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A floodplain-scale lake classification based on characteristics of macroinvertebrate assemblages and corresponding environmental properties

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ABSTRACT

Floodplain lakes have been experiencing great pressures by human activities, and ecological functions in different types of lakes show different degrees of degradation. For facilitating conservation and management of different types of floodplain lakes, it is necessary to classify the lakes into similar groups according to certain standards. In this study, on basis of consideration of macroinvertebrate assemblages and corresponding environmental properties, the Yangtze floodplain lakes were classified into three major types grouping five groups of lakes: (1) river-disconnected lakes (algal lakes, macrophytic-algal transition lakes, and macrophytic lakes), (2) semi-connected lakes (oxbow lakes), (3) river-connected lakes. The classification of floodplain lakes mainly reflects the gradients of trophic and hydrological connectivity. The key factors structuring macroinvertebrate assemblages in the Yangtze floodplain lakes were mainly hydrological (connectivity rating, water depth), trophic (total phosphorus, macrophytes biomass) and morphometric (development of lake shoreline). Among the floodplain lakes, ecological status of river-connected lakes, where biodiversity, biomass and production of macroinvertebrates reached maxima, has been confirmed to be the best. From the view of conservation and management of the entire floodplain lakes, it is suggested that protecting the remnants of river-connected lakes, controlling eutrophication and linking disconnected lakes freely with the mainstream are crucial.

Introduction

Floodplain lakes have many functions such as water supply, irrigation, food production, sightseeing, as well as the maintenance of the unique and diverse biota of the entire floodplain ecosystem. In recent decades, the floodplain lakes have been experiencing great pressures by human activities that alter the hydrological, physico-chemical, and biological processes. Therefore, for facilitating conservation and management of these lakes, it is necessary to classify the lakes into similar groups according to certain standards.

Many classifications of lakes have been developed during the past several decades. Some researchers were keen on differences of physical characteristics including location, origin, shape and morphometry (Hutchinson, 1957; Pennak, 1958; Lewis, 1983; Canfield et al., 1984; George and Maitland, 1984). Certainly, chemical characteristics (i.e. total dissolved solids, pH, salinity, and nutrient concentrations related to trophic levels) were also used to differentiate lakes (Stockner and Benson, 1967; Kemp, 1971; Hutchinson, 1973; Schneider, 1975; Pitblado et al., 1980; Chapra and Dobson, 1981; Håkanson and Jansson, 1983). Still other researchers identified differences in lakes on basis of biological characteristics such as macrophytes, plankton, macroinvertebrates, fish and so on (Rawson, 1956; Jensen and Van Der Maarel, 1980; Harvey, 1981; Tonn and Magnuson, 1982). Recently the multi-metric approaches combined with a variety of characteristics have been gaining favor among scientists.

In the process of lake classification based on consideration of multiple factors, selection of good biological indicators is critical. Benthic macroinvertebrates are important components of aquatic ecosystems, and they are often considered as good indicators of long-term changes in environments due to their confinement to the bottom, long life cycles and limited abilities of movement (Hart and Fuller, 1974; Liang and Wang, 1999; Timm and Mõls, 2012; Jiang et al., 2013). Macroinvertebrate quality indices to classify lakes have been developed from indicator values of a few selected species (Wiederholm, 1980; Lafont et al., 1991) and representative

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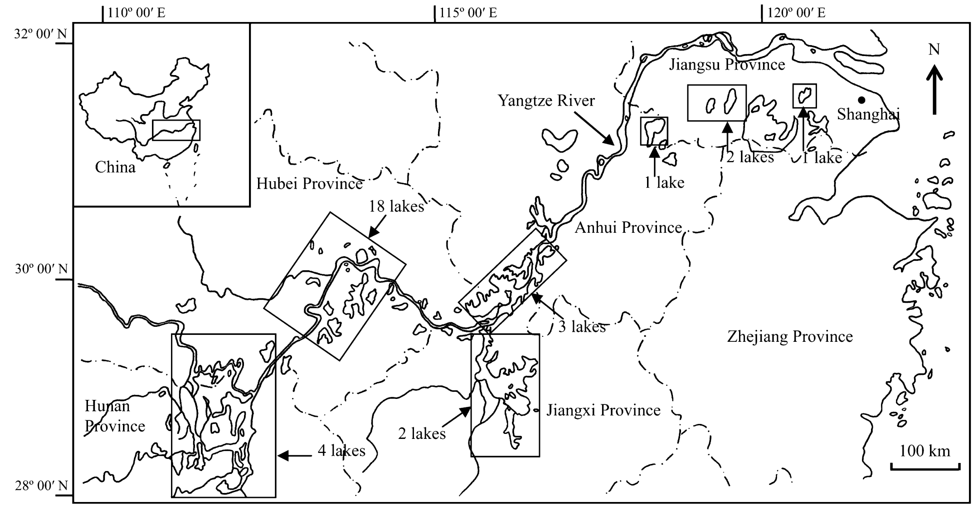

Fig. 1. Distribution of study lakes along the Yangtze River.

taxonomic groups such as chironomids and oligochaetes (Sæther, 1979; Lang, 1990) to species richness and abundance of the entire assemblage (Verneaux et al., 2004). Therefore, it's of significance to differentiate lakes using indication of macroinvertebrate assemblages in combination with other environmental variables.

