 (0 to 0.02)	0.01 (0.01 to 0.02)	0.01 (0.01 to 0.02)	0.01 (0.01 to 0.02)	0.01 (0 to 0.02)	0.01 (0 to 0.02)
TDS (g L^{-1})	0.18 (0.04 to 0.26)	0.18 (0.11 to 0.26)	0.18 (0.11 to 0.25)	0.18 (0.11 to 0.26)	0.18 (0.05 to 0.26)	0.16 (0.04 to 0.25)
ORP	−204 (−243 to −135)	−201 (−243 to −140)	−209 (−235 to −164)	−206 (−239 to −157)	−193 (−224 to −135)	−210 (−233 to −184)
Cl^- (mg L^{-1})	11.84 (5.09 to 32.80)	11.97 (5.49 to 18.50)	11.28 (5.35 to 16.9)	11.18 (5.49 to 17.20)	13.15 (5.09 to 32.80)	12 (5.78 to 25.20)
Ca^{2+} (mg L^{-1})	2.97 (2.42 to 3.64)	2.97 (2.69 to 3.30)	2.95 (2.69 to 3.52)	3 (2.63 to 3.42)	2.95 (2.51 to 3.64)	2.94 (2.42 to 3.34)
Velocity (m s^{-1})	0.41 (0 to 1.80)	0.74 (0.27 to 1.80)	0.37 (0 to 0.81)	0 (0 to 0)	0.58 (0.21 to 1.03)	0.46 (0 to 0.95)
Width (m)	17.09 (1.75 to 45.00)	15.07 (4.23 to 34.00)	19.27 (5.00 to 34.83)	21.39 (1.75 to 45.00)	12.68 (3.30 to 26.60)	15.73 (5.27 to 28.6)
Depth (m)	0.48 (0.10 to 1.16)	0.33 (0.16 to 0.63)	0.48 (0.17 to 0.95)	0.69 (0.32 to 1.16)	0.29 (0.10 to 0.58)	0.57 (0.27 to 1.01)

Table 3 Fractions of variance explained and fractions of variation of dependent variables predicted by PLS models for diatom species richness and total diatom density at unregulated sites (H1)

PLS models	With 15 environmental variables			Excluding flow velocity		
	R_x^2	R_y^2	Q_y^2	R_x^2	R_y^2	Q_y^2
Diatom species richness	0.45	0.64	0.38	0.45	0.56	0.26
Total diatom density	0.24	0.26	0.12	0.26	0.20	0.06

R_x^2 is the fraction of the variance of all the independent variables and R_y^2 of all the dependent variables explained by the model. Q_y^2 is the fraction of the total variation of the dependent variable that can be predicted by the model, as estimated by cross-validation

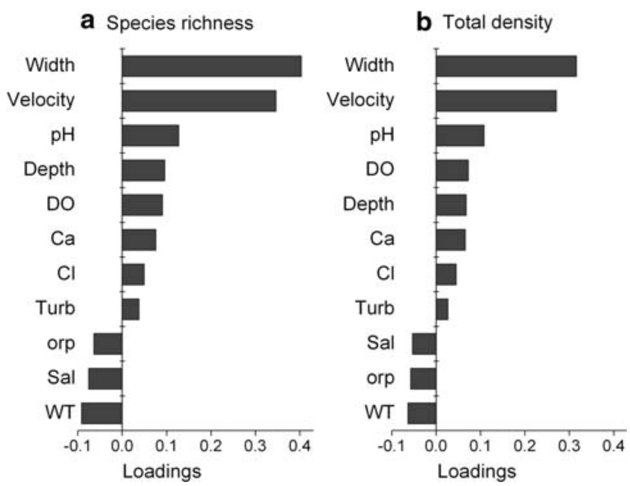

Fig. 2 Loadings for the most influential variables in PLS regression models of (**a**) diatom species richness and (**b**) total diatom density

did not differ from zero (Fig. 5b), indicating no significant effect of flow regulation on total diatom density.

