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Journal of Freshwater Ecology

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tjfe20

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Published online: 06 Jan 2011.

To cite this article: Meiling Shao , Yaoyang Xu & Qinghua Cai (2010) Effects of Reservoir Mainstream on Longitudinal Zonation in Reservoir Bays, Journal of Freshwater Ecology, 25:1, 107-117, DOI: 10.1080/02705060.2010.9664363

To link to this article: http://dx.doi.org/10.1080/02705060.2010.9664363

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Effects of Reservoir Mainstream on Longitudinal Zonation in Reservoir Bays

Meiling Shao[a,b], Yaoyang Xu[a,c], and Qinghua Cai[a,d]

ABSTRACT

Spatial longitudinal zonation in reservoir bays is poorly documented, and most published papers considered that longitudinal zonation in bays is similar to that in reservoirs. Our results from analyses of the benthic macroinvertebrate community in the bays of the Three-Gorges Reservoir, China, showed that a typical bay contains four distinct zones—one more zones than a reservoir. This newly distinguished zone lies along the mouth stretch of a reservoir bay, and we call it a *mainstream zone* because it is disturbed by the reservoir mainstream. The mainstream zone is characterized by a lower standing crop and a more unstable macroinvertebrate community than in the lacustrine zone. Longitudinal zonation of reservoir bays is related to their lengths, and lacustrine zones develop only where the bay is sufficiently long. Similar to reservoirs, longitudinal zonation in bays is also dynamic and is to some extent influenced by the ages of bays and seasons.

INTRODUCTION

It is widely accepted that three longitudinal zones can be distinguished in a typical reservoir—riverine zone, transitional zone, and lacustrine zone in the direction of inflow (Straškraba and Tundisi 1999, Wetzel 2001). Various physics and chemistry gradients exist from the riverine to the lacustrine zone, including mainly gradients of width, depth, flow, nutrients, organic matter, and eutrophic properties (Straškraba and Tundisi 1999). Other gradients can also exist, such as sediment deposition (e.g., Baxter 1977), water clarity (e.g., Hart 1990, Bernot et al. 2004). Correspondingly, biotic gradients, such as those of zooplankton community (e.g., Seda and Devetter 2000, Nogueira 2001, Bernot et al. 2004), also have been observed in these zones. Recognition of longitudinal zonation in a reservoir is of great practical importance for effectively managing and utilizing reservoirs. For example, different zones should have respective assessment methodology and standards for nutrition status because these zones have different eutrophication sensitivity (Zhang et al. 2006).

Numerous bays are of great importance for reservoir environments (e.g., Nogueira et al. 1999, González et al. 2004) and reservoir biotic communities (e.g., Matsumura-Tundisi and Tundisi 2005) and have been studied extensively. Spatial longitudinal zonation in reservoir bays, however, is poorly documented. Bays of canyon-shaped reservoirs are usually long and narrow, which promote the development of the longitudinal zonation. On the other hand, these bays often the have severe water-quality degradation. For example, after the first impoundment of the Three-Gorges Reservoir (TGR), a number of bays underwent severe eutrophication, and phytoplankton blooms often developed in these bays in the spring (Cai and Hu 2006). By contrast, the blooms in the mainstream were much more scarce. The surface area of bays of the TGR will account for 1/3 of the total surface area of the TGR when the project is completed (Huang et al. 1999). Therefore, the importance of the bays is obvious. Moreover, places

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where phytoplankton blooms originate are often different within a bay. For example, Ye et al. (2007) noted that the two blooms that occurred in Xiangxi Bay of the TGR during the spring of 2005 originated in the upstream reach and also in the middle reach. Is there a substantial difference between blooms that originate in different places within a bay? It is reasonable to believe that understanding where blooms develop may aid in possible control of blooms. Thus, scientific investigations of longitudinal zonation in reservoir bays may often benefit for reservoir management.

