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Macroinvertebrate community succession in the Three-Gorges Reservoir ten years after impoundment

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ABSTRACT

The Three-Gorges Reservoir (TGR) is one of the world's largest reservoirs, whose ecological effects have attracted much attention. Focusing on the macroinvertebrate community dynamics and its relationship with hydrological factors ten years after impoundment, we provide an overview of the macroinvertebrate community succession in the TGR including determining factors. Pioneer species in the TGR was *Polypedilum scalaenum* while *Nais inflata* became dominant during non-flooding seasons commencing the second impounding year with extremely high relative abundance (up to 97%). An increase of water-level fluctuation range in the third impoundment stage did not significantly alter the steady seasonal pattern of macroinvertebrate community which formed following the second impounding year. MRPP (Multi-response Permutation Procedure) analysis showed significant differences between-season ($A < 0.3$, $P < 0.01$) except between summer and autumn ($A = -0.0165$, $P = 0.773$). Macroinvertebrate assemblages were evidently correlated with inflow discharge during flood seasons and water retention time during non-flood seasons. Macroinvertebrate density showed severe reduction in summer following high velocity inflow current, and disappeared in autumn following vast sedimentation. The macroinvertebrate community gradually became reestablished following reduction of inflow discharge and sedimentation and increase of water retention time in winter and spring. Our analyses suggest that macroinvertebrate community in the TGR is regulated by the subtropical monsoon climate, commencing with seasonal cycles of destruction followed by reestablishment.

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1. Introduction

The Three-Gorges Reservoir (TGR) was initially impounded in June, 2003. After the water level reached the normal storage level 175 m in October 26, 2010, the TGR became a giant reservoir with a surface area of 1080 km², a length of 600 km and a capacity of 3.93×10^{10} m³ (Huang et al., 2006). The impoundment in the TGR could be divided into three stages, among which the water fluctuation range increased gradually (Fig. 1). The hydrological regime of the TGR accounts for the operational pattern called "storing clear and releasing muddy". During the flooding season, water level (145 m) is maintained in order to increase capacity for flood, when the reservoir becomes more like a river with a high water velocity and short water retention time and large amounts of sediment discharge. After the flood season, water level rises to 175 m, during

which water retention time become longer and water with corresponding minor sediment load is retained in the reservoir (Wang, 2008; Xu et al., 2009a). The Three Gorges Dam (TGD) is located in Sandouping (Yichang, China) within the middle of the Yangtze River whose drainage basin covers an area of 1.8 million km², and experiences a subtropical monsoon climate (Chen et al., 2008). Influenced by monsoon activities and seasonal motion of subtropical highs, the annual precipitation and runoff vary significantly seasonally (Jiang et al., 2006). Most precipitation in the TGR area occurs in summer, 40%–50% of the annual total; only about 5% happens in winter (Cai et al., 2010).

The macroinvertebrate environment within reservoir experienced significant changes after impoundment (Hall et al., 1999; Scasso et al., 2001), followed by colonization and succession of organisms (Youngman et al., 1976; Wolfinbarger, 1999; Domingues et al., 2007; Jorcin et al., 2009). Ecologists have studied macroinvertebrate community colonization and secondary succession in newly formed reservoirs (Voshell and Simmons, 1984; Bass, 1992; Ruhí et al., 2010). However, little research on macroinvertebrate

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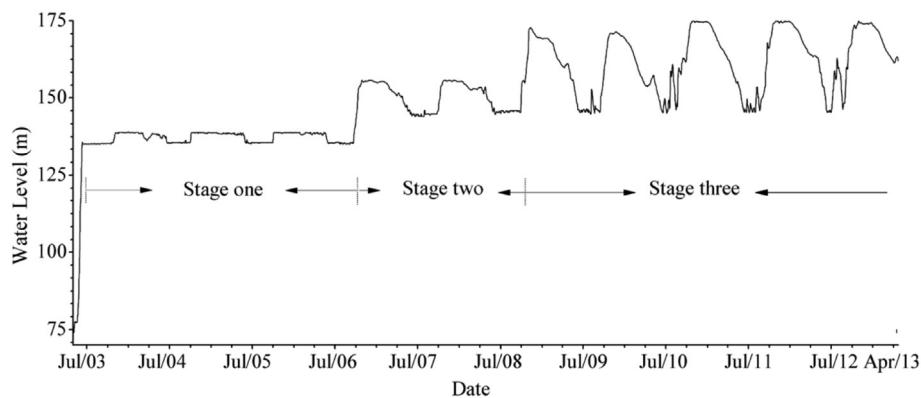


Fig. 1. Water level fluctuation of Three-Gorges Reservoir during ten years (from May 1st, 2003 to April 23rd, 2013.).