Discussion

Effects of flow disturbance

The establishment of cascade run-of-river dams caused habitats of the lower reach (H3) to have a significantly lower flow velocity, resulting in a potential change of many parameters. Flow velocity is one of the most significant factors impacting the development of aquatic organisms, particularly periphyton (Sand-Jensen et al. 1988; Chételat et al. 1999). As a main factor of hydrological regime, current velocity affects species composition, succession of species colonization, physiology of organisms, as well as periphyton metabolism (Biggs 1996). In our study, we investigated potential impacts of flow regulation on benthic algal indices and found strong evidence for such effects. Observed species richness at H3, H4 and H5 were significantly higher—70.6, 63.9 and 46.6%, respectively—than predicted values, although no significant effect of flow regulation at H2 was observed.

Diatom species richness is used commonly in bioassessments (Wang et al. 2005; Wu et al. 2009). The impacts of a disturbance on diatom species richness are unpredictable and depend on the type of stressors involved (Stevenson 1984). Thomson et al. (2005) indicated that diatom species richness in downstream reaches declined significantly following complete removal of a small run-of-river dam in Manatawny, Pennsylvania, while Wu et al. (2009) found that diatom species richness decreased at downstream sites following dam construction in a tributary of the Xiangxi River, China. Nevertheless, observed diatom species richness in our study at impacted sites (H3, H4 and H5) was significantly higher than predicted values. These different responses to flow regulations may be explained by disturbance pattern (dam removal, flow increasing vs. dam construction, flow decreasing) and total installed capacity of SHP, which determines the proportion of flow left in the waterway.

The absence of dam impacts at H2 was probably related to dam size and impoundment residence time (Velinsky et al. 2006). Water residence time, determined mostly by dam size, is a useful system-level index that has similar ecological implications for rivers, lakes and reservoirs (Soballe and Kimmel 1987). Where water has a long residence time, uptake of elements by aquatic organisms or populations could have significant effects on water-quality (Kurunc et al. 2006), which may significantly influence the benthic algal community. However, the dams in our study are run-of-river structures with a relatively small impoundment area, and water flows directly into the intake weirs with a very low residence time.

Possible mechanisms for observed impacts

Predictive models have been used to estimate the magnitude of effects of dams on invertebrate, net-spinning caddis larvae, and blackfly larvae (e.g. Armitage et al. 1987; Englund et al. 1997; Zhang et al. 1998). Here we take one step further and try to elucidate the mechanism causing observed impacts, a necessary step since hydropower plants and dams affect the environment in many different ways. For example, effects on benthic algal communities

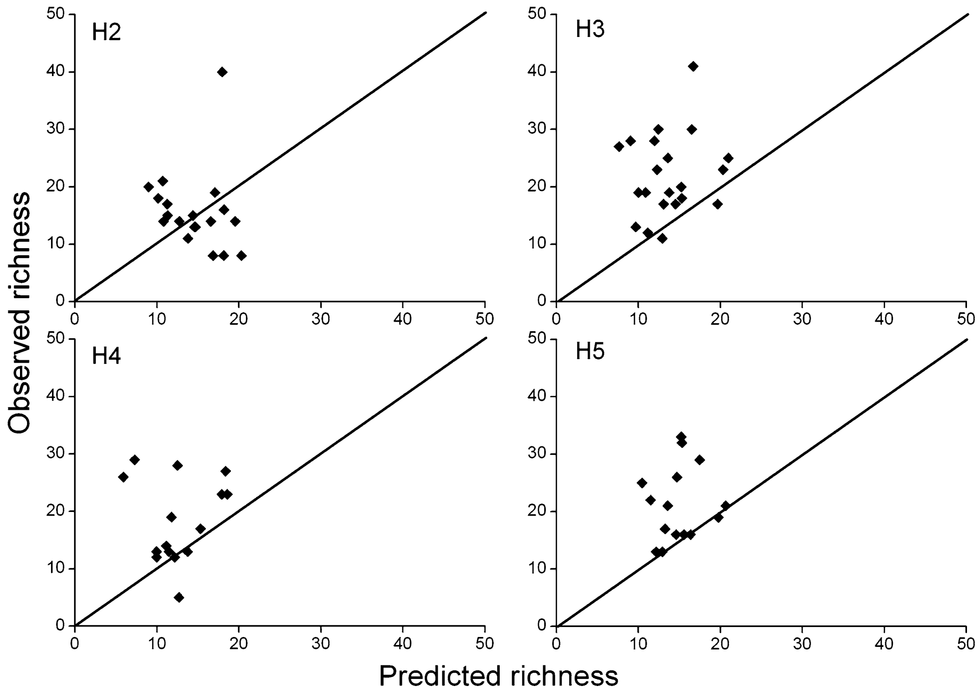

Fig. 3 Predicted versus observed values of diatom species richness at four different habitat groups (H2–H5). The predicted values were estimated with PLS models based on data from unregulated sites (H1)