In the Yangtze basin of China, belonging in the monsoon region of East Asia subtropical zone, floodplain lakes are numerous, with a total area over 16,600 km^2. Historically, most lakes were connected freely with the main river course of the Yangtze, where floods occur periodically. To prevent villages and cultivated lands along lakeshore from being flooded, embankments and sluice gates were constructed during the 1950s–1970s and eventually isolated most lakes from the river (Pan et al., 2011). Thus, some lakes freely connected with river mainstream can maintain natural ecological health, however, these river-disconnected lakes may lose water self-purification ability due to reduced hydrological connectivity degree, and they also have been facing the threat of eutrophication, so their service functions are severely damaged. In view of this, to conserve and manage the floodplain lakes, it's necessary to classify the lakes into several similar groups.

This paper deals with systematic limnological investigations in the Yangtze floodplain quarterly during 2004–2005. The purpose of this study is threefold: to differentiate Yangtze floodplain lakes based on macroinvertebrate assemblages and environmental variations; to analyze the potential factors structuring macroinvertebrate assemblages in the Yangtze floodplain lakes; to put forward some implications for lake conservation and management.

Study area and methods

All these 31 river-disconnected lakes are situated in the mid-lower Yangtze Basin, in other words, located in the monsoon region of East Asia subtropical zone. The locations of study lakes are given in Fig. 1.

Field investigations were quarterly conducted in April–May 2004 (spring), June–August 2004 (summer), September–November 2004 (autumn) and December 2004–Janurary 2005 (winter). Average values from the seasonal investigations were used for analyses. Water depth (Z) and Secchi depth (Z_{SD}) were measured with a sounding lead and a Secchi Disc, respectively. Water samples were taken near the surface and at the bottom, and combined for laboratory analyses. Total nitrogen (TN) was analyzed by the alkaline potassium persulfate digestion-UV spectrophotometric method. Total phosphorus (TP) was analyzed by the ammonium molybdate method. Phytoplankton chlorophyll *a* concentration (Chl *a*) was measured after acetone extractions by reading absorbance at 665 nm and 750 nm using spectrophotometer (Unico UV-2000, Shanghai, China). All variables were analyzed according to Standard Methods for the Examination of Water and Wastewater (2002). In the same habitat adjacent to benthic sampling site, macrophytes were sampled with a scythe (0.2 m^2), 2–4 times at each site, then cleaned, removed superfluous water and weighed for wet weight (B_{Mac}). Principal component analysis (PCA) was used to assess environmental differences between floodplain lakes.

Benthic animals dwelling in the sediment were taken with a weighted Petersen grab (0.0625 m^2) and then sieved with a 420-μm sieve. The collected animals were preserved in 10% formalin. Benthic animals were identified to the lowest feasible taxonomic level according to relevant references (Morse et al., 1994; Wiggins, 1996; Dudgeon, 1999; Wang, 2002; Zhou et al., 2003). Wet weight of animals was determined with an electronic balance after being blotted, and then dry mass (mollusks without shells) was calculated according to the ratios of dry-wet weight and tissue-shell weight reported by Yan and Liang (1999). In the study of Yan and Liang (1999), the data were collected from mid-lower Yangtze lakes, and mollusk samples were treated according to Banse and Mosher (1980) (the shells were removed and then shell and tissue were dried separately). All taxa were assigned to functional feeding groups (shredders, collector–gatherers, collector–filterers, scrapers, and predators) according to Morse et al. (1994) and Liang and Wang (1999). When a taxon had several possible feeding activities, its functional designations were equally proportioned, e.g. that if a taxon can be both collector–gatherer and scraper, the abundance of it is divided 50:50 into these groups. Two-way indicator species analysis (TWINSPAN) was performed to explore differences between macroinvertebrate assemblages in these floodplain lakes.

PC-ORD 4.0 (MjM Software Design, Gleneden Beach, Oregon) was used for two-way indicator species analysis (TWINSPAN), a divisive clustering method widely used to determine significant differences between assemblages (Hill, 1979). STATISTICA 8.0 (StatSoft, Inc., Tulsa, Oklahoma) was used for principal component analysis (PCA). CANOCO 4.53 (Microcomputer Power, Ithaca, New York) was used for detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). DCA indicated that a normal model (gradient lengths >2.0 standard units) would best fit the data, and CCA was used to analyze the relation between animal assemblages and environments. In CCA, analyses of forward selection and Monte Carlo permutation test were used to yield important environmental factors influencing abundance and distribution of macroinvertebrates. Altogether 11 environmental