community succession within large deep-water reservoirs within a relatively long time scale has been conducted. The Three-Gorges Project (TGP) is the world's largest water-power project, and the TGR is one of the world's biggest reservoirs, whose ecological effect has been attracting much attention (Wu et al., 2003; Cai and Sun, 2012). After impoundment, variations were observed in water physicochemical characteristics (Kuang et al., 2005; Cao et al., 2006), trophic status (Ye et al., 2009; Xu et al., 2011), suspended solid (Xu et al., 2009a), sedimentation (Shao et al., 2008a), phytoplankton community (Ye et al., 2007; Xu et al., 2009b; Wang et al., 2011), zooplankton community (Xue et al., 2006; Zhou et al., 2008), and macroinvertebrate community (Shao et al., 2006, 2008b, 2010; Zhang et al., 2010). However, no systematic research has been conducted on the ecological evolution of the TGR during the ten years since first impoundment stage to the termination of the third impoundment stage. Before impoundment, Borutsky et al. (1959) investigated the macroinvertebrate community in the unfilled reservoir area. Chironomidae larvae were reported as most common, and Naididae was collected in some sites, while Tubificidae were rare. In addition, other taxa including larval Ceratopogonidae were also reported. After impoundment, the macroinvertebrate community within the mainstream of the TGR mainly comprised Naididae, Tubificidae and Chironomidae (Shao et al., 2008b; Zhang et al., 2010). The macroinvertebrate community changed significantly in the first year (Shao et al., 2008b). Evident seasonal pattern had formed since the second year, and this pattern remained during the second impoundment stage (Zhang et al., 2010). During the third impoundment stage, the water level fluctuation range increased from 11 m to 30 m. One purpose of our study was to determine if this fluctuation would have a significant effect on the macroinvertebrate community.

We analyze the evolution of macroinvertebrate community within the mainstream of the TGR and its relationship with hydrological factors during ten years after impoundment in order to reveal the succession rule of macroinvertebrate community within the TGR, and discuss the factors determining this rule. Our results may aid in evaluating macroinvertebrate community succession within other giant deep-water reservoirs.

2. Materials and methods

Two transects (CJ01, CJ04) were selected from routine sites in the long-time monitoring of the "Xiangxi River ecosystem monitoring station of Chinese Academy of Sciences/China Three Gorges Project Corporation". CJ01 is located upstream of the dam, and CJ04 lies in the upper mouth of Xiangxi Bay. A site was

selected on the left, middle, and right of each transect respectively (Fig. 2). A global positioning system (GPS) was used for locating the sites.

Samples were collected seasonally in winter (January), spring (April), summer (July) and autumn (October) with a modified Petersen grab (area 0.0625 m²) once at each site. 40 surveys were performed during ten years from 2003 to 2013. A 200 µm mesh sieve was used for filtering samples, and materials remaining on the sieve were hand-picked and preserved in 10% formaldehyde. Most taxa were identified to genus or species, and the densities were expressed as individuals/m² (ind./m²). Sampling methods refer to protocols for standard observation and measurement of the Chinese Ecosystem Research Network (CERN) (Cai, 2007). No samples were collected from a few sites due to high water velocity and coarse sediment.

The data of water level and inflow discharge of the TGR were provided by China Three Gorges Project Corporation. Storage capacity computational methods of the TGR at specific water levels are from Xu (2010). Water retention time (WRT) was calculated as:

$$WRT = \frac{V_T}{Q_T},$$

following the method outlined by George and Hurley (2003) where V_T equals average capacity (m³) of the period T (Day); Q_T represents the average inflow discharge (m³ d⁻¹) of the period T (Day).

Diversity of the community was evaluated by species richness (R) and Shannon–Wiener diversity index (H'):

$$H' = -\sum_{i=1}^s P_i \log_2 P_i$$

$$P_i = N_i/N$$

Where N_i is the density of species i ; N is the total density of macroinvertebrates.

As the distance between the two transects (30 km) is negligible compared to the total length of the reservoir (600 km), spatial variation was not taken into account and the mean value of all sites was calculated for analyses. Univariate two-way analysis of variance (SPSS 19.0) was performed with the two hydrological variables WRT, inflow discharge (D) and the six community variables, total density (TD), richness (R), Shannon–Wiener diversity index (H'), relative abundance of Tubificidae (%T), relative abundance of Chironomidae (%C), relative abundance of Naididae (%N)

