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Author(s): Bao-Zhu Pan, Hai-Jun Wang, Xiao-Min Liang, and Hong-Zhu Wang

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## Macrozoobenthos in Yangtze floodplain lakes: patterns of density, biomass, and production in relation to river connectivity

Bao-Zhu Pan<sup>1</sup>, Hai-Jun Wang<sup>2</sup>, Xiao-Min Liang<sup>3</sup>, AND Hong-Zhu Wang<sup>4</sup>

State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, Hubei 430072, China

**Abstract.** A systematic investigation of macrozoobenthos was conducted in Yangtze floodplain waters to reveal patterns of density, biomass, and production in relation to river connectivity. In the Yangtze-connected lakes, 78 taxa belonging to 33 families and 62 genera were identified. Macrozoobenthos density was 327 individuals/m<sup>2</sup>, biomass was 1.40 g dry mass/m<sup>2</sup>, and production was 3.23 g dry mass m<sup>-2</sup> y<sup>-1</sup>. The assemblages were characterized by high diversity, high production, and high bivalve-filterer abundance. The key factor determining the macrozoobenthic assemblages was river connectivity. As river connectivity increased, 3 types of response patterns were observed: 1) density, biomass, and production of collector-filterers (mainly Bivalvia), shredders (e.g., *Stictochironomus*), and predators (e.g., Dytiscidae) showed unimodal changes, i.e., first increased and then decreased; 2) density, biomass, and production of collector-gatherers (mainly Tubificidae and Chironomidae) decreased continuously; and 3) density of scrapers (mainly Gastropoda) decreased, whereas their biomass and production changed unimodally. At an intermediate level of river connectivity, biomass and production of total macrozoobenthos reached maxima, whereas density decreased with increasing river connectivity. Previous research showed that  $\alpha$  diversity of zoobenthos also peaks at moderate connectivity with rivers. Therefore, to maintain high productivity as well as high biodiversity in the Yangtze floodplain, protecting the remnants of river-connected lakes and linking disconnected lakes freely with the mainstream are crucial.

**Key words:** macrozoobenthos, water current, connectivity, Yangtze floodplain lakes.

The riverine floodplain is one of the most endangered landscapes worldwide (Tockner and Stanford 2002). In floodplain waters, macrozoobenthos play an important role in trophic dynamics by cycling nutrients and providing food for higher trophic levels, such as fish and birds (Van den Brink et al. 1994). A better understanding of macrozoobenthic assemblages is of great significance to floodplain conservation and management.

Previous research on macrozoobenthos in floodplains has been mostly restricted to the Danube, Rhine, and Mississippi basins (Castella et al. 1991, Obrdlik and Fuchs 1991, Van den Brink and Van der Velde 1991, Van den Brink et al. 1994, Tockner et al. 1999b). Hydrological connectivity with rivers and pertinent variables, i.e., flood-pulse duration, flood frequency, water velocity, and water-level fluctuation,

are key factors structuring macrozoobenthic assemblages (Van den Brink and Van der Velde 1991, Amoros and Bornette 2002, Paillex et al. 2007).

Alpha diversity of macrozoobenthos reaches a maximum at an intermediate level of river–floodplain connectivity (Obrdlik and Fuchs 1991, Ward 1998, Tockner et al. 1999b, Ward et al. 1999, Amoros and Bornette 2002), whereas  $\beta$  diversity tends to be higher when river connectivity is weaker (Castella et al. 1991, Reckendorfer et al. 2006). The relationship between macrozoobenthic standing crops and hydroperiod has been studied less often (Corti et al. 1997, Flinn et al. 2008), but knowledge of responses of macrozoobenthic standing crops and production to river connectivity is important to ecosystem management. Therefore, our goal was to explore the patterns of standing crops and production of zoobenthos along river connectivity gradients.

In the Yangtze basin of China, floodplain lakes are numerous, with a total area >16,600 km<sup>2</sup>. Historically, most lakes were connected freely with the main river course of the Yangtze, where floods occur periodically. To protect villages and cultivated land along the

<sup>1</sup> E-mail addresses: zhuzipan@163.com

<sup>2</sup> wanghj@ihb.ac.cn

<sup>3</sup> liangxm@ihb.ac.cn

<sup>4</sup> To whom correspondence should be addressed. E-mail: wanghz@ihb.ac.cn

lakeshore from flooding, embankments and sluice gates were constructed between the 1950s and the 1970s. These structures eventually isolated most lakes from the river. At present, only 3 medium- to large-sized lakes (Dongting Lake, Poyang Lake, and Shijiu Lake) remain connected with the Yangtze mainstream. Although they are now few in number, these river-connected lakes are important for maintaining the unique and diverse biota of the entire Yangtze ecosystem. However, our knowledge concerning the macrozoobenthos of these lakes is still limited, and only a few works describing these assemblages have been published (Dai et al. 2000, Wang et al. 2007, Xie et al. 2007).

Our paper reports the results of a systematic investigation of macrozoobenthos in all 3 Yangtze-connected lakes. The purpose of our study was 2-fold: 1) to describe the overall character of macrozoobenthic assemblages in these lakes, and 2) to reveal patterns of density, biomass, and production of different macrozoobenthic groups in relation to river connectivity.

## Methods

### *Study area*

Dongting Lake, Poyang Lake, and Shijiu Lake are situated in mid-to-lower Yangtze basin in the monsoon region of the East Asia subtropical zone. Locations, sampling sites, and limnological variables of study lakes are given in Fig. 1 and Table 1.

Field investigations were conducted in May to July (high-water level) and September to December (low-water level) 2004. The data from the 2 investigations were combined for analyses. Water depth ( $Z$ ) and Secchi depth ( $Z_{SD}$ ) were measured with a sounding lead and a Secchi disc, respectively. Water velocity ( $U$ ) was measured with a propeller-type current meter (Model LS 1206B; Nanjing Automation Institute of Water Conservancy and Hydrology, Nanjing, China). One-liter water samples were taken near the surface and at the bottom of each lake and combined for laboratory analyses. Total N (TN) was analyzed by the alkaline potassium persulfate digestion-ultraviolet spectrophotometric method. Total P (TP) was analyzed by the ammonium molybdate method. Total dissolved N (TDN),  $\text{NO}_3\text{-N}$ ,  $\text{NO}_2\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and total dissolved P (TDP) were analyzed according to Huang (1999). Phytoplankton chlorophyll  $a$  concentration (Chl  $a$ ) was measured after acetone extraction by reading absorbance at 665 nm and 750 nm with a spectrophotometer (Unico UV-2000; Unico Instruments Co., Ltd., Shanghai, China). Macrophytes were sampled with a scythe ( $0.20 \text{ m}^2$ ), 2 to 4 times in the

same habitat adjacent to the benthic sampling site, then cleaned and weighed for determination of wet mass ( $B_{Mac}$ ). Sediment samples of 500 mL were taken from the hyporheic zone (depth: 0–0.15 m), and particle size was analyzed using the sieving method. Sediment was classified according to the Wentworth scale. Particle diameters of coarse sand, medium sand, fine sand, silt, and clay were 0.5 to 2, 0.25 to 0.5, 0.0625 to 0.25, 0.004 to 0.0625, and  $<0.004$  mm, respectively (Allan and Castillo 2007).