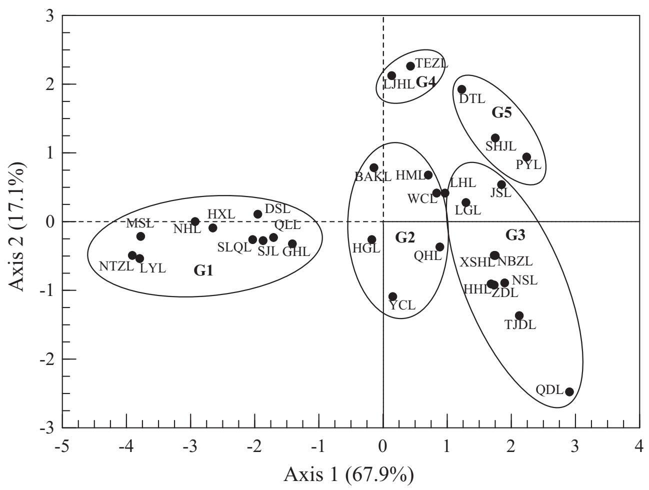

Fig. 2. Principal component analysis (PCA) ordination of the study lakes. Lake groups are G1, G2, G3, G4, and G5.

variables (A – lake surface area; D_L – development of lake shoreline; D_V – development of lake volume; DR, dynamical ratio of lake; Z; Z_{SD}; TN; TP; Chl a; B_{Mac}; CR, connectivity rating) and 101 macroinvertebrate taxa were used for CCA. CRs were ranked on a 4-point scale: 1 (river-disconnected lakes), 2 (oxbow lakes), 3 (Shijiu Lake, a river-connected lake with weaker hydrological connectivity), and 4 (Dongting Lake and Poyang Lake, two river-connected lakes with stronger hydrological connectivity). Before statistical analyses, data were $\log_{10}(x+1)$ transformed to reduce heterogeneity of variances.

Results

Classification of the study lakes

The principal component analysis (PCA) ordination diagram of sampling lakes is demonstrated that five groups of lakes were distinguishable, ordinated by the first and second axes (Fig. 2). PCA revealed that axes 1 and 2 accounted for 67.9% and 17.1% information of the measured environmental variations, respectively. The first axis was predominantly a trophic gradient. The factors strongly correlated with the first axis were total phosphorus concentration of water (TP), total nitrogen concentration of water (TN) and phytoplankton chlorophyll a concentration (Chl a). The second axis mainly reflected hydrological information. The factors strongly correlated with the second axis were connectivity rating and water depth. Morphometric, water physico-chemical and biological variables of the study lakes are given in Table 1, which indicates that large discrete differences occurred among different groups of lakes.

The classification of all the 31 lakes using TWINSPAN is shown in Fig. 3. At the first level of division, the 31 lakes were split by 2 indicator species into two groups (16 lakes characterized by abundant pollution-tolerant taxa and no pollution-sensitive ones, while 15 lakes supporting no pollution-tolerant taxa and many pollution-sensitive ones). The pollution-tolerant taxa included *Limnodrilus hoffmeisteri*, *Limnodrilus Claparèdeianus*, *Propsilocerus akamusi*, *Tanypus* sp., et al. The pollution-sensitive taxa included *Parafossarulus striatulus*, *Stenothyra glabra*, Ephemeroptera, Plecoptera, Trichoptera, et al. Further analyses divided all lakes into five groups.

According to the standard suggested by Bachmann et al. (2002) for macrophytic and algal classification of lake system, the TWINSPAN first group of lakes belongs to algal lakes which were characterized by high phytoplankton chlorophyll a concentration with a concentration range of 36.1–113.3 mg/m^3, the TWINSPAN third group of lakes belongs to macrophytic lakes which were characterized by dense macrophytes with a wet biomass range of 600.0–6488.3 g/m^2, while ecological status of the TWINSPAN second group of lakes (viz. macrophytic-algal transition lakes) ranged between the first group and the third group. The TWINSPAN fourth group of lakes (viz. oxbow lakes) results from the natural cutoff of meanders or artificial cutoffs, and these lakes are intermittently connected with river mainstream. The TWINSPAN fifth group of lakes (viz. river-connected lakes) is freely connected with river mainstream. Thus, the Yangtze floodplain lakes were classified into three major types of five groups: (1) river-disconnected lakes (algal lakes, macrophytic-algal transition lakes, and macrophytic lakes), (2) semi-connected lakes (oxbow lakes), (3) river-connected lakes.

TP-Chl a relationships in different groups of lakes

The TP-Chl a relationship is an important ecological relationship, and it reflects the conversion efficiency from total phosphorus concentration into phytoplankton biomass. Positive relationships between $\log_{10}$TP and $\log_{10}$Chl a in the Yangtze-disconnected lakes were found (Fig. 4a), and the slopes were in descending order from algal lakes, macrophytic-algal transition lakes to macrophytic lakes. The river-connected lakes have lentic and lotic regions, and analyses referring to $\log_{10}$TP-$\log_{10}$Chl a relationships are given according