To our knowledge, longitudinal zonation in reservoir bays is only mentioned by a few researchers, such as Straškraba and Tundisi (1999), who noted that larger bays may have similar zonation to the reservoir. Indeed, bays can be regarded as small reservoirs. Nevertheless, bays lack dams, resulting in a significant difference between bays and reservoirs. Therefore, the mouth stretch of a bay may be disturbed by the mainstream of a reservoir. Beckmann et al. (2005) also noted that increased flow in the mainstream of the Rhine River would influence the invertebrate communities of its tributary mouths. Therefore, we hypothesized that reservoir bays contain at least one additional zone that lies within the bay's mouth stretch. We term this zone the *mainstream zone* because it is formed by the disturbance of the reservoir mainstream.

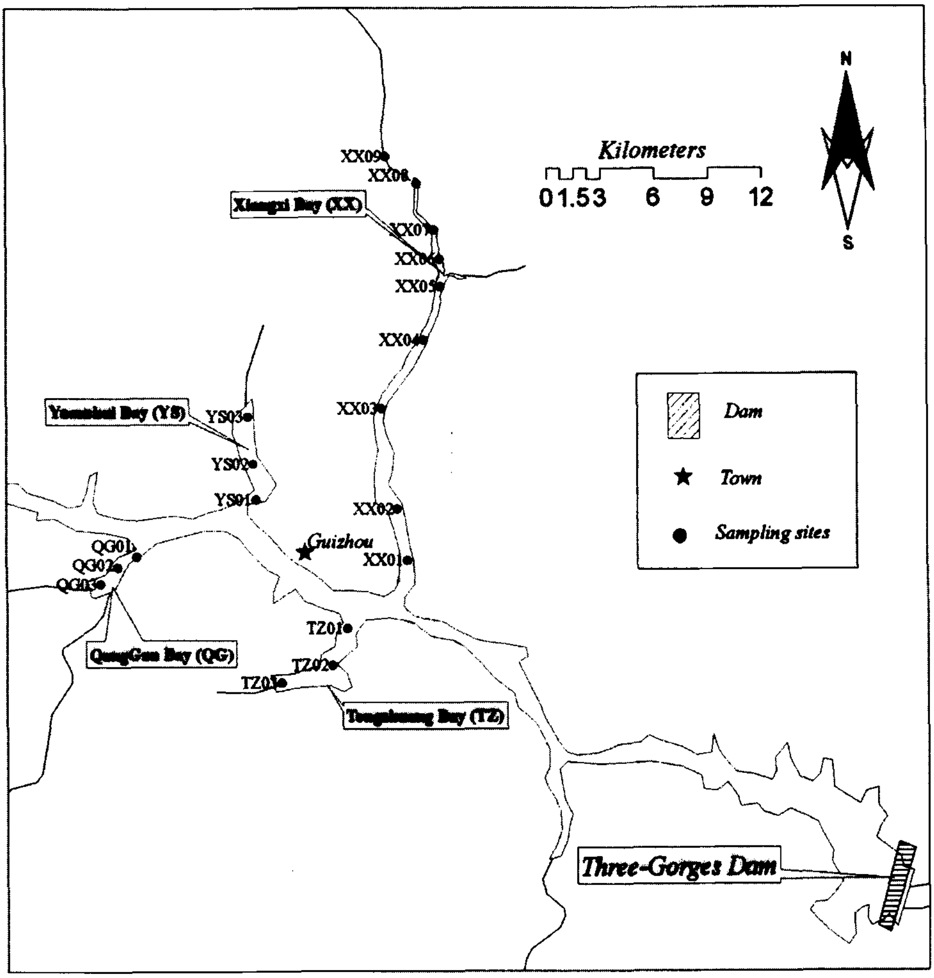

Figure 1. Location of sampling sites in the bays of the Three-Gorges Reservoir.

Macroinvertebrate communities are widely used in environmental evaluation (e.g., Blocksom et al. 2002, Moreno and Callisto 2006), mainly in water quality assessment (e.g., Fleituch 1992, Shao et al. 2007), because of their sensitivity to environmental variations and comparatively long life cycle. Moreover, macroinvertebrate communities can reflect hydrographic conditions of their habitats (Palacín et al. 1991, Donohue and Irvine 2004). In the present study we investigated longitudinal zonation in reservoir bays by examining benthic macroinvertebrate communities.