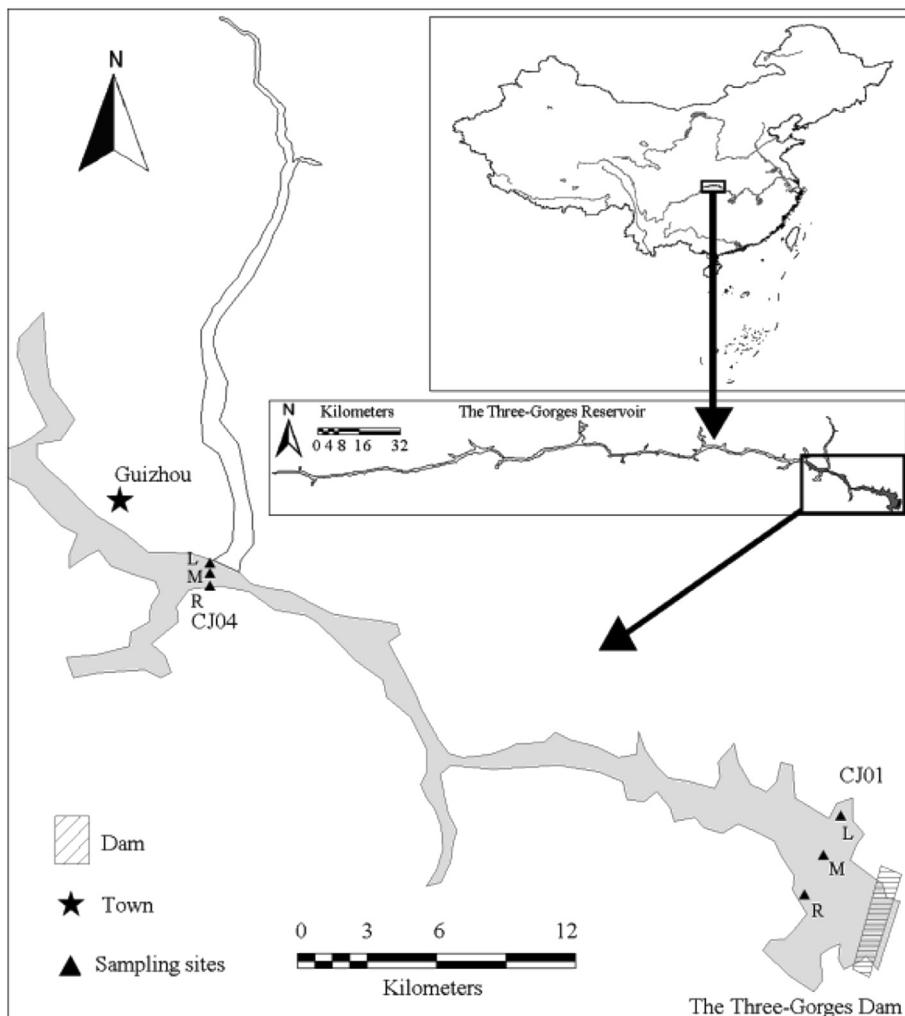


Fig. 2. Distribution of sampling sites in the TGR.

in order to examine the difference of each variable among seasons and the three impoundment stages. To improve the normality and homogeneity, D, TD, R, H', %T, %C and %N were transformed by $\log(y + 1)$. If interaction between the two factors (season and stage) was not significant, it was removed from the model. If the among-groups difference was significant, multiple comparisons were performed. LSD (Least Significant Difference) test was carried out only when homogeneity was found. Otherwise, the Tamhane test was performed. Canonical correspondence analysis (CCA, Canoco for Windows 4.5) was conducted to explore the relationship between the hydrological variables and macroinvertebrate community. Five-day mean values of WRT and inflow discharge preceding fifteen days from the sampling day were calculated for variance analyses and CCA (e.g., if sample was collected in July 15th, mean value of WRT and inflow discharge from June 28th to July 2nd was calculated) (Zhang, 2012). Non-Metric Multidimensional Scaling (NMS) ordination was used for grouping all seasons, and Bray–Curtis was selected as the distances measure method. Multi-response Permutation Procedure (MRPP) was conducted for examining specific similarity between groups, which was expressed as A (Zhang et al., 2010). As the macroinvertebrate community of the TGR was chaotic in the first impounding year (Shao et al., 2008b; Zhang et al., 2010), the winter of 2005 was taken as the starting point in variance analyses, CCA, NMS

ordination, and MRPP analyses. As no macroinvertebrates were collected in the summer of 2012, this season was removed from the CCA, NMS ordination and MRPP analyses, the latter two analyses both performed with PC-ORD 5.0.

3. Results

A total of 49 taxa were collected during the ten years' surveys, and mainly comprised three groups: Chironomidae, Tubificidae and Naididae (Fig. 3). Ten taxa were found in common among the three impoundment stages as follows: *Polyphemus scutatum*, *Branchiura sowerbyi*, *Limnophilus hoffmeisteri*, *Nais inflata*, *Stictochironomus* sp., *Teneridrilus mastix*, *Nais variabilis*, *Paranais frici*, *Procladius* sp., *Bothrioneurum vejdovskyanum*, and *Nematoda* spp. *Polyphemus scutatum* was the most frequent taxon, occurring in 70% of all the 40 surveys. Other frequent taxa included: *B. sowerbyi* and *Procladius* sp., 50%; *N. inflata* and *Nematoda* spp., 45%; *T. mastix*, 37.5%; *Stictochironomus* sp., 35% and *L. hoffmeisteri*, 32.5%.