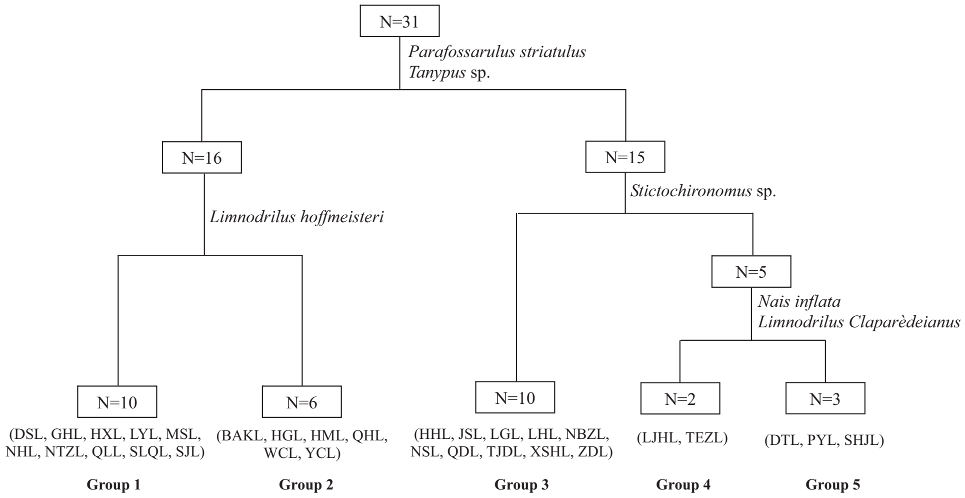

Fig. 3. TWINSPAN dendrogram of 31 lakes with seven pseudospecies cut-levels: 0, 0.5, 1.5, 4.5, 13.5, 40.5 and 121.5. Species names are the indicators for each of the dichotomies.

Table 1
Basic morphometric, physico-chemical and biological variables in the study lakes.

Code	Lake	A (km^2)	D_L	D_V	DR	Z (m)	Z_{SD} (m)	TN (mg/m^3)	TP (mg/m^3)	Chl *a* (mg/m^3)	B_{Mac} (g/m^2)
1	Dianshan Lake (DSL)	63.7	2.20	1.76	2.22	2.2	0.4	6043	232	36.1	0
2	Gehu Lake (GHL)	146.5	1.18	1.88	6.37	1.2	0.4	3197	218	47.7	0
3	Hongxing Lake (HXL)	0.5	2.12	2.90	0.24	2.8	0.5	7882	384	57.6	0
4	Longyang Lake (LYL)	1.8	2.00	2.40	0.67	1.7	0.4	8171	1017	113.3	0
5	Moshui Lake (MSL)	1.5	2.50	2.40	0.67	2.2	0.4	6848	1050	103.6	0
6	Nanhu Lake (NHL)	7.9	2.17	2.00	1.12	2.5	0.4	8259	346	79.9	0
7	Nantaizi Lake (NTZL)	5.6	2.03	2.21	1.87	1.5	0.3	13690	760	96.0	0
8	Qingling Lake (QLL)	2.0	1.81	2.60	0.94	1.3	0.4	2514	293	83.2	0
9	Sanliqi Lake (SLQL)	2.7	2.10	2.71	0.78	1.9	0.5	7096	306	36.8	0
10	Sanjiao Lake (SJL)	0.5	2.00	2.50	0.50	1.8	0.5	6073	205	50.2	0
11	Bao'ankou Lake (BAKL)	3.0	1.67	1.67	1.62	1.8	0.5	2129	81	13.2	0
12	Houguan Lake (HGL)	12.7	2.37	1.88	1.11	2.8	1.2	2038	59	14.7	0
13	Huama Lake (HML)	10.3	9.07	1.29	0.76	2.2	0.6	1138	51	12.1	103.9
14	Qihu Lake (QHL)	1.3	2.66	1.80	0.77	1.2	0.9	1145	78	10.3	0
15	Wuchang Lake (WCL)	86.6	1.50	2.55	2.96	2.6	0.9	1032	48	5.8	122.6
16	Yangcheng Lake (YCL)	113.0	2.93	1.02	2.53	1.5	0.8	2452	94	13.2	422.4
17	Honghu Lake (HHL)	355.0	1.54	1.75	8.12	1.3	0.9	918	40	5.0	795.0
18	Junshan Lake (JSL)	192.5	3.25	1.88	2.17	3.6	2.2	610	33	1.4	600.0
19	Longgan Lake (LGL)	252.0	3.20	1.37	6.30	1.4	0.5	615	42	1.1	609.0
20	Luhu Lake (LHL)	29.8	5.21	2.20	1.82	2.5	0.9	641	31	4.2	798.1
21	Nanbeizui Lake (NBZL)	66.7	6.40	1.96	1.78	3.0	1.6	770	16	3.1	762.4
22	Niushan Lake (NSL)	38.0	4.80	2.10	1.23	4.2	3.2	804	33	2.2	897.6
23	Qiaodun Lake (QDL)	8.0	1.95	1.91	0.86	2.7	2.0	536	48	3.8	6488.3
24	Taojiada Lake (TJDL)	3.0	2.53	1.88	0.72	1.5	1.2	633	46	3.4	1471.9
25	Xiaosihai Lake (XSHL)	1.5	3.63	2.62	0.57	2.0	0.9	700	19	3.1	1123.4
26	Zhangdu Lake (ZDL)	35.2	1.22	1.57	2.58	1.7	1.1	717	49	4.5	1226.1
27	Laojianghe Lake (LJHL)	18.4	1.48	0.95	0.23	4.9	0.6	829	118	8.7	0
28	Tian'ezhou Lake (TEZL)	20.0	1.41	0.54	0.18	7.6	0.9	880	66	3.3	0
29	Dongting Lake (DTL)	2432.0	7.70	0.82	7.70	3.7	0.7	902	109	3.5	333.7
30	Poyang Lake (PYL)	2933.0	5.90	0.52	10.62	2.7	1.4	1009	24	2.0	532.9
31	Shijiu Lake (SHJL)	210.4	4.70	2.32	3.54	2.5	1.0	536	89	5.9	346.3