METHODS AND MATERIALS

The TGR is located in the upper Yangtze River, and a humid subtropical monsoon climate prevails in this region, which has a mean annual temperature of 17–19 °C and a mean annual precipitation of 1140–1200 mm. Precipitation is concentrated from April to October, which amounts to more than 80% of the yearly total, and floods often occur during the monsoon season from May to September (Huang et al. 2006). The operational pattern of the TGR is to store clear water after the flood season and release muddy water during the flood season. During the course of our investigation, the water level of the TGR remained at about 135 m a.s.l. during the flood season, whereas the water level was about 139 m a.s.l. during the rest of the year.

We investigated four bays (Xiangxi, Tongzhuang, Yuanshui, and Qinggan) of the TGR (Fig. 1). These four bays formed simultaneously and are close to the dam (approximately 31.5, 33.2, 40.8 and 45.1 km, respectively). They are all canyon-shaped, with minimally developed littoral zones, and aquatic macrophytes are scarce. Xiangxi Bay is the longest (approximately 25.9 km in length) and the one most investigated (e.g., Shao et al. 2006 and 2007, Ye et al. 2007, Zhou et al. 2007). The other three bays are short and similar in length (all approximately 6.0 km).

Eight sites, XX01–XX08, were set up in a lengthwise transect of Xiangxi Bay (Fig. 1). Site XX01 was located close to the mouth of the Xiangxi River, and site XX08 was located upstream of the water level at 135 m a.s.l. and downstream of the water level at 139 m a.s.l. A reference site, XX09, was set up immediately upstream of the level at 139 m a.s.l. Three sites were sampled in the other three bays respectively, and all were downstream of the water level at 135 m a.s.l. Additionally, 14 sites were sampled in the mainstream of the TGR (Shao et al. 2008).

Twelve surveys were performed seasonally from October 2003 to July 2006 in the mainstream and in Xiangxi Bay. We were unable to sample site XX08 during the flood season because low water levels in the mainstream prevented us from reaching the site by boat. When the water level increased in autumn, the site usually could not be sampled because of the hard substratum. Because no integrated annual samples were collected from site XX08, this site was excluded in our analysis. Four surveys were performed seasonally from July 2004 to April 2005 at site XX09. The other three bays were sampled seasonally from October 2005 to July 2006.

Macroinvertebrates were collected using a modified Peterson grab sampler (area 0.0625 m^2) once at each site, except at site XX09, where the benthic samples were collected with a Surber net (area 0.09 m^2). Samples were passed through a 200-μm mesh sieve, and the material retained was preserved in 4% formaldehyde. Most specimens were identified at least to genus, and all macroinvertebrate densities and biomass (wet weight) were expressed as individuals m^{-2} and g m^{-2}, respectively.

Two-way indicator species analysis (TWINSPAN; PC-ORD 4, MjM software, Gleneden Beach, Oregon, U.S.A.) was used on relative abundance data to group samples into clusters and identify characteristic species of each group. Species with a constancy of ≥ 30%, and with fidelity between 3 and 5 (on a scale from 1 to 5) were termed *characteristic species* (modified from Vogiatzakis et al. 2003). We performed multi-response permutation procedures (MRPP; PC-ORD 4), with Sorensen (Bray-Curtis) distance as the distance measure, to examine significant differences in community structure between groups determined by TWINSPAN. MRPP is a nonparametric statistical method for testing the hypothesis of no difference in community structure between two or more *a priori* groups (Bestelmeyer and Wiens 2001, Hylander et al. 2005).

One-way analysis of variance (SPSS 13.0, SPSS Inc., Chicago, Illinois, U.S.A.) was used to examine significant spatial differences in density, biomass, and taxon number. Density and biomass data were square-root transformed to improve normality and homoscedasticity. Richness data were not transformed. If the between-groups effects of one-way ANOVA were significant, multiple comparisons were performed. Tukey's honestly significant difference (HSD) *post hoc* tests were carried out only when homoscedasticity was found. Otherwise, Games-Howell tests were performed (Beckmann et al. 2005).