Quantitative samples of macrozoobenthos were taken from the hyporheic zones with a weighted Petersen grab ( $0.0625 \text{ m}^2 \times 0.15 \text{ m}$ ) and then passed through a 420- $\mu\text{m}$  sieve. Specimens were sorted manually from sediment on a white porcelain plate and preserved in 10% formalin. Wet mass of zoobenthos was determined with an electronic balance after the specimens were blotted, and dry mass (mollusks without shells) was calculated according to the ratios of dry:wet mass and tissue-shell weight reported by Yan and Liang (1999). In the study by Yan and Liang (1999), the data were collected from mid-lower Yangtze lakes, and mollusk samples were treated according to the method described by Banse and Mosher (1980) (the shells were removed and then shell and tissue were dried separately). Production of zoobenthos was calculated mainly according to the ratio of production to biomass (P/B) reported from Yangtze lakes (Yan 1998). In the study by Yan (1998), 12 samples of macrozoobenthos were taken monthly over a period of 1 y from 2 lakes, and the production was estimated by the size-frequency method. The P/B ratio of *Corbicula* was taken from Marsh (1985). For taxa without production data, P/B ratios of similar forms were used (Liang and Wang 1999). 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.

Two-Way Indicator Species Analysis (TWINSPAN, PC-ORD 4.0; MjM Software Design, Gleneden Beach, Oregon) is a divisive clustering method widely used to determine significant differences between assemblages (Hill 1979). Based upon indicator species of benthic assemblages, TWINSPAN was used to classify the sampling sites into several groups that were subject to different degrees of riverine influence. Canonical correspondence analysis (CCA, CANOCO 4.5; Microcomputer Power, Ithaca, New York) was used to examine the relationships among 13 environmental variables ( $U$ ,  $Z$ ,  $Z_{SD}$ , TN, TDN,  $\text{NO}_3\text{-N}$ ,  $\text{NO}_2\text{-N}$ ,  $\text{NH}_4\text{-N}$ , TP, TDP, Chl  $a$ ,  $B_{Mac}$  and substrate type

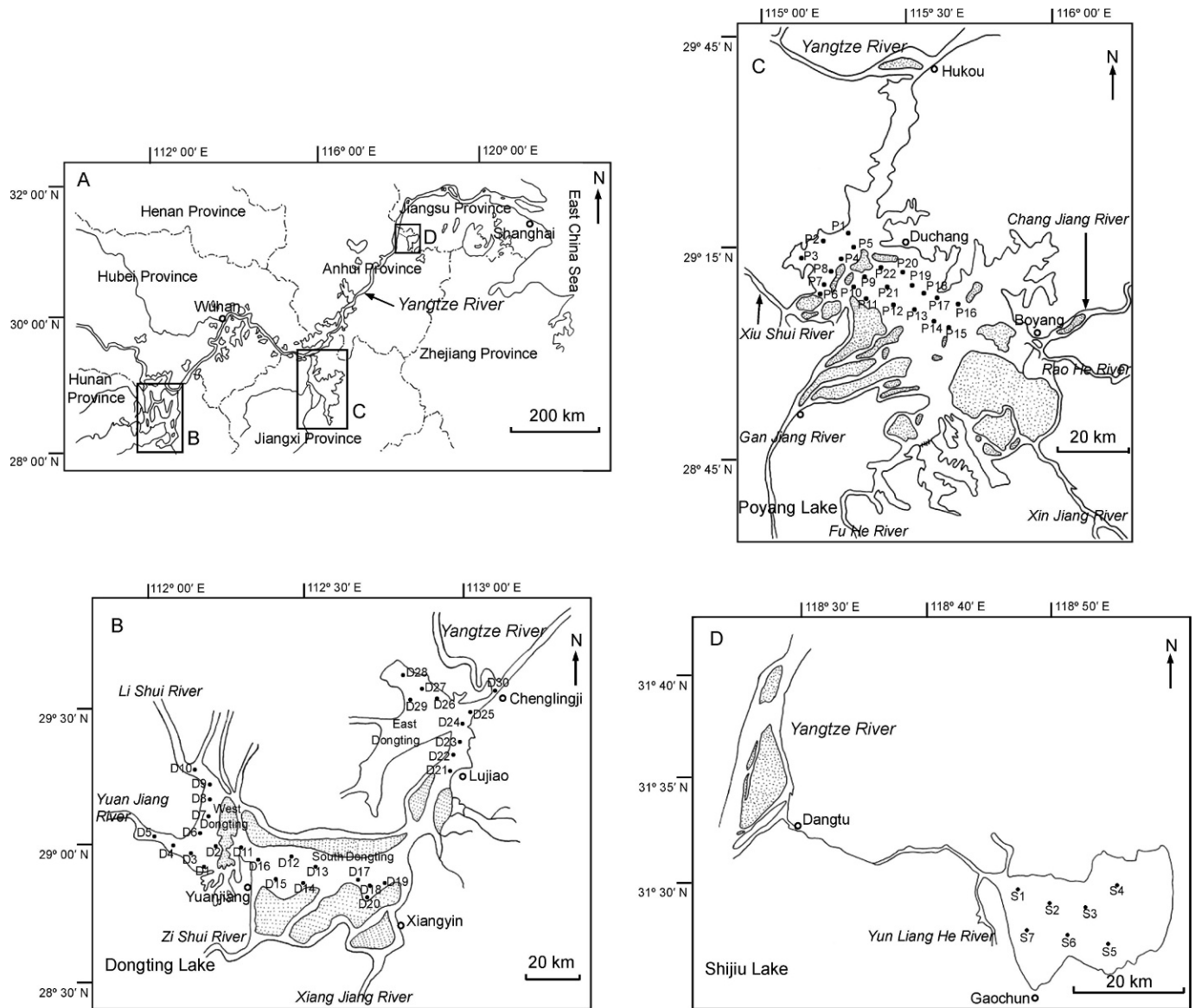


FIG. 1. Locations of study lakes and sampling sites in the Yangtze basin (A). Lakes in panel A are labeled and enlarged in subsequent panels to show Dongting Lake (sites D1–30) (B), Poyang Lake (sites P1–22) (C), Shijiu Lake (sites S1–7) (D). The stippled areas are islands.

[ST]) and 78 macrozoobenthic taxa across all sampling sites. STs were ranked on a 5-point scale: 1 (clay), 2 (silt), 3 (fine sand), 4 (medium sand), and 5 (coarse sand). In both analyses, biological and environmental data were  $\sqrt{(x)}$ -transformed to stabilize variances.

## Results

### Taxa, densities, biomass, production, and functional structure

Seventy-eight taxa of macrozoobenthos belonging to 33 families and 62 genera were identified (Appendix). Among them were 12 oligochaetes, 27

mollusks, 30 insects, and 9 miscellaneous zoobenthos. The average density, biomass, and production of macrozoobenthos in the 3 lakes were 327 individuals (ind.)/m<sup>2</sup>, 1.40 g dry mass (DM)/m<sup>2</sup>, and 3.23 g DM m<sup>-2</sup> y<sup>-1</sup>, respectively (Table 2). Mollusks (gastropods and bivalves) were the predominant group and made up 62.7% of the total density, 91.5% of total biomass, and 83.9% of total production. Variations in densities, biomass, and production were evident among lakes. Densities of total benthos, oligochaetes, and gastropods were highest in Shijiu Lake, whereas biomass and production of total benthos and gastropods were highest in Poyang Lake (Table 2). With regard to

TABLE 1. Limnological variables in the Yangtze-connected lakes. Data were from related materials (Zhu and Zhang 1997, Wang and Dou 1998, Dou and Jiang 2000). asl = above sea level.