Polyphemus scutatum was the pioneer species of the TGR. The pioneer community lasted for half a year until the spring of 2004, when other taxa became established. The community makeup in the following year was labile, as the dominant taxon changed. After that, *N. inflata* was always the dominant species in the spring macroinvertebrate community commencing in 2005. In winter,

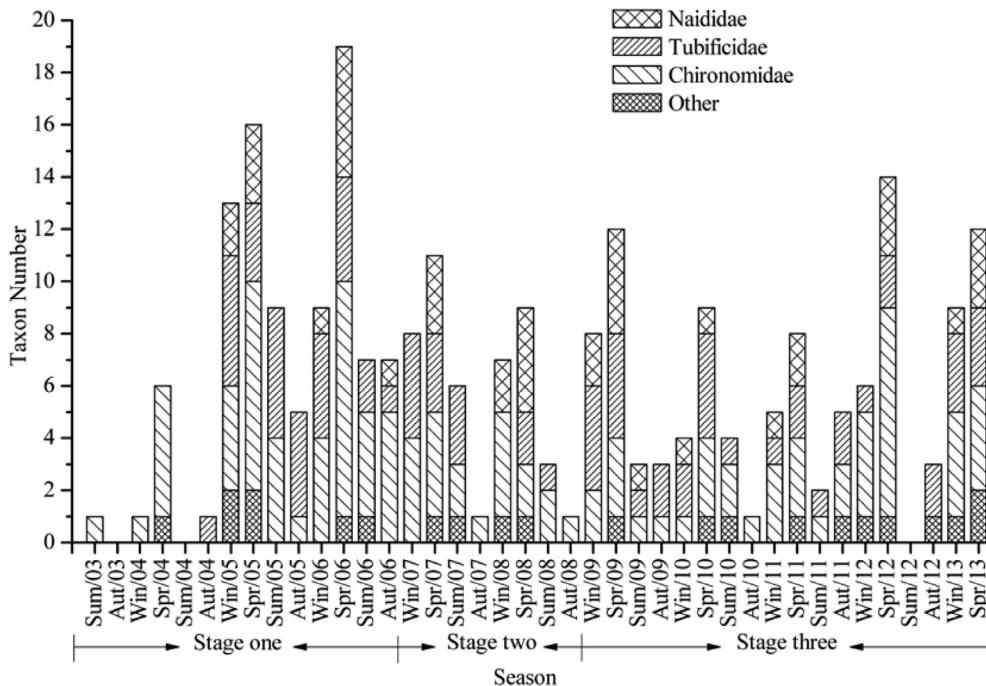


Fig. 3. Taxon composition of macroinvertebrate community in each season.

Polydendron scalaenum was predominant from 2005 to 2007, after which they were replaced by *N. inflata* or *Stictochironomus* sp. A stochastic dynamic was presented in the evolution of the community in summer and autumn (Table 1, Fig. 4).

variables showed significant differences among seasons, while only WRT, R and H' showed significant differences among stages. WRT significantly increased while R noticeably decreased in the subsequent two stages compared to the first stage. H' exhibited a sig-

Table 1
Dominant species of each season during the ten years after impoundment.

Season	Dominant species	Relevant abundance (%)	Season	Dominant species	Relevant abundance (%)
Sum/03	<i>Polydendron scalaenum</i>	100	Spr/09	<i>N. inflata</i>	81.3
Win/04	<i>Polydendron scalaenum</i>	100	Sum/09	<i>N. inflata</i>	45.7
Spr/04	<i>Tanytarsus</i> sp.	28.6	Aut/09	<i>B. sowerbyi</i>	50.0
Aut/04	<i>Tubificidae</i> sp.1	100	Polypedilum scalaenum	33.3	
Win/05	<i>Polydendron scalaenum</i>	44.3	Win/10	<i>Stictochironomus</i> sp.	67.1
	<i>N. inflata</i>	32.1	Spr/10	<i>N. inflata</i>	88.4
Spr/05	<i>N. inflata</i>	93.8	Sum/10	<i>Chironominae</i> sp.2	33.3
Sum/05	<i>L. hoffmeisteri</i>	46.7	Aut/10	<i>Chironominae</i> sp.2	100
Aut/05	<i>Polydendron scalaenum</i>	64.7	Win/11	<i>N. inflata</i>	71.9
Win/06	<i>Polydendron scalaenum</i>	44.9	Spr/11	<i>N. inflata</i>	86.0
Spr/06	<i>N. inflata</i>	97.7	Sum/11	<i>Procladius</i> sp.	66.7
Sum/06	<i>Procladius</i> sp.	52.9	Aut/11	<i>Procladius</i> sp.	53.1
Aut/06	<i>Procladius</i> sp.	68.8		<i>B. sowerbyi</i>	30.5
Win/07	<i>Polydendron scalaenum</i>	64.4	Win/12	<i>Stictochironomus</i> sp.	42.1
Spr/07	<i>N. inflata</i>	91.1		<i>B. sowerbyi</i>	21.1
Sum/07	<i>Nematoda</i> spp.	47.1		<i>Polydendron scalaenum</i>	21.1
Aut/07	<i>Procladius</i> sp.	100	Spr/12	<i>N. inflata</i>	69.9
Win/08	<i>N. inflata</i>	90.6		<i>Polydendron scalaenum</i>	19.4
Spr/08	<i>N. inflata</i>	96.3	Aut/12	<i>T. tubifex</i>	76.9
Sum/08	<i>Procladius</i> sp.	81.8	Win/13	<i>N. inflata</i>	47.4
Aut/08	<i>Procladius</i> sp.	100		<i>Nematoda</i> spp.	24.1
Win/09	<i>N. inflata</i>	71.4	Spr/13	<i>N. inflata</i>	91.9