RESULTS

An obvious longitudinal zonation of density existed in Xiangxi Bay (Fig. 2). The middle stretch of the bay was characterized by high density, whereas density in the two ends of the bay was low. Similar patterns were also found for biomass and taxon number.

Eight samples with no macroinvertebrates, which were collected during the first five sampling periods, were excluded from TWINSPAN. TWINSPAN clustered the other 80 samples into five groups (Table 1). Community types with their characteristic species are presented in Table 2. The five groups differed significantly, as shown by the strong chance-corrected, within-group agreement ($A = 0.329$) and test statistic ($T = -26.28$, $p < 0.001$), which resulted from group comparisons by MRPP. Samples from sites XX03–XX05 belonged to Group 3 from October 2004 (Table 1); the community type, *Limnodrilus*, was stable. Community types from sites at the ends of the bay were unstable and changed over time. Community types of samples from sites XX06 and XX07 changed mainly among a *Limnodrilus*, a *Procladius–Limnodrilus*, and a *Polypedilum–Limnodrilus–Tanytarsus* community type, whereas community types of samples from sites XX01 and XX02 changed mainly among a *Nais*, a *Limnodrilus* and a *Procladius–Limnodrilus* community type. The community type of the reference site was different, being a typical stream community type. Therefore, longitudinal zonation also obviously existed in the community types.

From the above analyses, Xiangxi Bay could be divided into four zones: Zone I (XX01–XX02), Zone II (XX03–XX05), Zone III (XX06–XX07) and Zone IV (XX09). Density, biomass, and taxon number of the four zones (mean ± SE) are presented in Table 3.

It should be noted that only lentic communities were included in the following analysis. Therefore, the reference site was not analyzed. Significant spatial differences (among Zones I, II, III and the mainstream) were found for density, biomass, and taxon number (one-way ANOVA, $p < 0.001$, $p < 0.001$ and $p = 0.018$, respectively). The density and biomass in Zone II (14,742.7 ± 2,803.1 ind. m^{-2}, 9.39 ± 2.00 g m^{-2}, respectively) were significantly higher than those in Zone I (1,418.0 ± 497.7 ind. m^{-2}, 0.82 ± 0.45 g m^{-2}, respectively; $p < 0.05$ in both cases), Zone III (1,952.0 ± 848.0 ind. m^{-2}, 2.12 ± 0.87 g m^{-2}, respectively; $p < 0.05$ in both cases) and the mainstream (1,422.9 ± 931.2 ind. m^{-2}, 0.30 ± 0.12 g m^{-2}, respectively; $p < 0.05$ in both cases), whereas no differences were found among the latter three for these parameters. Moreover, the number of taxa in Zone II (7.1 ± 0.6) was higher than in the mainstream (3.1 ± 0.7; $p = 0.014$).