have been ascribed to changes in flow variability and particle sizes of bed sediments (Wu et al. 2009). Impacts on hydropsychids have been attributed to changes in temperature, food availability, substratum stability and flow variability (Parker and Voshell 1983; Boon 1993; Camargo 1993). Only when key mechanisms have been identified can we suggest cost-effective remedial measures (Englund et al. 1997).

One possible mechanism was biotic interactions (Fig. 6). In the Xiangxi River, biomass and density of benthic macroinvertebrates at impacted sites were lower than those of unregulated sites (Fu et al. 2008), although no influence of flow regulation on benthic rotifer and total zooplankton density (Zhou et al., unpublished data) was observed. We suggested that the underlying mechanism could be a negative effect of flow regulation on density and

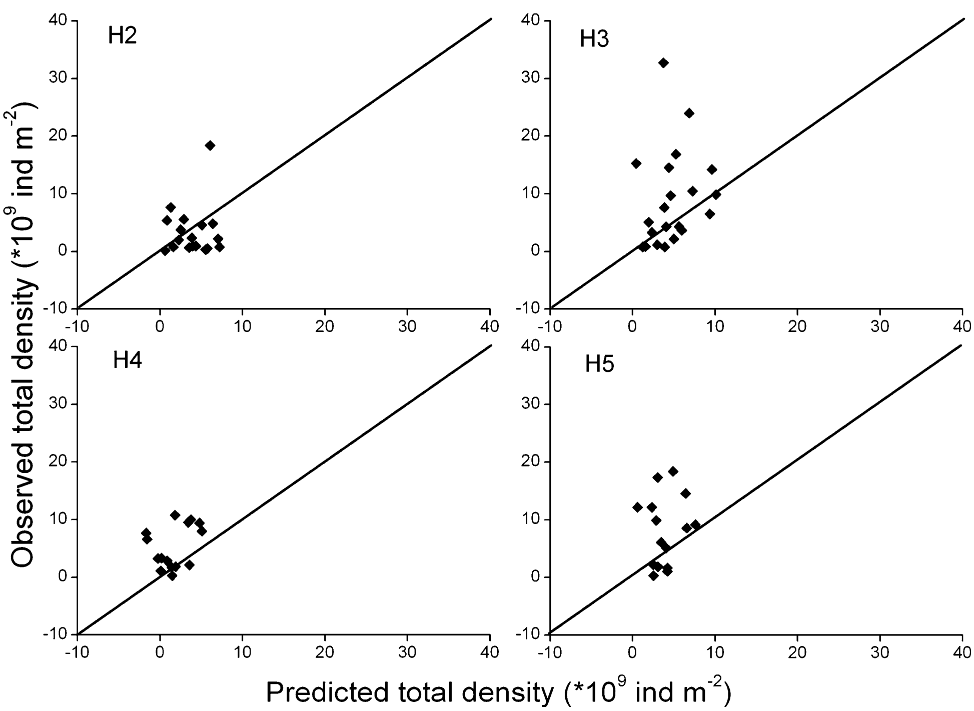

Fig. 4 Predicted versus observed values of total diatom densities at four different habitat groups (H2–H5). The predicted values were estimated with PLS models based on data from unregulated sites (H1)