Note: A – lake surface area; D_L – development of lake shoreline; D_V – development of lake volume; DR – dynamical ratio of lake; Z – mean water depth; Z_{SD} – Secchi depth; TN – total nitrogen concentration of water; TP – total phosphorus concentration of water; Chl *a*, chlorophyll *a* concentration; B_{Mac} – biomass of submersed macrophytes.

to respective regions. As shown in Fig. 4c and d, the regressions derived from lentic and lotic regions were linear and curvilinear, respectively.

Macroinvertebrate assemblages in different groups of lakes

Altogether 101 taxa of macroinvertebrates belonging to 34 families and 83 genera were identified from all the study lakes. Among them were 19 oligochaetes, 28 mollusks, 44 insects and 10 miscellaneous animals. Comparisons on densities and biomass of macroinvertebrates in different types of lakes are given in Table 2. It's indicated that variations in densities and biomass were evident among lakes. The density of total macroinvertebrates reached a maximum in the algal lakes, which were characterized by dominance of collector-gatherers (i.e. Tubificidae and Chironomidae). In the macrophytic lakes, scrapers (i.e. epiphytic gastropods) were predominant. In the oxbow lakes, the dominant group was insects belonging to collector-gatherers and shredders. In the river-connected lakes, macroinvertebrates were dominated by gastropod-scrapers and bivalve-filterers preferring hard sandy substrate.

Factors structuring macroinvertebrate assemblages in Yangtze floodplain

Forward selection analyses and Monte Carlo permutation test revealed that the important environments influencing densities of macroinvertebrates in the study lakes were connectivity rating (CR), water depth (Z), total phosphorus concentration (TP), biomass of submersed macrophytes (B_{Mac}), development of lake shoreline (D_L), Secchi depth (Z_{SD}), and dynamical ratio of lake (DR) (Fig. 5a). Axes 1 and 2 accounted for 30.7% and 19.5% of the variability in species-environment relations, respectively, and both axes were significant at $p < 0.05$ (Monte Carlo permutation test). The factors strongly correlated with the first axis were CR, TP, and Z_{SD}. The second axis was predominantly correlated with Z (Table 3).

The important environments influencing biomass of macroinvertebrates were CR, TP, B_{Mac}, Z, Z_{SD}, and D_L (Fig. 5b). Axes 1 and 2 accounted for 35.5% and 19.4% of the variability in species-environment relations, respectively, and both axes were significant at $p < 0.05$ (Monte Carlo permutation test). The factors strongly correlated with the first axis were CR and TP. The second axis was predominantly correlated with Z (Table 4).

Discussion

On basis of consideration of macroinvertebrate assemblages and corresponding environmental properties, the Yangtze floodplain lakes were classified into five groups. As shown in Fig. 3, two species were indicators for the first division. According to related materials, *P. striatulus* is closely associated with macrophytes and clean water (Newman, 1991; Jeppesen et al., 1998; Pan et al., 2011), while *Tanypus* is tolerant of moderate or heavy organic pollutions (Rosenberg and Resh, 1993; Morse et al., 1994). Thus, the first division reflected variations of trophic levels. Furthermore, 16 lakes were easily assigned to Group 1 and Group 2 according to abundance of a pollution-tolerant species (i.e. *L. hoffmeisteri*), and 15 other lakes were classified into two groups (i.e. 10 and 5 lakes) according to abundance of a potamophilus species (i.e. *Stictochironomus* sp.). At the third division level, the five lakes were assigned to Group 4 and Group 5 according to abundance of the potamophilus and psychrophilic species which were related to hydrological connectivity degree (Pringle, 2001; Amoros and Bornette, 2002). Therefore, lake classification with indication of macroinvertebrates incorporated trophic levels and a hydrological connectivity gradient, which was consistent with the ordination derived from principal component analysis (cf. Fig. 2).