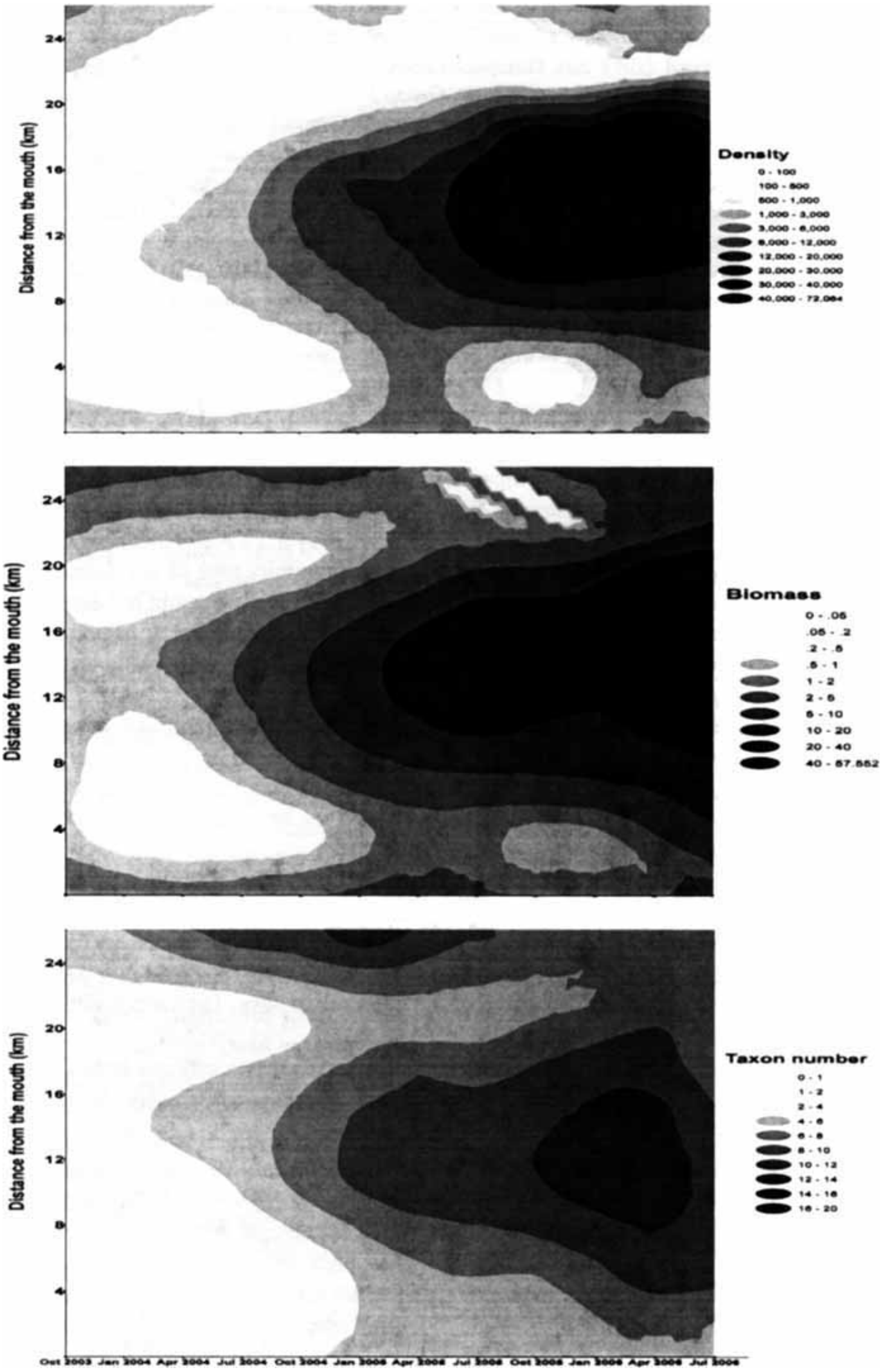

Figure 2. Distributions of density, biomass, and taxon number of benthic macroinvertebrates in Xiangxi Bay from October 2003 to July 2006.

Table 1. TWINSPAN classification of the samples collected from Xiangxi Bay. –, the densities of these samples were zero; therefore, they were excluded in TWINSPAN.

	XX01	XX02	XX03	XX04	XX05	XX06	XX07	XX09
Oct 2003	Group 2	–	Group 2	Group 3	Group 2	Group 3	–	
Jan 2004	Group 3	–	Group 2	Group 1	Group 2	Group 1	Group 2	
Apr 2004	Group 3	–	Group 4	Group 3	Group 3	Group 4	Group 2	
Jul 2004	–	–	Group 3	Group 3	Group 2	Group 2	–	Group 5
Oct 2004	–	Group 3	Group 3	Group 3	Group 3	Group 2	Group 2	Group 5
Jan 2005	Group 2	Group 2	Group 3	Group 3	Group 3	Group 2	Group 1	Group 5
Apr 2005	Group 3	Group 4	Group 3	Group 3	Group 3	Group 2	Group 3	Group 5
Jul 2005	Group 3	Group 3	Group 3	Group 3	Group 3	Group 3	Group 3	
Oct 2005	Group 3	Group 2	Group 3	Group 3	Group 3	Group 3	Group 2	
Jan 2006	Group 4	Group 2	Group 3	Group 3	Group 3	Group 3	Group 1	
Apr 2006	Group 4	Group 4	Group 3	Group 3	Group 3	Group 3	Group 3	
Jul 2006	Group 3	Group 3	Group 3	Group 3	Group 3	Group 3	Group 3	