In the third impounding year, density and richness of macroinvertebrates achieved a peak in spring, and reached their lowest level in autumn. Seasonal ordination of density and richness was: spring > winter > summer > autumn. This stable seasonal pattern was similar to that of the preceding two impounding stages and was supported by two-way ANOVA and multiple comparisons. All

nificant difference between the first two stages. Significant differences occurred among all variables between summer and spring but not between summer and autumn. Community variables were significantly different between winter and spring, but not hydrological variables. All variables except H' represented significant differences between spring and autumn. (Table 2)

Table 2

Multiple comparisons between variables in Two-Way ANOVA.

		WRT	D	TD	R	H'	C%	T%	N%
Stage one	Stage two	-11.639^b	-0.005	0.244	0.285^b	0.147^a	0.121	0.553	0.148
	Stage three	-27.697^b	0.020	0.392	0.272^b	0.064	0.174	0.184	-0.114
		-16.058^b	0.025	0.148	-0.013	-0.083	0.053	-0.369	-0.262
Stage two	Stage three	-16.058^b	0.025	0.148	-0.013	-0.083	0.053	-0.369	-0.262
	Winter	Spring	0.793	0.071	-1.197^b	-0.188^a	0.166^b	0.821^b	0.741^b
	Summer	-40.986^b	-0.393^b	0.911^b	0.279^b	0.046	0.108	-0.224	1.038^a
Spring	Autumn	-40.236^b	-0.432^b	0.919^b	0.349^b	0.145^a	-0.121	0.079	1.168^b
	Summer	40.193^b	-0.463^b	2.108^b	0.467^b	-0.120^a	-0.713^a	-0.965^a	1.745^b
	Autumn	39.443^b	-0.503^b	2.116^b	0.537^a	-0.021	-0.942^b	-0.662	1.874^b
Summer	Autumn	-0.002	-0.040	0.008	0.070	0.099	-0.229	0.302	0.130

WRT: water retention time (day); D: discharge ($10^3 \text{ m}^3/\text{s}$); TD: total density (ind./ m^2); R: richness; H': Shannon–Wiener diversity index; %C: relative abundance of Chironomidae; %T: relative abundance of Tubificidae; %N: relative abundance of Naididae.

^a Indicates difference is significant at 0.05 level.

^b Indicates difference is significant at 0.01 level.

Communities in winter and spring were clearly segregated from those of summer and autumn on the CCA axes (Fig. 5). Macroinvertebrate communities were principally regulated by inflow discharge in summer and autumn, and intensely correlated with WRT in winter and spring. Moreover, the NMS ordination demonstrated that macroinvertebrate community could be grouped by seasons in the third impoundment stage. Taking the three stages into consideration, MRPP analysis demonstrated extremely low but not significant similarity between summer and autumn ($A = -0.0165$, $P = 0.773$), which may be an indicator of stochastic dynamics of macroinvertebrate communities in these two seasons. In sharp contrast, the other between-season differences were all highly significant ($A < 0.3$, $P < 0.01$) (Fig. 6).

4. Discussion

4.1. Succession

At the initial stage of reservoir formation that includes sediment and nutrient loading, organic substances in sediment accumulate

and provide an abundance of high quality habitat and food for macroinvertebrate biomass (Popp and Hoagland, 1995). Pioneer colonists of a new reservoir are primarily facultative species from streams and ponds inundated by impoundment. Subsequent succession is related to limnophilic species probably from other nearby waters (Voshell and Simmons, 1984; Bass, 1992). *Polyphemus scalaenum* was the pioneer species of the TGR, while *Nais inflata* was dominant in spring and winter, commencing in the second year. Borutsky et al. (1959) reported *N. inflata* as common in the creeks of the TGR, which provided compelling evidence for why *N. inflata* could be prevalent in the macroinvertebrate community before flooding seasons. Generally, after the colonization of pioneer fauna, autochthonous factors begin to regulate succession, and the dominant species shift to other colonizers (Voshell and Simmons, 1984; Bass, 1992). Profiting from the fact that TGR is an almost lotic water system during the flooding season and a lentic water system in the non-flooding season, the facultative species *Polyphemus scalaenum* could be dominant for a long time. Statistical analyses demonstrated a greater variation among seasons than among years since the second year, which indicated that a seasonal