Lake	Dongting Lake	Poyang Lake	Shijiu Lake
Area (km <sup>2</sup> )	2432 (33.0 m asl)	2933 (21.7 m asl)	210.4 (9.3 m asl)
Maximum (mean) depth (m)	23.5 (6.4)	29.2 (5.1)	5.3 (4.1)
Annual mean water-level fluctuation (m)	5.90	5.86	3.10
Annual precipitation (mm)	1200–1450	1340–1780	569–1685
Annual evaporation (mm)	1174–1420	800–1200	900–1100
Annual water input (10 <sup>8</sup> m <sup>3</sup> )	3065.7	1501.2	78.4
Retention time (d)	18.2	10.0	41.0
Annual mean air temperature (°C)	16.8	16.6	16.0
Annual mean water temperature (°C)	16.7	16.5	–
pH	8.1	7.3	7.8
Annual mean water sediment concentration (g/m <sup>3</sup> )	127	66	–
Dominant algae	Cryptophyta Bacillariophyta	Bacillariophyta	Chlorophyta Euglenophyta

functional groups, scrapers were predominant and made up 46.5% of total density, 73.6% of total biomass, and 52.6% of total production. Collector-filterers also were frequent and made up 19.3% of total density, 17.9% of total biomass, and 31.3% of total production (Table 3).

#### TWINSPAN classification of sampling sites

At the 1<sup>st</sup> level of division in the TWINSPAN classification, the 59 sites were split by 3 indicator species into 2 groups (34 sites with slow flow and clear water and 25 sites with fast flow and turbid water) (Fig. 2). Further analyses divided all sites into

5 groups. Density, biomass, and production of shredders (Fig. 3A), collector-filterers (Fig. 3B), and predators (Fig. 3E) showed unimodal changes among site groups, i.e., first increased and then decreased, as river connectivity increased. Collector-gatherers decreased (Fig. 3C), and densities of scrapers (Fig. 3D) and total benthos (Fig. 3F) decreased, but biomass and production changed unimodally.

#### Environmental factors influencing macrozoobenthic assemblages

Forward selection analyses and Monte-Carlo permutation tests revealed that the important environ-

TABLE 2. Mean ( $\pm 1$  SE) density (D; individuals/m<sup>2</sup>), biomass (B; g dry mass/m<sup>2</sup>; mollusks without shells), and production (P; g dry mass m<sup>-2</sup> y<sup>-1</sup>) of each taxonomic group of macrozoobenthos in the Yangtze-connected lakes. Numbers in parentheses are percentages (relative abundance).

Taxon	Variable	Dongting Lake	Poyang Lake	Shijiu Lake	Average
Total	D	271 $\pm$ 50 (100)	313 $\pm$ 43 (100)	398 $\pm$ 64 (100)	327 $\pm$ 37 (100)
	B	1.16 $\pm$ 0.36 (100)	1.71 $\pm$ 0.51 (100)	1.32 $\pm$ 0.65 (100)	1.40 $\pm$ 0.16 (100)
	P	2.46 $\pm$ 0.50 (100)	3.85 $\pm$ 0.60 (100)	3.39 $\pm$ 1.30 (100)	3.23 $\pm$ 0.41 (100)
Oligochaeta	D	33 $\pm$ 9 (12.2)	29 $\pm$ 7 (9.3)	89 $\pm$ 43 (22.4)	50 $\pm$ 19 (15.3)
	B	0.03 $\pm$ 0.01 (2.2)	0.01 $\pm$ 0.00 (0.7)	0.07 $\pm$ 0.04 (5.1)	0.04 $\pm$ 0.02 (2.9)
	P	0.12 $\pm$ 0.04 (4.9)	0.06 $\pm$ 0.02 (1.6)	0.28 $\pm$ 0.15 (8.3)	0.15 $\pm$ 0.07 (4.6)
Gastropoda	D	61 $\pm$ 20 (22.5)	155 $\pm$ 38 (49.5)	209 $\pm$ 45 (52.5)	142 $\pm$ 43 (43.4)
	B	0.84 $\pm$ 0.32 (72.3)	1.36 $\pm$ 0.50 (79.4)	0.89 $\pm$ 0.44 (67.2)	1.03 $\pm$ 0.16 (73.6)
	P	1.22 $\pm$ 0.52 (49.6)	2.31 $\pm$ 0.64 (60.0)	1.58 $\pm$ 0.47 (46.6)	1.70 $\pm$ 0.32 (52.6)
Bivalvia	D	94 $\pm$ 33 (34.7)	58 $\pm$ 16 (18.5)	38 $\pm$ 15 (9.5)	63 $\pm$ 16 (19.3)
	B	0.20 $\pm$ 0.07 (16.8)	0.29 $\pm$ 0.15 (17.0)	0.27 $\pm$ 0.25 (20.4)	0.25 $\pm$ 0.03 (17.9)
	P	0.77 $\pm$ 0.27 (31.3)	1.18 $\pm$ 0.60 (30.6)	1.08 $\pm$ 1.00 (31.9)	1.01 $\pm$ 0.12 (31.3)
Insecta	D	54 $\pm$ 11 (19.9)	56 $\pm$ 10 (17.9)	47 $\pm$ 30 (11.8)	52 $\pm$ 3 (15.9)
	B	0.08 $\pm$ 0.04 (7.1)	0.03 $\pm$ 0.01 (1.6)	0.08 $\pm$ 0.07 (6.1)	0.06 $\pm$ 0.02 (4.3)
	P	0.33 $\pm$ 0.13 (13.4)	0.13 $\pm$ 0.04 (3.4)	0.39 $\pm$ 0.34 (11.5)	0.28 $\pm$ 0.08 (8.7)
Others	D	29 $\pm$ 8 (10.7)	15 $\pm$ 5 (4.8)	15 $\pm$ 6 (3.8)	20 $\pm$ 5 (6.1)
	B	0.01 $\pm$ 0.00 (0.9)	0.02 $\pm$ 0.01 (1.2)	0.01 $\pm$ 0.00 (0.8)	0.02 $\pm$ 0.01 (1.4)
	P	0.02 $\pm$ 0.00 (0.8)	0.17 $\pm$ 0.08 (4.4)	0.06 $\pm$ 0.01 (1.8)	0.08 $\pm$ 0.04 (2.5)



TABLE 3. Mean ( $\pm$  SE) density (D; individuals/m<sup>2</sup>), biomass (B; g dry mass/m<sup>2</sup>; mollusks without shells), and production (P; g dry mass m<sup>-2</sup> y<sup>-1</sup>) of each functional feeding group of macrozoobenthos in the Yangtze-connected lakes. Numbers in parentheses are percentages (relative abundance).