Studies in the mainstream showed that the benthic community during the first year of the reservoir existence was unstable (Shao et al. 2008). Therefore, the data from the first year were excluded in comparisons of community types between the mainstream and Xiangxi Bay. In the mainstream, from the second year, a *Limnodrilus* community type occurring in autumn and summer, was followed by a *Nais–Polypedilum* community type in winter and spring (Shao et al. 2008). The community type of the mainstream in autumn and summer was the same as that in Zone II. Hence, we could not determine which community – the community of Zone II or of the mainstream or of both – disturbed the community in Zone I during this period. Evidence that could testify to the influence of the mainstream on Zone I was the *Nais* community type, which occurred in winter and spring in Zone I. This community type was similar to that occurring simultaneously in the mainstream.

No significant differences were found for density, biomass, and taxon number between the mainstream and each site in the other three bays (Table 4). Therefore, Zone II of Xiangxi Bay was not present in these three bays.

We analyzed winter and spring community types of sites in the three bays because these two seasons could most reflect the influence of the mainstream on tributary community types, as demonstrated above. Results of TWINSPAN were similar between January and April 2006. Samples from TZ03 and YS03 were clustered into two different groups, differing from the third group of the other seven sites. The community types of

Table 2. Community types with their characteristic species of samples collected from Xiangxi Bay.

Group	Community type	Characteristic species	Degree of fidelity	Constancy (%)	Relative abundance (mean ± SE)
1	*Polypedilum–*	*Polypedilum scalaenum* gr.	5	100	55.9 ± 16.0
	Limnodrilus–	*Limnodrilus hoffmeisteri*	5	50	18.0 ± 12.1
	Tanytarsus	*Tanytarsus* sp.	5	50	16.4 ± 9.6
2	*Procladius–*	*Procladius* sp.	5	67	45.0 ± 8.2
	Limnodrilus	*L. hoffmeisteri*	5	56	31.5 ± 7.2
3	*Limnodrilus*	*L. hoffmeisteri*	5	100	79.0 ± 2.7
4	*Nais*	*Nais infalta*	5	100	71.9 ± 11.1
5	*Baetis*	*Baetis* sp.	4	50	8.1 ± 4.6

TZ03 and YS03 could not be analyzed because of insufficient samples. Therefore, we only determined the community types of the third group. A *Polypedilum* community type appeared in winter and was followed by a *Nais* community type in spring. These two types were similar to community types that occurred simultaneously in the mainstream, reflecting the influence of the mainstream on these sites. Therefore, these seven sites were all in Zone I of each bay. Correspondingly, sites TZ03 and YS03 were in Zone III.

Table 3. Density, biomass, and taxon number of the four zones in Xiangxi Bay (mean ± SE, n = 12 and 4). T, total; C, chironomids and O, oligochaetes.