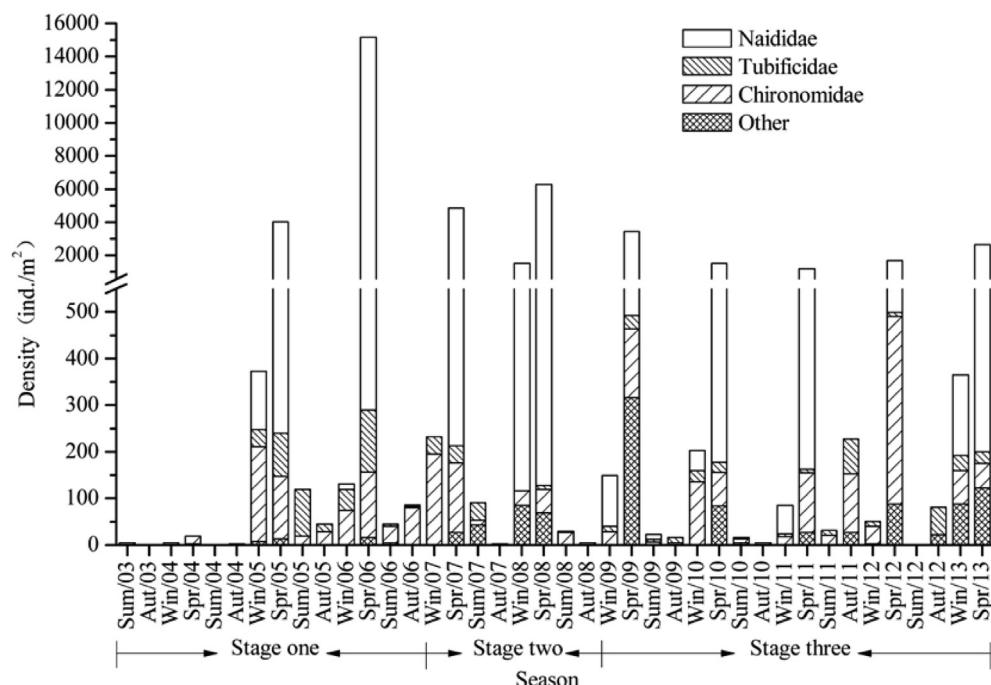


Fig. 4. Density of macroinvertebrate in each season.

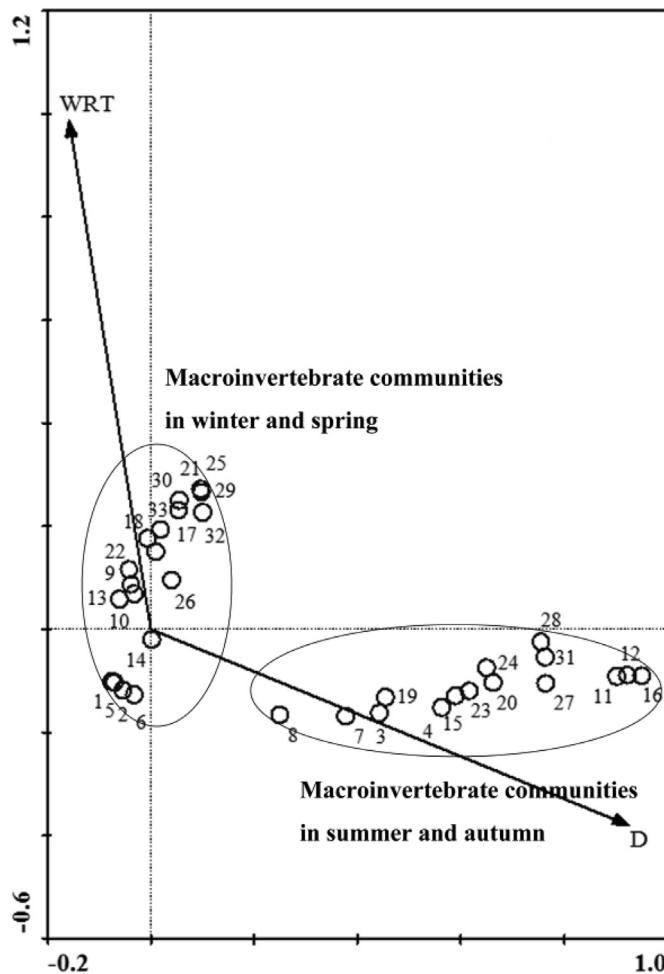


Fig. 5. Distribution of macroinvertebrate communities and hydrological variables on the CCA axes.

pattern was formed in the macroinvertebrate community of the TGR. Hydrological stability and sedimentation are significant factors regulating the secondary succession of macroinvertebrate community in a reservoir (Popp and Hoagland, 1995; Ruhí et al., 2010). Collectively, our results lead to the assumption that water-level fluctuation and sedimentation may be the key factors controlling macroinvertebrate community succession of the TGR.