Taxon	Variable	Dongting Lake	Poyang Lake	Shijiu Lake	Mean
Shredders	D	32 $\pm$ 11 (11.8)	7 $\pm$ 2 (2.2)	0 $\pm$ 0 (0.0)	13 $\pm$ 10 (4.0)
	B	0.04 $\pm$ 0.02 (3.4)	0.00 $\pm$ 0.00 (0.0)	0.00 $\pm$ 0.00 (0.0)	0.01 $\pm$ 0.00 (0.9)
	P	0.16 $\pm$ 0.08 (6.5)	0.00 $\pm$ 0.00 (0.0)	0.00 $\pm$ 0.00 (0.0)	0.05 $\pm$ 0.05 (1.5)
Collector-filterers	D	94 $\pm$ 33 (34.7)	58 $\pm$ 16 (18.5)	38 $\pm$ 15 (9.5)	63 $\pm$ 16 (19.3)
	B	0.20 $\pm$ 0.07 (16.8)	0.29 $\pm$ 0.15 (17.0)	0.27 $\pm$ 0.25 (20.4)	0.25 $\pm$ 0.03 (17.9)
	P	0.77 $\pm$ 0.27 (31.3)	1.18 $\pm$ 0.60 (30.6)	1.08 $\pm$ 1.00 (31.9)	1.01 $\pm$ 0.12 (31.3)
Collector-gatherers	D	57 $\pm$ 11 (21.0)	43 $\pm$ 16 (13.7)	127 $\pm$ 49 (31.9)	76 $\pm$ 26 (23.2)
	B	0.05 $\pm$ 0.02 (4.3)	0.04 $\pm$ 0.01 (2.3)	0.16 $\pm$ 0.11 (12.1)	0.08 $\pm$ 0.04 (5.7)
	P	0.20 $\pm$ 0.08 (8.1)	0.25 $\pm$ 0.05 (6.5)	0.73 $\pm$ 0.50 (21.5)	0.39 $\pm$ 0.17 (12.1)
Scrapers	D	67 $\pm$ 23 (24.7)	165 $\pm$ 40 (52.7)	225 $\pm$ 48 (56.5)	152 $\pm$ 46 (46.5)
	B	0.84 $\pm$ 0.32 (72.3)	1.36 $\pm$ 0.50 (79.4)	0.89 $\pm$ 0.44 (67.2)	1.03 $\pm$ 0.16 (73.6)
	P	1.22 $\pm$ 0.52 (49.6)	2.31 $\pm$ 0.64 (60.0)	1.58 $\pm$ 0.47 (46.6)	1.70 $\pm$ 0.32 (52.6)
Predators	D	21 $\pm$ 4 (7.7)	40 $\pm$ 8 (12.8)	8 $\pm$ 4 (2.0)	23 $\pm$ 9 (7.0)
	B	0.04 $\pm$ 0.02 (3.4)	0.02 $\pm$ 0.01 (1.2)	0.00 $\pm$ 0.00 (0.0)	0.02 $\pm$ 0.01 (1.4)
	P	0.11 $\pm$ 0.04 (4.5)	0.11 $\pm$ 0.05 (2.9)	0.00 $\pm$ 0.00 (0.0)	0.07 $\pm$ 0.04 (2.2)

mental factors influencing macrozoobenthos densities were U, B<sub>Mac</sub>, TP, NO<sub>2</sub>-N, TN, and ST (Fig. 4A). Axes 1 and 2 accounted for 35.9% and 18.8% of the variability in species–environment relationships, respectively, and both axes were significant at  $p < 0.05$  (Monte Carlo permutation test). The factors strongly correlated with the 1<sup>st</sup> axis were U and B<sub>Mac</sub>. The 2<sup>nd</sup> axis was predominantly a water-chemistry gradient. The important environmental factors influencing macrozoobenthos biomass were U, Z<sub>SD</sub>, B<sub>Mac</sub>, TP, and ST (Fig. 4B). Axes 1 and 2 accounted for 35.4% and 25.0% of the variability in species–environment relationships, respectively, and both axes were significant at  $p < 0.05$  (Monte Carlo permutation test).

The factors strongly correlated with the 1<sup>st</sup> axis were U, Z<sub>SD</sub>, and B<sub>Mac</sub>. The 2<sup>nd</sup> axis was predominantly correlated with TP. From site group 1 to 5, Z<sub>SD</sub> (Fig. 5B), B<sub>Mac</sub> (Fig. 5F), and Chl *a* concentration (Fig. 5G) decreased, whereas U (Fig. 5A), TN (Fig. 5C), NO<sub>2</sub>-N (Fig. 5D), TP (Fig. 5E), and % sand (Fig. 5H) increased.

## Discussion

### Characteristics of macrozoobenthos in the Yangtze-connected lakes

In comparison with those of the Yangtze main-stream and disconnected lakes (Table 4), macrozoo-

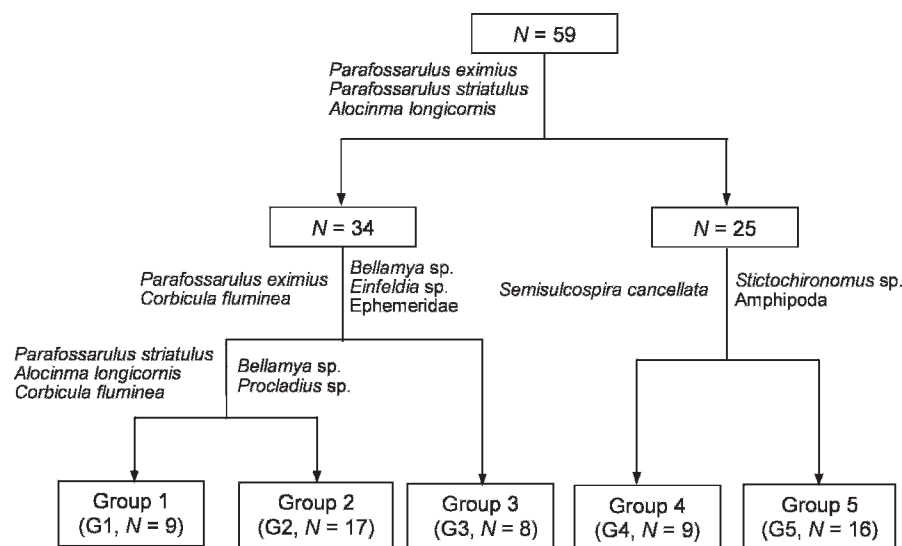


FIG. 2. TWINSPAN dendrogram of 59 sites with 6 pseudospecies cut levels: 0, 5, 10, 20, 40, and 80. Taxon names are the indicators for each of the dichotomies.

