Macroinvertebrate responses to regime shifts caused by eutrophication in subtropical shallow lakes

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Abstract: The ecological status of subtropical floodplain lakes is threatened by eutrophication, which can shift lakes from a clear, macrophyte-dominated equilibrium state to a turbid, phytoplankton-dominated state. Such a shift is reflected in their macroinvertebrate assemblages, which may serve as good indicators of long-term changes in such lake ecosystems. We conducted a survey of benthic macroinvertebrates in 20 lakes in the Yangtze floodplain that were disconnected from the river channel to identify invertebrate response patterns along a gradient of eutrophication. Macroinvertebrate assemblages changed in parallel to the observed regime shift of a subgroup of those lakes. The most abundant groups were epiphytic invertebrates (e.g., Bithyniidae) in the macrophyte-dominated lakes and pollution-tolerant invertebrates (e.g., Tubificidae, *Tanypus*) in the phytoplankton-dominated lakes. Planktonic chlorophyll *a* concentration and wet biomass of submersed macrophytes were the key factors structuring macroinvertebrate assemblages. Macroinvertebrate taxon richness decreased along the eutrophication gradient, but density reached a minimum at a moderate eutrophication level and then increased. Scraper density (e.g., Bithyniidae) dropped abruptly at the moderate eutrophication level and did not increase again, whereas collector–gatherers (mainly Tubificidae and Chironomidae) and predators (e.g., *Tanypus*) increased continuously along the eutrophication gradient. We conclude that the abrupt disappearance of macrophytes during the regime shift means the loss of key habitat for biota associated with aquatic plants. Therefore, ecological restoration projects should be designed to reduce the nutrient concentration of floodplain lakes enough to allow re-establishment of a clear-water lake equilibrium dominated by aquatic macrophytes.

Key words: benthic macroinvertebrates, regime shift, eutrophication, Yangtze lakes

Lewontin (1969) proposed that freshwater ecosystems could theoretically have more than one equilibrium state. Since that time, empirical evidence has been gathered that supports this idea (Holling 1973, May 1977, Dublin et al. 1990, Knowlton 1992, Scheffer et al. 1993, 2001, Dent et al. 2002). Subtropical shallow lakes are among the best-understood examples of aquatic ecosystems exhibiting alternative states. In these systems, several ecological interactions, i.e., vegetation–turbidity, fish–turbidity, and vegetation–fish, shed light on the theoretical background for existence of alternative stable states over a certain nutrient range (Scheffer 1990). During shifts between alternative stable states in subtropical shallow lakes, a clear macrophyte-dominated state may switch to a turbid state dominated by planktonic algae. Analyses of how alternative stable states switch have significant implications for the management of freshwater ecosystems (Scheffer et al. 2001).

Floodplain lakes in subtropical regions provide many ecosystem services including water supply, food production, and recreation and, therefore, are important in people's lives and in agricultural production. Eutrophication is considered as the greatest threat to water quality and ecological health of floodplain lakes (Hart and Fuller 1974, Gyorgy and Judit 1983, Hargeby et al. 1994, Gong and Xie 2001, Dodds 2002, Jiang et al. 2011). Eutrophication, a consequence of intense human activity, can cause toxic algal blooms, water turbidity, low dissolved O_2, and reduction of macrophyte cover, all of which seriously damage the ability of such lake ecosystems to provide ecosystem services (Scheffer 1989, Dodds 2002). Therefore, lake managers would benefit from awareness of biological indicators of the alternative stable states.