4.2. Water-level fluctuation

Water-level fluctuation has always been thought to have a considerable effect on macroinvertebrates (Richardson et al., 2002; Wantzen et al., 2008; McEwen and Butler, 2010). Moderate fluctuation can be beneficial to the development of macroinvertebrate communities, whereas intense and sustaining fluctuation may reduce diversity and even destroy the structure of a macroinvertebrate community (Valdovinos et al., 2007; Aroviita and Hämaläinen, 2008; Bond et al., 2008). Water-level fluctuations of the TGR are mainly of two kinds: periodic variation caused by reservoir regulation; and drastic fluctuation within a short time caused by flooding (Figs. 1 and 7). Based on the conclusions of Shao et al. (2008b) and Zhang et al. (2010), along with our results, we outlined the general insights that steady seasonal pattern had been formed since the second impounding year for the macroinvertebrate community in the TGR. In the third impoundment stage, water-level fluctuation range rose by 173% from 11 m to 30 m.

Nevertheless, differences among the three stages were not obvious. Periodic fluctuation did not significantly affect the macroinvertebrate community in the TGR. It had previously been confirmed that water-level fluctuation induced by flood in summer had no statistical effect on the macroinvertebrate community in the estuary area of Xiangxi Bay (Zhang, 2012). Intensely influenced by the mainstream of Yangtze River, the macroinvertebrate community in the estuary area of Xiangxi Bay is similar to that in the mainstream of the TGR (Shao et al., 2010). Therefore, these surveys demonstrate that the effects of the drastic fluctuation caused by flooding in summer to the macroinvertebrate community in the TGR were also finite.

4.3. Sedimentation

Sedimentation is also a crucial factor influencing macroinvertebrate communities (Chou et al., 2004; Kaller and Hartman, 2004). Sediment input alters macroinvertebrate habitats, giving rise to changes in community structure (Voshell and Simmons, 1984; Popp and Hoagland, 1995). Sedimentation can severely destroy the macroinvertebrate communities by degrading their food quality (Graham, 1990), impeding their normal ingestion (Cohen et al., 1993; Wood and Armitage, 1997), or even burying organisms (Wood et al., 2005). After impoundment, macroinvertebrate communities of the TGR comprised mainly Chironomidae, Tubificidae, and Naididae (Shao et al., 2008b; Zhang et al., 2010). Owing to their sensitivity to suspended solids, naidids tended to prefer clear water with high transparency and less suspended solids (Shao et al., 2008b; Zhang et al., 2010). Being more tolerant of stress environments (Zhang et al., 2010), tubificids and chironomids have different preferences to habitat. Tubificids can adapt to conditions with fine sediment and rich organic matter (Takamura et al., 2009), while chironomids can accommodate to water disturbance and particle sedimentation (Bazzanti and Seminara, 1987). We suggest that composition and dynamics of macroinvertebrate community in the TGR are closely related to the sedimentation.

Affected by the monsoon precipitation, the runoff within the Yangtze River basin reveals an evident seasonal pattern (Chen et al., 2001; Jiang et al., 2006). Sediment load is strongly correlated with runoff volume in both wet- and dry-seasons (Chen et al., 2001). As a consequence, sedimentation in the Yangtze River shows a significant seasonal pattern with a varying runoff volume (Chen et al., 2008). Chen et al. (2008) reported that about 87% of the sediment transportation took place during May to October. Intercepted by the TGD, a large amount of suspended solid was retained in the TGR (Wang et al., 2007; Ran et al., 2013). Flushed out of the TGR by high velocity currents, the sedimentation attained its maximum in the subsequent two months of the maximal runoff volume period (Chen et al., 2001), which took place during the flooding season (June to August). Consequently, the most severe sedimentation occurred at the end of the flooding season (September to October).

Significant correlations were revealed between inflow discharge and community variables (Zhang et al., 2010). As displayed in the variations of macroinvertebrate community in the TGR, total density and richness always reached their peak in spring, rapidly decreased in summer, degraded to their lowest level in autumn, and rose again in winter (Figs. 3 and 4). In winter and spring, due to inflow discharge and sediment load reducing, with water retention time increasing as well as water disturbance lessening, optimal habitats were formed within the TGR, which resulted in the expansion of the macroinvertebrate community. In summer, exposed to the drastic disturbance caused by the high velocity current carrying a large amount of sediment, the density of Naididae declined dramatically (Shao et al., 2008b; Zhang et al., 2010),