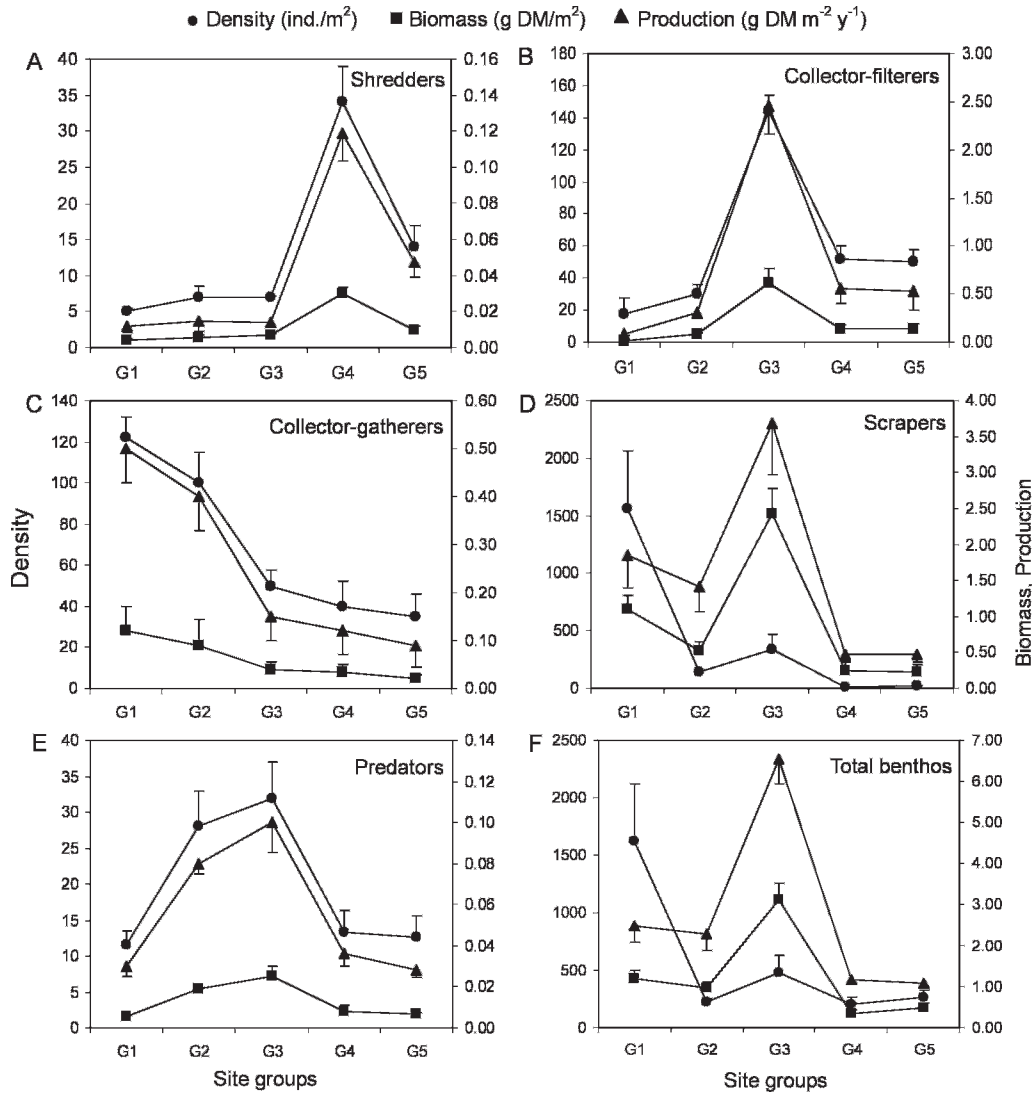


FIG. 3. Comparisons of mean (±1 SE) densities, biomass, and production of shredders (A), collector-filterers (B), collector-gatherers (C), scrapers (D), predators (E), and total benthos (F) among site groups in the Yangtze-connected lakes. Ind. = individuals, DM = dry mass.

benthos of the Yangtze-connected lakes are characterized by high diversity, high production, and high bivalve-filterer abundance. Similar features of diversity and dominant taxa also have been found in frequently flooded European lakes (Van den Brink and Van der Velde 1991, Obrdlik and Garcia-Lozano 1992, Van den Brink et al. 1994). In the 3 Yangtze-connected lakes, mollusks were predominant and insect abundance was about the same as in the European lakes. However, some differences still existed among these connected lakes. First, species with marine affinity (e.g., Nemertinea and Polychaeta) were present only in downstream lakes (Shijiu and Poyang), which are nearer to the East China Sea. Second, potamophilic taxa (e.g., Polycentropodidae,

Gomphidae, *Stictochironomus*, *Xenochironomus*, and *Corbicula fluminea*) occurred mainly in large lakes (Dongting and Poyang), which have several large tributaries and are closer to the Yangtze mainstream (Fig. 1A). Third, oligochaetes were most numerically abundant in Shijiu Lake, where the bottom was largely silt and rich in fine organic matter, and bivalves were most numerically abundant in Dongting Lake, where the current was faster and, thus, a hard bottom prevailed.

*Primary factors governing the macrozoobenthic assemblages*

According to our analyses, factors that regulated macrozoobenthic assemblages in the Yangtze-con-

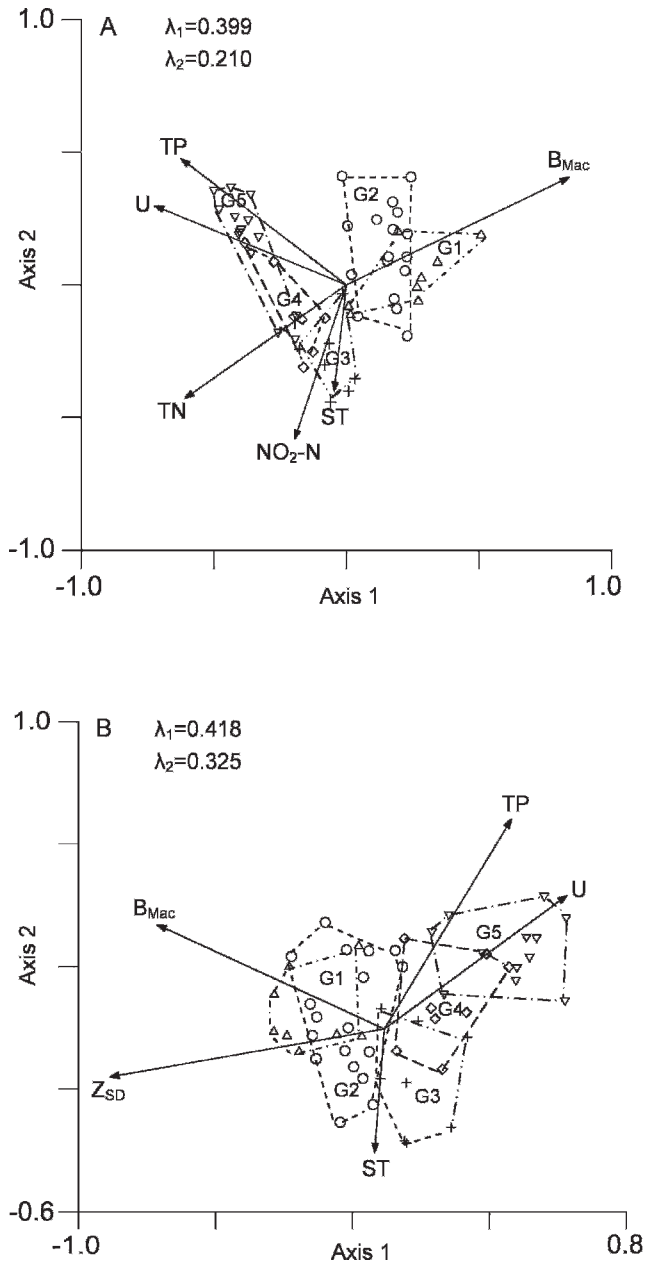


FIG. 4. Canonical Correspondence Analysis (CCA) bi-plots of 6 environmental variables influencing benthos density (A) and 5 environmental variables influencing benthos biomass (B). Site groups are G1, G2, G3, G4, and G5. U = water velocity (m/s),  $Z_{SD}$  = Secchi depth (m), TN = total N concentration of water ( $mg/m^3$ ), TP = total P concentration of water ( $mg/m^3$ ),  $NO_2-N$  ( $mg/m^3$ ),  $B_{Mac}$  = wet biomass of macrophytes ( $g/m^2$ ), ST = substrate type,  $\lambda$  = eigenvalue.

ected lakes were mainly water velocity, macrophytes, substrate, and nutrients (Fig. 4B). Among these, water velocity is regarded as the most important factor because it scours zoobenthos directly and determines other habitat conditions. First, rapid

current inhibits the growth of submersed macrophytes, as shown by the negative relationship between  $U^{0.5}$  and  $\log_{10}B_{Mac}$  ( $r = -0.49, n = 59, p < 0.001$ ), because rapid flow erodes sediment and plant roots and increases water turbidity (Sparks et al. 1990). Second, water velocity determines substrate properties and subsequently influences benthos (Nowell and Jumars 1984, Allan and Castillo 2007). Third, water velocity is closely related to suspended food particles. The positive relationship between  $U^{0.5}$  and  $\log_{10}TP$  ( $r = 0.66, n = 59, p < 0.001$ ) demonstrated that fast flow was linked closely to more external nutrients (see also Søballe and Kimmel 1987). Moreover, fast flow inhibits the growth of phytoplankton and zooplankton (Reckendorfer et al. 1999, Allan and Castillo 2007). Water flow in the Yangtze-connected lakes was mainly the result of river input, and lake depth was not highly variable among different regions. Thus, water velocity may be considered a measure of hydrological connectivity between the lakes and the river. Therefore, it could be concluded that river connectivity plays the leading role in governing macrozoobenthic assemblages of the Yangtze-connected lakes.