		Zone I	Zone II	Zone III	Zone IV
Density (ind. m^{-2})	T	1418.0 ± 497.7	14742.7 ± 2803.1	1952.0 ± 848.0	864.6 ± 745.4
	C	148.0 ± 49.2	162.7 ± 45.9	62.7 ± 15.0	580.6 ± 536.2
	O	1244.0 ± 464.9	14530.9 ± 2791.9	1877.0 ± 843.5	86.1 ± 82.4
Biomass (g m^{-2})	T	0.82 ± 0.45	9.39 ± 2.00	2.12 ± 0.87	2.12 ± 0.80
	C	0.06 ± 0.02	0.08 ± 0.03	0.02 ± 0.01	0.17 ± 0.15
	O	0.76 ± 0.44	9.28 ± 2.00	2.10 ± 0.87	0.00 ± 0.00
Taxon number	T	4.1 ± 0.8	7.1 ± 0.6	4.2 ± 0.6	12.3 ± 3.4
	C	1.9 ± 0.4	1.9 ± 0.2	1.4 ± 0.2	5.3 ± 2.0
	O	1.9 ± 0.4	4.6 ± 0.5	2.5 ± 0.5	1.0 ± 0.4

DISCUSSION

Generally, profundal zones of lakes or zones just upstream from a dam are characterized by high-standing crops of oligochaetes (Thut 1969, Jiang et al. 1995, Liu and Liang 1997). Therefore, Zone II could be described as a lacustrine zone because of extremely high-standing crops of oligochaetes in this zone. Zone III could be described as a transitional zone, and, correspondingly, Zone I could be determined as a mainstream zone. Therefore, a typical reservoir bay could be divided into four general zones. However, the zone upstream from the transitional zone was more disturbed by inflow and fluctuations of the water level (135 ↔ 139 m a.s.l.). Therefore, longitudinal zonation in this zone became more complicated and was not analyzed in the present study.

The sheltered lacustrine zone was characterized by high density and biomass, the stable community type, reflecting the stable environment of this zone. Nogueira et al. (1999) also noted that the environment of the lacustrine zone of the Jurumirim Reservoir was relatively stable and was little affected by periodic pulses produced by intensive rains in comparison with upstream regions. Samples with no macroinvertebrates in the present study were all collected in the transitional and the mainstream zones (mainly in the mainstream zone), indicating the unstable environments in these zones. However, no significant difference was found in taxon number among the three zones, which was probably related to the reservoir mainstream. Reservoir construction eliminated the riffle habitat required by many species that inhabited the original river, and the resultant habitat homogenization resulted in biotic homogenization (Rahel 2002). Thus the taxon number was comparatively low in this reservoir. All four types of lentic communities were completely dominated by few (1–3) taxa, whereas the community of the reference site was diverse, and the relative abundance of the characteristic species was only 8.1 ± 4.6%.

Our data demonstrated the existence of a mainstream zone (Zone I) and a transitional zone (Zone III) in all four bays. The presence of the mainstream zone in all bays suggests that this zone was indeed formed by disturbances from the mainstream. The absence of a lacustrine zone in the other three bays reflected the fact that longitudinal zonation was associated with the length of a bay. Theoretically, bays in close vicinity should have mainstream zones of similar lengths because the mainstream disturbed these bays in similar frequency and intensity. Therefore, we could infer that the length of the mainstream zones of these bays was ≥ 5.2 km (distance from site XX02 to the mouth in Xiangxi Bay). However, the total lengths of the other three bays were a slightly more than 5.2 km. Further, the upstream end of a bay is always disturbed by inflow. Therefore, the lacustrine zone could not develop in these bays because of the insufficient lengths of the bays. Hence, only when a bay is sufficiently long, four zones can be distinguished. Understanding this point can provide guidance to researchers for selecting representative bays.