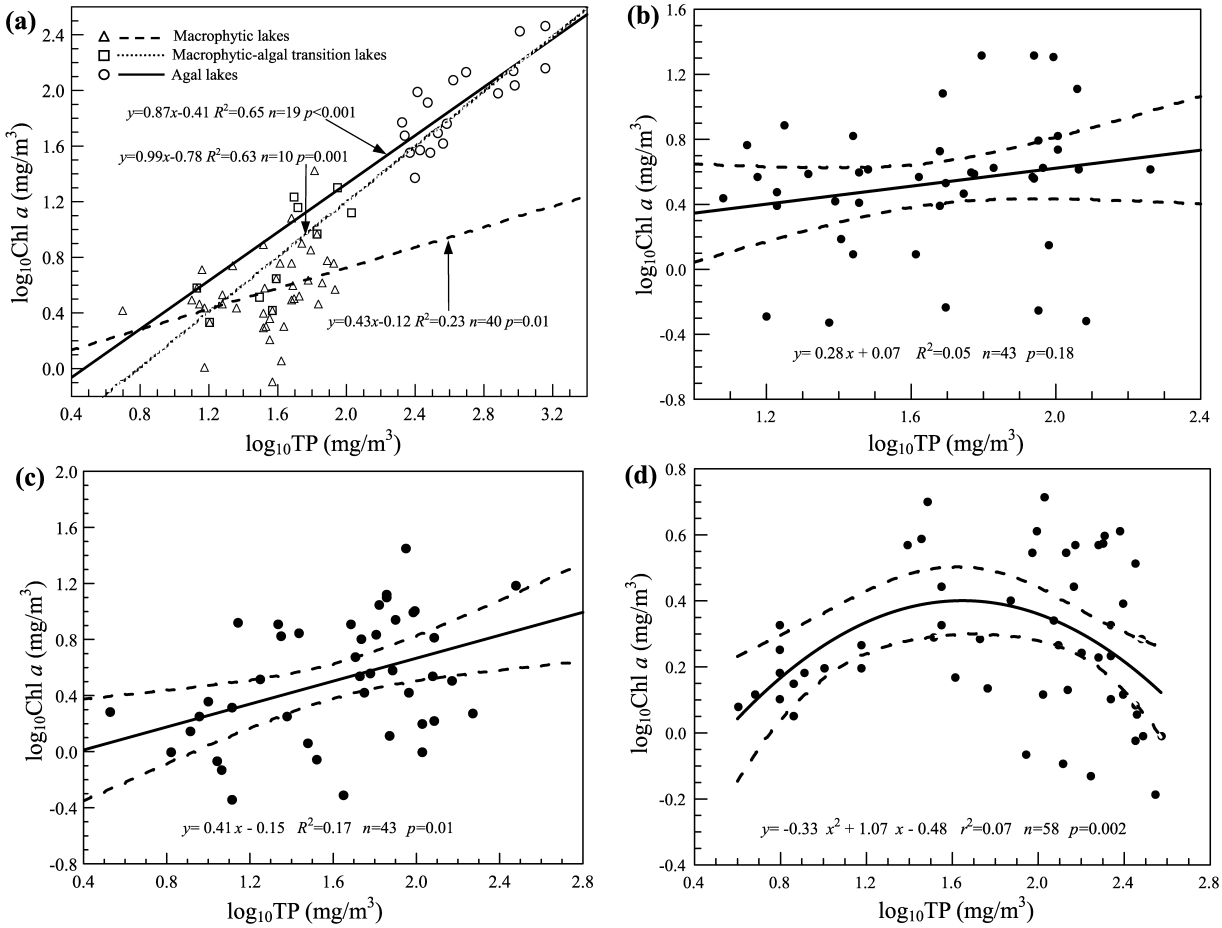

Fig. 4. Regressions of chlorophyll *a* concentration ($\log_{10}$Chl *a*) against total phosphorus ($\log_{10}$TP) in the Yangtze-disconnected lakes (a), in the Yangtze oxbows (b), in the lentic regions (c) and the lotic regions (d) of the Yangtze-connected lakes.

According to our analyses, factors regulating macroinvertebrate assemblages were mainly hydrological (connectivity rating, water depth), trophic (total phosphorus, macrophytes biomass) and morphometric (development of lake shoreline). Hydrological connectivity reflects the interference intensity by river, and the river disturbs its associated waters mainly through the function of water flow. First, water flow determines substrate properties and subsequently affects benthic animals (Nowell and Jumars, 1984; Allan and Castillo, 2007). Second, water flow is closely related to external nutrients (Søballe and Kimmel, 1987), and it is the driving force for delivering nutrients to macroinvertebrates. Third, water flow influences abundance of suspended food particles. Fast flow

Table 2
Mean (±SE) density (*D* – ind./m²) and biomass (*B* – g dry mass/m²) (mollusks without shells) of macroinvertebrates in different Yangtze lakes. All the samples were taken by a weighted Petersen grab with a sampling area of 0.0625 m².