*Patterns of density, biomass, and production in relation to river connectivity*

To illustrate the patterns of density, biomass, and production of zoobenthos along river connectivity gradients, the results of Figs 3 and 5 and Table 4 were combined to form a series of curves showing general patterns (Fig. 6A–C) in which the Yangtze-disconnected lakes were treated as the least-influenced group, the 5 site groups in the Yangtze-connected lakes were treated as intermediately influenced, and the Yangtze mainstream as the most-influenced group. The change patterns could be classified into 3 types.

First, density, biomass, and production of shredders, collector-filterers, and predators show unimodal changes. Shredders (e.g., *Stictochironomus*) feed on coarse particulate organic matter, such as decaying leaves (Cummins et al. 1989), so that their abundance should increase with more external organic matter brought by increasing river inflow, but over-disturbance may inhibit them. At an intermediate level of river connectivity, the substrate is hard and sandy in general (Figs 5H, 6C), and suspended organic particles are relatively abundant (Figs 5G, 6C). Thus, the substrate favors filterers (mainly bivalves) (Dillon 2000). At a high level of river connectivity, the substrate becomes unstable and water is full of inorganic particles (Tockner et al. 1999a), so that



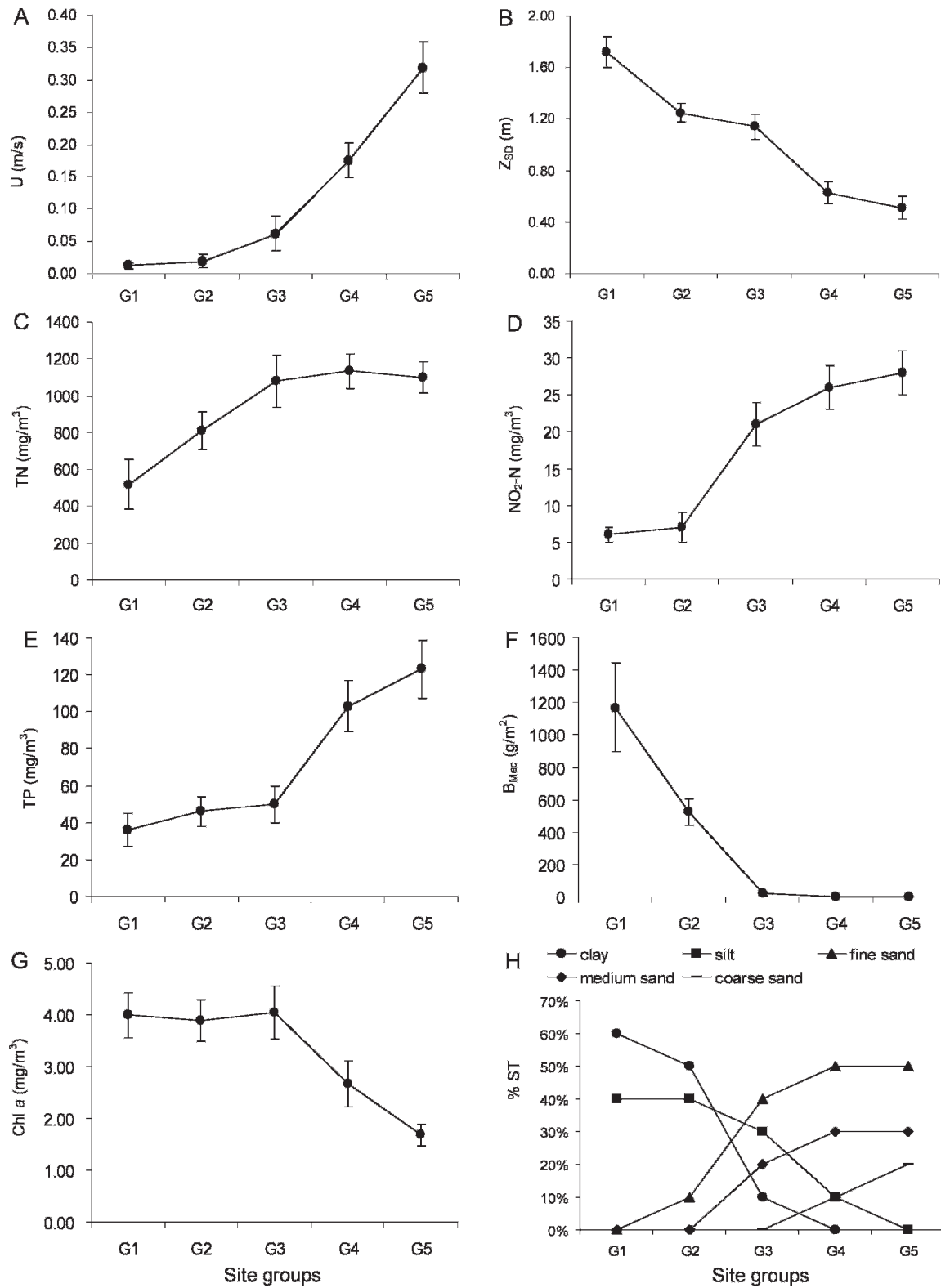


FIG. 5. Mean ( $\pm 1$  SE) values of water velocity (U) (A), Secchi depth ( $Z_{SD}$ ) (B), total N (TN) (C), NO<sub>2</sub>-N (D), total P (TP) (E), macrophyte biomass ( $B_{Mac}$ ) (F), chlorophyll *a* (Chl *a*) concentration (G), and percentage of each substrate type (% ST) (H) among site groups in the Yangtze-connected lakes. Groups are G1, G2, G3, G4, and G5.

TABLE 4. Mean ( $\pm 1$  SE) number of species (SN), density (D; individuals/m<sup>2</sup>), biomass (B; g dry mass/m<sup>2</sup>), and production (P; g dry mass m<sup>-2</sup> y<sup>-1</sup>) of macrozoobenthos and environmental variables in different waters of the Yangtze floodplain. All the samples were taken by a weighted Petersen grab with a sampling area of 0.0625 m<sup>2</sup>. Data from the same seasons (spring and autumn) are used for the comparison. Species number was calculated only from quantitative samples. U = water velocity (m/s), Z<sub>SD</sub> = Secchi depth (m), TN = total N (mg/m<sup>3</sup>), TP = total P (mg/m<sup>3</sup>), B<sub>Mac</sub> = macrophyte biomass (g/m<sup>2</sup>), Chl *a* = chlorophyll *a* concentration (mg/m<sup>3</sup>).