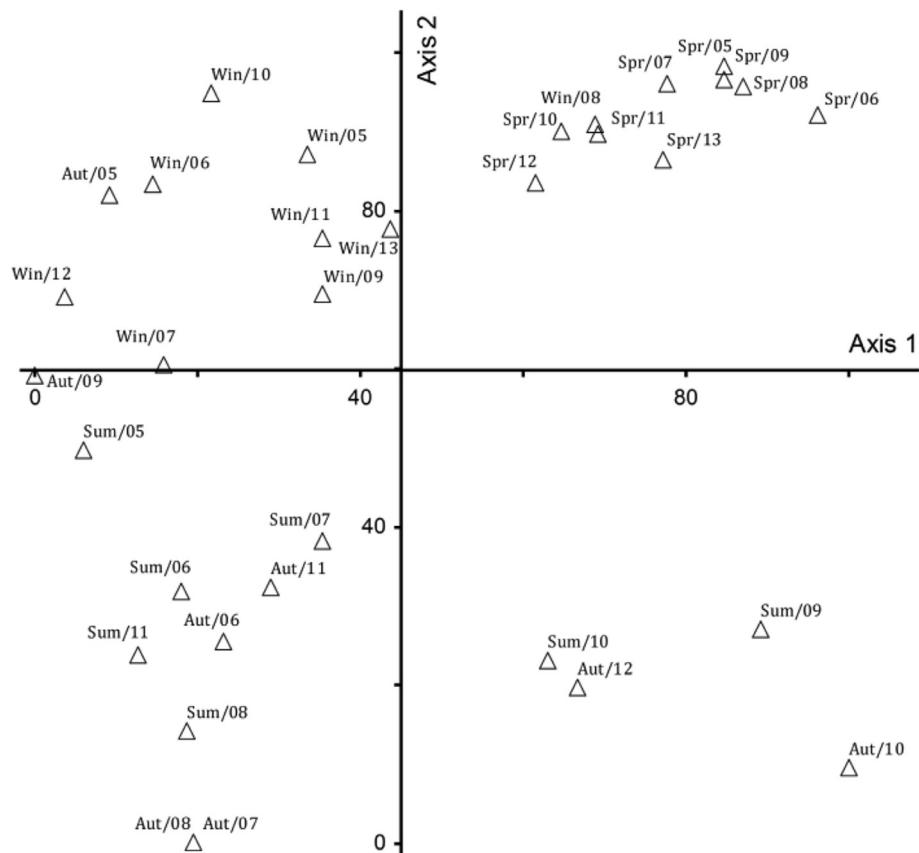


Fig. 6. Results of NMS ordination.

whereas some tolerant tubificids and chironomids survived (Zhang et al., 2010). This explains why richness sustained a relatively high level in spite of the intense decrease of total density. In autumn, total density and richness were lowest, likely due to sedimentation in the TGR. At the end of flooding season, the TGR began to store

water. As water-level rose, flow velocity decreased and water retention time became longer. Sedimentation in the TGR was peak in autumn (Chen et al., 2001). The vast sedimentation buried the macroinvertebrates (Wood et al., 2005), and destroyed the community. As a consequence, macroinvertebrate abundance in

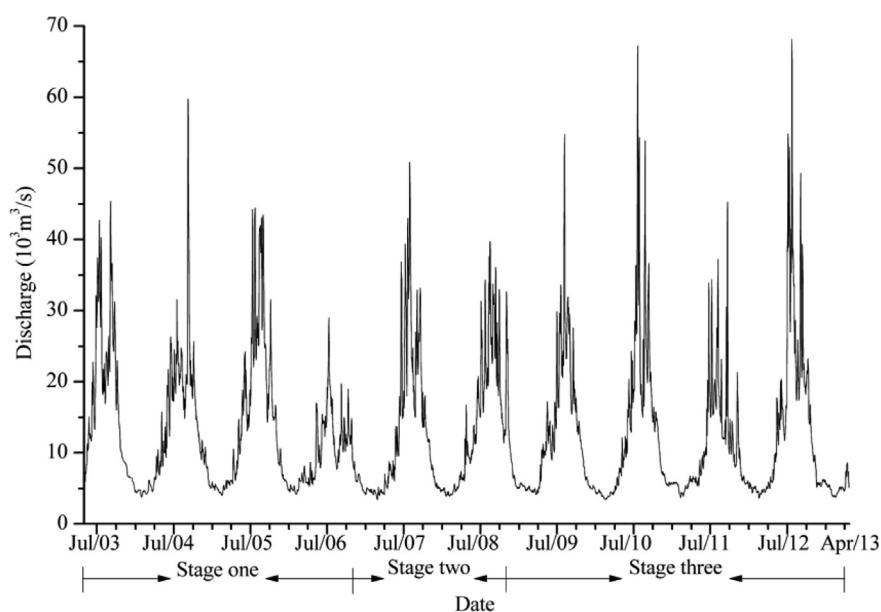


Fig. 7. Inflow discharge of the TGR from May 1st, 2003 to April 23rd, 2013.

autumn was rare, and no individuals were found in some sites especially in the middle transects.

5. Conclusion

Affected by the vast inflow discharge in flood season and the intense sedimentation at the end of flood season, the macroinvertebrate community in the TGR will be destroyed every year. The macroinvertebrate community is destroyed in autumn, gradually reconstructed in winter, and then peaks in spring following by drastic decrease in summer. Inflow discharge and sedimentation ultimately are both determined by the subtropical monsoon climate (Chen et al., 2001; Jiang et al., 2006). An and Jones (2002) found that water quality and longitudinal gradients in Asian reservoirs were regulated by the subtropical monsoon, the influence of which was long-term and relatively steady (An and Park, 2002). Based on all these data collected, it is predictable that macroinvertebrate community in the TGR will retain the seasonal pattern in the future. Nevertheless, the sampling period intervals are too long to predict a specific macroinvertebrate community turnover in a year. Consequently, high-frequency sampling will be necessary for an in-depth study.

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