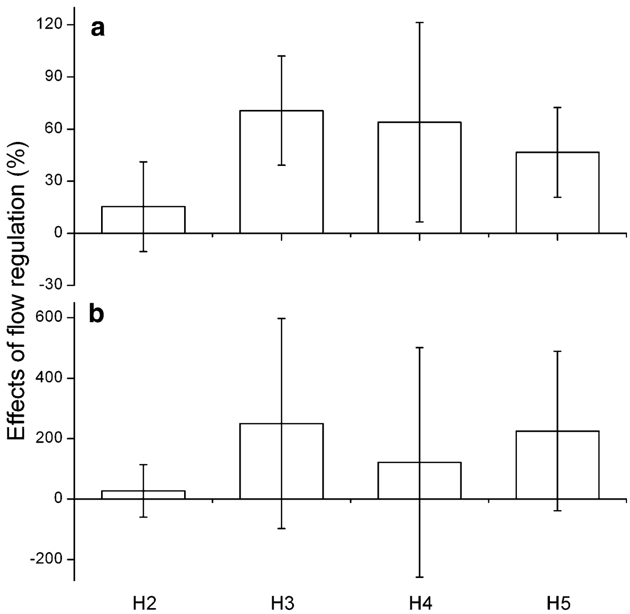

Fig. 5 Effects of flow regulation at four different habitat groups (H2–H5) on (**a**) diatom species richness and (**b**) total diatom density. *Error bars* indicate 95% confidence intervals. If the confidence interval did not include zero, the effect was regarded as significant ($P < 0.05$)

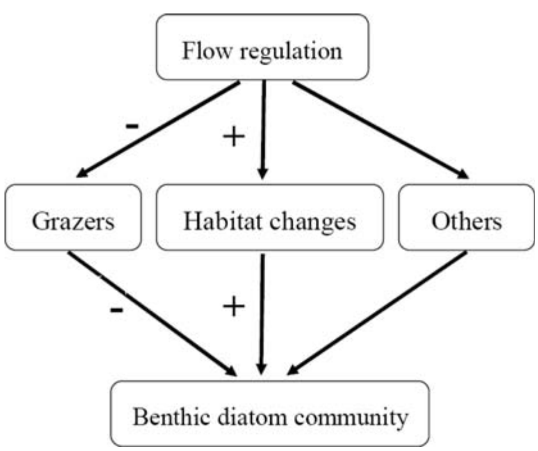

Fig. 6 Hypothesized relationships among flow regulation, predators, habitat changes and the benthic diatom community. *Arrows* indicate directions of interactions and *plus* (+) and *minus* (−) *signs* represent positive and negative effects, respectively

biomass of grazers, which increased diatom species richness under more benign conditions. Several studies have shown that herbivorous zooplankton and macroinvertebrates can reduce diatom species richness. Koetsier (2005) investigated the effects of top predator manipulations on the community structure of benthic diatoms in a small stream ecosystem, and demonstrated that top predators can alter the community composition and structure of benthic diatoms indirectly through grazer suppression and directly by disruption due to foraging activity. McCauley and Briand (1979) found that lowering herbivorous zooplankton levels may cause an intensification of exploitative competition among phytoplankton, which favors edible species and a few inedible algae like *Synedra*.

Another potential reason was that river water downstream of the dams was relatively shallow due to water abstraction, and habitat was thus relatively stable and conducive to algal growth (Tang et al. 2004). Wu et al. (2009) suggested that changes in algae-based metrics downstream of dams probably reflect frequent hydraulic disturbances after dam construction, because sediments deliberately or accidentally released from reservoirs can cause pronounced reductions in benthic densities and diversity (Gray and Ward 1982; Marchant 1989). Nevertheless, there was almost no hydraulic disturbance during the dry seasons in the Xiangxi River because the entire flow was abstracted for hydroelectric power generation. Moreover, shallow depths downstream of the dams could translate into stream differences in light availability, which may substantially influence the photosynthesis of the benthic diatom community. Therefore, we hypothesized that habitat changes created by flow reduction also played an important role in increasing diatom species richness (Fig. 6).

In conclusion, a combination of biotic interactions and habitat changes may explain why diatom species richness was positively affected by flow regulation. However, other possible mechanisms for observed effects may exist, and the influences we observed might increase, decrease, or remain unchanged with time. Thus further research is necessary to address the potential negative impacts of cascade run-of-river dams in different seasons, and explore more appropriate mechanisms for such influences, which may lead to sustainable management strategies for the Xiangxi River. Furthermore, it is strongly warranted to continue this research on other aquatic organisms (fish, macroinvertebrate, phytoplankton and zooplankton) and explore the negative impacts of cascade run-of-river dams, which would help to determine the optimal ecological water requirement for the Xiangxi River.

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