Variable		Disconnected lakes <sup>a</sup>	Connected lakes <sup>b</sup>	Yangtze mainstream <sup>c</sup>
Macrozoobenthos				
Shredders	D	3 $\pm$ 1	13 $\pm$ 10	15 $\pm$ 5
	B	0.00 $\pm$ 0.00	0.01 $\pm$ 0.00	0.02 $\pm$ 0.01
	P	0.00 $\pm$ 0.00	0.05 $\pm$ 0.05	0.04 $\pm$ 0.02
Collector-filterers	D	3 $\pm$ 1	63 $\pm$ 16	24 $\pm$ 10
	B	0.01 $\pm$ 0.00	0.25 $\pm$ 0.03	0.10 $\pm$ 0.05
	P	0.04 $\pm$ 0.01	1.01 $\pm$ 0.12	0.40 $\pm$ 0.20
Collector-gatherers	D	128 $\pm$ 24	76 $\pm$ 26	40 $\pm$ 8
	B	0.14 $\pm$ 0.03	0.08 $\pm$ 0.04	0.03 $\pm$ 0.01
	P	0.50 $\pm$ 0.10	0.39 $\pm$ 0.17	0.09 $\pm$ 0.03
Scrapers	D	1624 $\pm$ 360	152 $\pm$ 46	2 $\pm$ 1
	B	1.12 $\pm$ 0.25	1.03 $\pm$ 0.16	0.01 $\pm$ 0.01
	P	1.91 $\pm$ 0.48	1.70 $\pm$ 0.32	0.03 $\pm$ 0.03
Predators	D	9 $\pm$ 3	23 $\pm$ 9	10 $\pm$ 4
	B	0.01 $\pm$ 0.00	0.02 $\pm$ 0.01	0.01 $\pm$ 0.00
	P	0.03 $\pm$ 0.00	0.07 $\pm$ 0.04	0.02 $\pm$ 0.00
Total	SN	40	78	33
	D	1767 $\pm$ 385	327 $\pm$ 37	91 $\pm$ 13
	B	1.28 $\pm$ 0.21	1.40 $\pm$ 0.16	0.17 $\pm$ 0.05
	P	2.48 $\pm$ 0.43	3.23 $\pm$ 0.41	0.58 $\pm$ 0.20
Environmental				
U		0.00 $\pm$ 0.00	0.13 $\pm$ 0.02	0.44 $\pm$ 0.03
Z <sub>SD</sub>		1.45 $\pm$ 0.26	1.01 $\pm$ 0.07	0.37 $\pm$ 0.02
TN		695 $\pm$ 36	899 $\pm$ 55	1356 $\pm$ 115
TP		36 $\pm$ 4	75 $\pm$ 7	244 $\pm$ 65
B <sub>Mac</sub>		1579 $\pm$ 620	409 $\pm$ 110	0 $\pm$ 0
Chl <i>a</i>		3.80 $\pm$ 0.40	3.05 $\pm$ 0.41	1.44 $\pm$ 0.11

<sup>a</sup> 68 sites in 10 lakes, 850 km<sup>2</sup> in total area (Liang et al. 1995, Gong et al. 2000, Pan 2009)

<sup>b</sup> 59 sites in 3 lakes, 5575 km<sup>2</sup> in total area (this study)

<sup>c</sup> 40 sites in 23 segments, 1060 km in length range (Xie et al. 1999, Xia et al. 2006, Wang et al. 2007)

filterers would not be supported. The same pattern of filterer abundance was also described from the Rhine floodplain (Van den Brink et al. 1994). The increase of predators (e.g., Dytiscidae) at the initial stage may be the result of reduction in macrophytes because plants can provide refuges for zoobenthos and impede predation (Allan and Castillo 2007). The decrease at later stages seems to be caused by high turbidity and habitat instability. High turbidity may prevent predators from seeing prey (Corbet 1980, see also Figs 5B, 6C).

Second, density, biomass, and production decrease when river connectivity increases. This pattern is represented by collector-gatherers (mainly Tubificidae and Chironomidae). The same pattern has been found in the Mississippi River floodplain (Galat et al. 1998). Collector-gatherers mainly consume fine particulate organic matter (Liu and Wang 2008), so their

decrease probably is caused by the fact that the organic-rich silt diminishes with increasing river connectivity (Figs 5H, 6C).

Third, density decreases with increasing river connectivity, whereas biomass and production change unimodally. Scrapers exhibit this trend. The decrease of scraper density could be ascribed to the reduction of macrophytes, which small-sized gastropods prefer (Figs 5F, 6C). The increase of biomass and production at the initial stage could be ascribed to the replacement of small-sized epiphytic gastropods (mainly Bithyniidae) by large-sized bottom dwellers (mainly *Bellamyia*). The decrease at later stages may result from the increase of sand fractions (Fig. 5H). Because of instability and detritus shortage (Allan and Castillo 2007), sandy bottoms in the Yangtze-connected lakes should not be suitable for scrapers, which feed mainly on detritus there (Liu and Wang 2008).

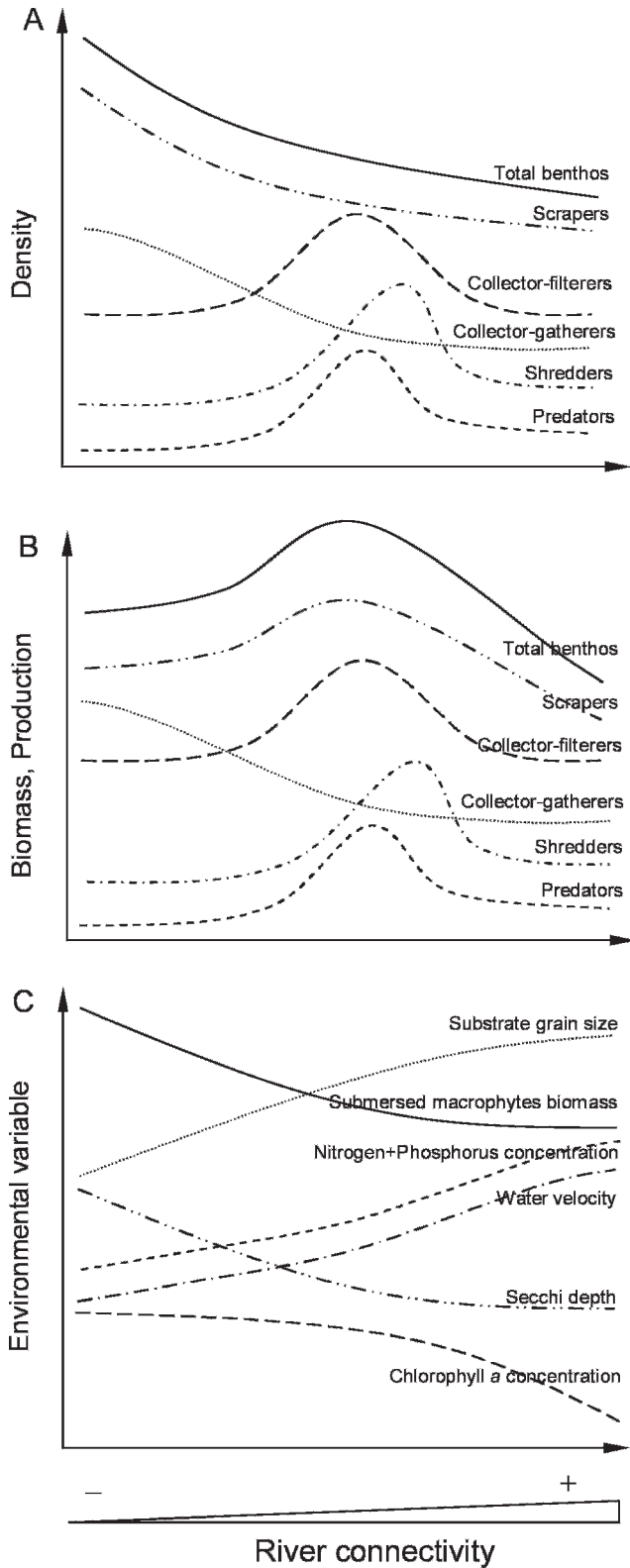


FIG. 6. Tendency diagrams to illustrate responses of density of different functional feeding groups (A), biomass and production of different functional feeding groups (B), and environmental variables (C) to river connectivity in the Yangtze floodplain.