	Macroinvertebrates		Algal lakes	Macrophytic-algal transition lakes	Macrophytic lakes	Oxbow lakes	River-connected lakes
Taxonomic groups	Total	D	2563 ± 1580	292 ± 58	1881 ± 400	586 ± 88	327 ± 37
		B	1.33 ± 0.58	1.22 ± 0.31	1.48 ± 0.24	1.95 ± 0.52	1.40 ± 0.16
	Oligochaetes	D	2033 ± 1512	101 ± 51	25 ± 4	150 ± 40	50 ± 19
		B	0.72 ± 0.45	0.15 ± 0.04	0.10 ± 0.02	0.12 ± 0.05	0.04 ± 0.02
	Gastropods	D	5 ± 3	43 ± 19	1752 ± 394	29 ± 11	142 ± 43
		B	0.21 ± 0.17	0.94 ± 0.27	1.29 ± 0.24	1.47 ± 0.55	1.03 ± 0.16
	Bivalves	D	0 ± 0	0 ± 0	6 ± 5	0 ± 0	63 ± 16
		B	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.04	0.00 ± 0.00	0.25 ± 0.03
	Insects	D	521 ± 123	145 ± 32	92 ± 31	385 ± 81	52 ± 3
		B	0.38 ± 0.11	0.12 ± 0.05	0.04 ± 0.02	0.35 ± 0.07	0.06 ± 0.02
Functional feeding groups	Shredders	D	1 ± 1	2 ± 1	3 ± 1	156 ± 40	13 ± 10
		B	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00	0.12 ± 0.04	0.01 ± 0.00
	Collector-filterers	D	0 ± 0	0 ± 0	7 ± 5	2 ± 1	63 ± 16
		B	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.04	0.00 ± 0.00	0.25 ± 0.03
	Collector-gatherers	D	2326 ± 1558	200 ± 49	83 ± 20	336 ± 55	76 ± 26
		B	0.97 ± 0.57	0.25 ± 0.08	0.13 ± 0.03	0.45 ± 0.24	0.08 ± 0.04
	Scrapers	D	5 ± 3	43 ± 19	1752 ± 394	39 ± 13	152 ± 46
		B	0.21 ± 0.17	0.94 ± 0.27	1.29 ± 0.24	1.35 ± 0.54	1.03 ± 0.16
	Predators	D	231 ± 50	47 ± 19	36 ± 15	53 ± 17	23 ± 9
		B	0.14 ± 0.04	0.02 ± 0.00	0.01 ± 0.01	0.02 ± 0.01	0.02 ± 0.01

Table 3
Summary statistics of the CCA for densities of macroinvertebrates in the Yangtze floodplain lakes.

CCA axes	1	2	3	4
Eigenvalues	0.609	0.386	0.288	0.239
Species-environment correlations	0.969	0.960	0.919	0.934
Cumulative percentage variance				
Of species data	13.5	22.0	28.4	33.7
Of species-environment relation	30.7	50.2	64.7	76.8
Inter-set correlations with axes				
Connectivity rating (CR)	0.9144	0.2905	−0.1265	0.0937
Water depth (Z, m)	0.3397	0.8416	0.1029	0.0649
Total phosphorus (TP, mg/m^3)	−0.8874	0.1439	−0.2901	0.2255
Macrophytes biomass (B_{Mac}, g/m^2)	0.5402	−0.4132	0.3263	0.5635
Development of lake shoreline (D_L)	0.5366	−0.1455	−0.6379	−0.2019
Secchi depth (Z_{SD}, m)	0.7331	−0.2260	0.1948	0.2107
Dynamical ratio of lake (DR)	0.6270	−0.2032	−0.5845	0.2162

can inhibit the growth of plankton, while plankton assemblages well develop in the river regions with low water velocity (Allan and Castillo, 2007; Pan et al., 2009). Water depth was one main influencing factor of macroinvertebrates, which indicates that water level fluctuation played a certain role in structuring benthic assemblages. The trophic variables directly or indirectly determine food resources of macroinvertebrates. Development of lake shoreline is closely related to input of external nutrients (Horne and Goldman, 1994), furthermore, affects benthic animals also through determining the amount of food.

Chlorophyll *a* concentration (Chl *a*) is widely used as a measure of phytoplankton biomass. Studies in temperate and subtropical lakes confirmed the strong dependence of Chl *a* on total phosphorus (TP). The TP-Chl *a* relationship was generally a linear function (Nicholls and Dillon, 1978; Schindler, 1978; Brown et al., 2000). However, in the lotic waters associated with river, Chl *a* was usually found to be influenced more strongly by water flow than nutrients (Pace et al., 1992; Tockner et al., 1999a; Lewis et al., 2000). The distinct relationships of $\log_{10}$TP-$\log_{10}$Chl *a* in five types of Yangtze lakes are compared (Fig. 5). The disparity of slopes in three Yangtze-disconnected lakes was ascribed to the large or small amount of macrophytes. In macrophytic lakes, abundant macrophytes can inhibit the growth of algae through nutrients competition and secretion of allelochemicals (Voinov and Tonkikh, 1987; Nakai et al., 1999; Zhang et al., 2009), so the slope of $\log_{10}$TP-$\log_{10}$Chl *a* was the smallest. Although both regressions of $\log_{10}$TP-$\log_{10}$Chl *a* in river-disconnected lakes and lentic regions of river-connected lakes were linear, the slope of the latter was smaller, which is mainly attributed to the different residence times. The regression derived from lotic regions in river-connected lakes is curvilinear. This character is considered to be a result of synthetic effects of TP and water flow (Pan et al., 2009).