Spatial longitudinal gradients of reservoir bays have been observed by previous authors. However, these previous studies either simply described spatial distributions of biotic communities or physicochemical variables in bays (e.g., de Oliveira et al. 2005, Ye et al. 2006) or simply applied rules of reservoir longitudinal zonation to bays (e.g., Zheng et al. 2006). All these studies did not sufficiently take into account the effects of the reservoir mainstream on the reservoir bays. Hence, they could not establish longitudinal zonation in reservoir bays theoretically and practically. We demonstrated, by macroinvertebrates, that spatial longitudinal zonation in reservoir bays was different from that in reservoirs. However, as demonstrated for reservoirs, longitudinal zonation is a dynamic process, influenced by retention time and season (e.g., Nogueira et al. 1999, Straškraba and Tundisi 1999). Therefore, longitudinal zonation in the reservoir bays discussed here is just a generality. For example, the community type of site XX06 was stable from July 2005, and standing crops of oligochaetes at this site were also relatively high, probably suggesting a transition to the lacustrine zone. This fact may be a reflection that the temporal development of a lacustrine zone is associated with age of the bay. The seasons also appreciably influenced zonation in Xiangxi Bay. Community types of sites XX01-XX07 in July 2005 and July 2006 were all of the *Limnodrilus* community type, consistent with the community type that occurred simultaneously in the mainstream (Shao et al. 2008). High discharges in summer and the low water level (135 m a.s.l.) during this period resulted in a shorter summer residence time (Shao et al. 2008). Therefore, rapid currents and a shorter residence time accounted for temporary disappearances of zonation in community types. However, zonation in density and biomass existed consistently.

We wanted to find out whether longitudinal zonation distinguished by macroinvertebrates was representative. Did longitudinal zonation also exist for other organisms or physicochemical variables? We took Xiangxi Bay for an example. Zhou et al. (2006) investigated rotifer communities in Xiangxi Bay during the first year of the bay's existence. They observed that rotifer density increased with increasing distance from the mouth. The cluster analysis showed that sites I (XX01) and II (XX02) could be grouped into one group, sites III (XX03) and IV (XX04) into one group, site V (XX05) into one group and sites VII (XX06), and VIII (XX07) into one group. Therefore, similar longitudinal zonation also existed for the rotifer community. Besides investigating organism communities, Xu et al. (2006) investigated the vertical attenuation coefficient (Ks_d) of downward visible irradiance in Xiangxi Bay during the spring of 2005. Spatial

Table 4. Significance tests (p) of density, biomass, and taxon number between the mainstream (October 2005 – July 2006) and each site in the other three bays by one-way ANOVA.

		Tongzhuang Bay			Yuanshui Bay			Qinggan Bay		
		TZ01	TZ02	TZ03	YS01	YS02	YS03	QG01	QG02	QG03
Mainstream	Density	0.690	0.670	0.372	0.986	0.744	0.540	0.774	0.821	0.811
	Biomass	0.925	0.990	0.681	0.586	0.848	0.426	0.819	0.611	0.829
	Taxon number	0.597	0.378	0.544	0.280	0.285	0.255	0.319	0.597	0.367

gradient distribution of Ks_d was observed in this study. In comparison with the middle stretch of the bay, the mouth stretch was characterized by low Ks_d, and the end of the bay was characterized by high Ks_d. Also during the spring of 2005, Han et al. (2006) analyzed contents of phytoplankton chlorophyll *a*, total nitrogen, and total phosphorus of water. Cluster analysis based on these three variables showed that the whole bay could be placed into four groups Group I (the mouth stretch), Groups II–III (the middle stretch) and Group IV (the end stretch). The mouth stretch (Group I) was substantially different from the other three groups owing to frequent disturbances from the mainstream. All these studies exhibited zonations similar to our results. Therefore, we conclude that our longitudinal zonation in reservoir bays, determined by macroinvertebrates, was sound. Further, the objects of all the studies mentioned above were not constant, including some plankton rotifers floating in the water column. Hence, it is reasonable to think that macroinvertebrates are good indicators of longitudinal zonation.

ACKNOWLEDGMENTS

This work was funded by the National Natural Science Foundation of China (No. 40671197), the Key Project of Knowledge Innovation Program of CAS (No. KZCX2-YW-427) and Doctoral Research Initiation Fund of Anhui Normal University. We thank Xiaodong Qu, who contributed the macroinvertebrate data of site XX09. Lin Ye, Xinqin Han, Guangjie Zhou, Hongbo Tang, Daofeng Li, Ming Cao, Jianlin Hu, Jing Chen, Junqian Zhang, Xinghuan Jia, Fengqing Li, Xiaocheng Fu and Aijiao Zhu helped with the field sampling.

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Received: 8 September 2009 Accepted: 9 November 2009