In terms of total benthos, density decreases with increasing river connectivity (Fig. 6A), showing the same pattern with the dominant groups in density, i.e., scrapers and collector-gatherers. Biomass and production change unimodally (Fig. 6B), showing the same pattern with the dominant groups in biomass, i.e., scrapers and collector-filterers.

*Concluding remarks*

Macrozoobenthic assemblages of the Yangtze-connected lakes are distinguished by high diversity, high production, and high bivalve-filterer abundance. The key factor affecting benthos is river connectivity. Biomass and production of macrozoobenthos peak at an intermediate level of river connectivity, whereas density decreases with increasing river connectivity. Previous research (Obrdlik and Fuchs 1991, Ward 1998, Tockner et al. 1999b, Ward et al. 1999, Amoros and Bornette 2002) has confirmed that  $\alpha$  diversity of benthos also reaches a maximum at moderate river connectivity. Therefore, to maintain high production and high biodiversity in the Yangtze floodplain, the remnants of river-connected lakes should be protected and disconnected lakes should be linked freely with the mainstream.

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APPENDIX. List of macrozoobenthic taxa in the Yangtze-connected lakes

Taxa	Dongting Lake	Poyang Lake	Shijiu Lake
<b>Oligochaeta</b>			
<b>Naididae</b>			
<i>Allonais gwaliorensis</i> (Stephenson)			+
<i>Pristina acuminata</i> Liang		+	
<b>Tubificidae</b>			
<i>Aulodrilus plurisetus</i> (Piguet)	+	+	+
<i>Aulodrilus japonicus</i> Yamaguchi	+		
<i>Branchiura sowerbyi</i> Beddard	+	+	+
<i>Limnodrilus amblysetus</i> Brinkhurst, Qi et Liang			
<i>Limnodrilus claparedeianus</i> Ratzel			
<i>Limnodrilus grandisetosus</i> Nomura	+		
<i>Limnodrilus hoffmeisteri</i> Claparede	+		
<i>Limnodrilus</i> sp.	+	+	+
<i>Spirosperma nikolskyi</i> (Lastockin et Sokolskaya)	+	+	
<i>Rhyacodrilus sinicus</i> (Chen)	+		
<b>Mollusca</b>			
<b>Gastropoda</b>			
<b>Viviparidae</b>			
<i>Angulyagra polyzonata</i> (Frauenfeld)	+	+	
<i>Bellamyia purificata</i> (Heude)	+	+	+
<i>Bellamyia aeruginosa</i> (Reeve)	+	+	+
<i>Cipangopaludina chinensis</i> (Gray)	+		+
<i>Rivularia auriculata</i> (Martens)	+	+	
<i>Rivularia bicarinata</i> Kobelt	+		
<i>Rivularia ovum</i> Heude	+		
<b>Pilidae</b>			
<i>Pila gigas</i> Spix	+		
<b>Pomatiopsidae</b>			
<i>Oncomelania hupensis hupensis</i> Gredler	+	+	+
<b>Bithyniidae</b>			
<i>Alocinma longicornis</i> (Benson)	+	+	+
<i>Parafossarulus eximius</i> (Frauenfeld)	+	+	+
<i>Parafossarulus sinensis</i> (Neumayr)	+	+	+
<i>Parafossarulus striatulus</i> (Benson)	+	+	+
<i>Stenothyra glabra</i> (A. Adams)	+	+	
<b>Pleuroceridae</b>			
<i>Semisulcospira amurensis</i> (Gerstfeldt)	+		
<i>Semisulcospira cancellata</i> (Benson)	+	+	+
<i>Semisulcospira gredleri</i> (Boettger)	+	+	
<b>Lymnaeidae</b>			
<i>Radix plicatula</i> (Benson)		+	+
<i>Radix swinhoei</i> (H. Adams)	+	+	+
<b>Planorbidae</b>			
<i>Hippeutis cantori</i> (Benson)	+	+	+
<i>Hippeutis umbilicalis</i> (Benson)		+	
<i>Gyraulus compressus</i> (Hutton)	+	+	
<i>Gyraulus convexiusculus</i> (Hutton)		+	
<b>Bivalvia</b>			
<b>Mytilidae</b>			
<i>Limnoperna lacustris</i> (Martens)	+	+	+
<b>Corbiculidae</b>			
<i>Corbicula fluminea</i> (Müller)	+	+	+
<i>Corbicula largillierti</i> (Philippi)	+	+	+
<b>Sphaeriidae</b>			
<i>Sphaerium lacustre</i> (Müller)	+		
<b>Insecta</b>			
<b>Ephemeroptera</b>			
Caenidae		+	

## APPENDIX. Continued.

Taxa	Dongting Lake	Poyang Lake	Shijiu Lake
Ecdyuridae		+	
Ephemeraeidae	+	+	
<b>Trichoptera</b>			
Hydropsychidae	+		
Polycentropodidae	+	+	
<b>Odonata</b>			
<i>Dromogomphus</i> sp.	+		
Gomphidae	+		
<b>Coleoptera</b>			
Dytiscidae	+		
<i>Latreille</i> sp.		+	
<i>Peltodytes</i> sp.	+		
<b>Diptera</b>			
Ceratopogonidae	+	+	
Psychodidae	+		
Stratiomyidae	+		
<i>Axarus</i> sp.	+		
<i>Chironomus</i> sp.	+	+	+
<i>Clinotanypus</i> sp.	+	+	
<i>Cryptochironomus</i> sp.	+	+	+
<i>Demicryptochironomus</i> sp.	+		
<i>Dicrotendipes</i> sp.	+		
<i>Einfeldia</i> sp.	+	+	+
<i>Gillotia</i> sp.	+		
<i>Microchironomus</i> sp.	+	+	
<i>Nanocladius</i> sp.	+		
<i>Parachironomus</i> sp.			+
<i>Paracladopelma</i> sp.	+		
<i>Polypedilum</i> sp.	+	+	
<i>Procladius</i> sp.	+	+	+
<i>Stictochironomus</i> sp.	+	+	
<i>Tanypus</i> sp.	+	+	+
<i>Xenochironomus</i> sp.	+		
<b>Others</b>			
Amphipoda	+		
<i>Barbronia</i> sp.	+		
Cirolanidae	+		
Erpobdellidae	+		
Glossiphoniidae	+		
<i>Hirudo</i> sp.		+	
Nematoda	+	+	
Nemertinea			+
Polychaeta		+	+
<b>Total taxa</b>	<b>64</b>	<b>44</b>	<b>27</b>