Among the floodplain lakes, ecological status of the lakes freely connected with river mainstream has been confirmed to be the best (Tockner et al., 1999b; Amoros and Bornette, 2002). In the Yangtze-connected lakes, biodiversity, biomass and production of macroinvertebrates reached maxima (Pan et al., 2011). The oxbow lakes cutted off from river mainstream are a special type of waterbody, and resources of macroinvertebrates were not abundant due to its deeper water (cf. Table 2). Previous research (Paillex et al., 2007; Gallardo et al., 2008) showed that diversity and abundance of macroinvertebrates would increase with the increase of hydrological connectivity. In the river-disconnected lakes, macroinvertebrate assemblages in the lakes at low level of eutrophication were characterized by dominance of epiphytic animals, and those in other lakes at high level of eutrophication were characterized by dominance of pollution-tolerant animals (Pan et al., 2012). In the last decades, the river-disconnected lakes have been facing the threat of eutrophication. In the process of eutrophication, the bottom gradually becomes a thick layer of organic-rich gyttja which is a potential internal pollution source, moreover, there is also an associated increase in phytoplankton, accompanied by decrease of the euphotic depth, thereby inhibiting the growth of submersed macrophytes (Jupp and Spence, 1977; Hough et al., 1989; Dodds, 2002), which play the critical role in the maintenance of diversity and abundance of macroinvertebrates through providing heterogeneous habitats and food sources (Rosine, 1955; Rooke, 1984; Newman, 1991; Jeppesen et al., 1998).

From the view of conservation and management of the entire floodplain lakes, to maintain high productivity as well as high biodiversity, protecting the remnants of river-connected lakes and linking disconnected lakes freely with the mainstream are crucial. Meanwhile, for river-disconnected lakes, it is also suggested that some effective restoration measures should be taken to shift from a turbid, algae-dominated state to a clear, macrophyte-dominated state, moreover, some effective restoration measures should be taken to control external pollution sources and remove potential internal pollution sources.

Table 4
Summary statistics of the CCA for dry weight of macroinvertebrates in the Yangtze floodplain lakes.

CCA axes	1	2	3	4
Eigenvalues	0.536	0.292	0.225	0.206
Species-environment correlations	0.935	0.918	0.874	0.872
Cumulative percentage variance				
Of species data	12.9	19.9	25.4	30.3
Of species-environment relation	35.5	54.9	69.8	83.5
Inter-set correlations with axes:				
Connectivity rating (CR)	0.8814	0.3774	0.0993	0.2354
Total phosphorus (TP, mg/m^3)	0.8791	0.3598	−0.1722	0.2021
Macrophytes biomass (B_{Mac}, g/m^2)	−0.4690	−0.3877	0.0422	0.7186
Water depth (Z, m)	−0.2977	0.5657	0.6891	0.0037
Secchi depth (Z_{SD}, m)	−0.6882	−0.2604	0.0698	0.2483
Development of lake shoreline (D_L)	−0.6084	0.4308	−0.4658	−0.0254

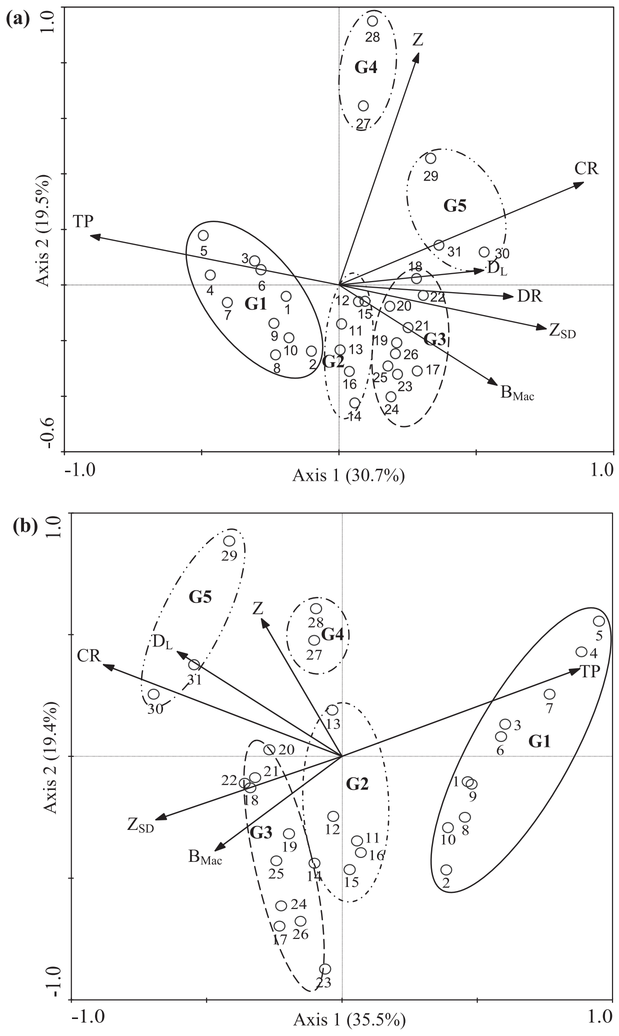

Fig. 5. Canonical correspondence analysis (CCA) biplots for lakes and environments. The important environmental variables influencing densities (a) and biomass (b) of macroinvertebrates are presented. CR, connectivity rating; Z, water depth; TP, total phosphorus concentration of water; B_{Mac}, biomass of submersed macrophytes; D_{L}, development of lake shoreline; Z_{SD}, Secchi depth; DR, dynamical ratio of lake. Lake groups are G1, G2, G3, G4, and G5. This figure shares the same lake codes with Table 1.

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