Macroinvertebrates are important in the trophic dynamics of aquatic ecosystems (Brauns et al. 2007b). They cycle

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nutrients and provide food for higher trophic levels, such as fish and birds. Moreover, they are good indicators of long-term changes in environments because of their confinement to the bottom, long life cycles, and limited abilities to move (Hart and Fuller 1974, Lindegaard 1994). Many macroinvertebrate taxonomic groups respond to trophic state. Ephemeroptera, Plecoptera, and Trichoptera (EPT) are generally intolerant of eutrophication (Roback 1974, Wiederholm 1984). In contrast, Tubificidae and Chironomidae increase with eutrophication (Brinkhurst and Cook 1974, Wiederholm 1980, Gyorgy and Judit 1983, Wolfram 1996). Increased levels of eutrophication are often accompanied by a decline in macroinvertebrate diversity (Donohue et al. 2009), an increase in density, and a decrease in wet biomass (mollusks with shells) (Crowns et al. 1992, Wollheim and Lovvorn 1995, Gong and Xie 2001, Xiong et al. 2003). However, most previous research has been restricted to local-scale studies, i.e., in a single lake or in a few lakes (Saether 1980, Kerovec et al. 1989, Gong et al. 2000, Xiong et al. 2003, Timm et al. 2006), and few studies have covered a complete range of nutrient concentrations (Brauns et al. 2007a, Donohue et al. 2009).

Floodplain lakes are numerous, with a total area >16,600 km^2 in the Yangtze basin in China, which belongs to the monsoon region of the East Asian subtropical zone. Historically, most lakes were connected freely with the main river course of the Yangtze, where floods occur periodically. Embankments and sluice gates were constructed during the 1950s to 1970s to prevent villages and cultivated lands along lakeshores from being flooded. These structures eventually isolated most lakes from the river (Pan et al. 2011). These river-disconnected lakes face a higher threat of eutrophication than do river-connected floodplain lakes, and their ability to provide ecosystem services is severely damaged.

Over a range of intermediate nutrient levels, these lakes possess 2 alternative equilibrium states, one with macrophyte vegetation and a more turbid one without vegetation, separated by an unstable equilibrium (Scheffer et al. 2001). In freshwater lakes, macrophytes create significant spatial heterogeneity that provides a physical template for distinct niches and food for benthic invertebrates (Brönmark 1989, Jeppesen et al. 1998, Pan et al. 2012). However, epiphytic invertebrates often were not considered in previous studies of these floodplain lakes. Our goals were to learn how epiphytic and benthic macroinvertebrates respond to regime shifts caused by eutrophication and to identify respective nutrient–macroinvertebrate relationships.

We surveyed 20 Yangtze-disconnected lakes to reveal macroinvertebrate response patterns along a gradient of eutrophication. The main purposes of our study were to: 1) describe the overall characteristics of macroinvertebrate assemblages in the subtropical lakes at a regional scale, 2) identify the response patterns of both epiphytic and benthic macroinvertebrates along the eutrophication gradient, and 3) test whether alternative equilibria exist in the relationship between eutrophication and macroinvertebrates. We expected that our results would have substantial implications for the management of lake ecosystems.

METHODS

The 20 river-disconnected lakes are situated in the mid-lower Yangtze Basin (Fig. 1) in the monsoon region of the eastern Asian subtropical zone. We conducted field investigations quarterly in April (spring), July (summer), October (autumn), and December (winter) 2004 and averaged seasonal results for further analyses. We measured water depth (Z) and Secchi depth (Z_{SD}). We collected water samples from 0.5 m below the surface and at ½ the water-column depth and combined them for laboratory analyses. We analyzed total (TN) by the alkaline potassium persulfate digestion–ultraviolet spectrophotometric method and total P (TP) by the ammonium molybdate method (APHA 2002). We measured phytoplankton chlorophyll *a* concentration (Chl *a*) after acetone extraction by reading absorbance at 665 nm and 750 nm using a spectrophotometer (Unico UV-2000: Unico, Shanghai, China) (APHA 2002).

At every sampling site, we collected epiphytic and benthic animals and combined them for further analyses. We used a scythe (0.2 m^2) to sample macrophytes in the habitat adjacent to benthic sampling sites 3 times at each site. We cleaned macrophytes and measured their wet mass (B_{Mac}). After scything, we gathered plants with a hand net (mesh size = 420 μm) and put them in plastic bags. In the laboratory, we picked epiphytic animals from the rinsed samples. We collected benthic animals with a weighted Petersen grab (0.0625 m^2) and sieved the samples through a 420-μm sieve. Benthic animals were identified to the lowest feasible taxonomic level according to the keys provided by Morse et al. (1994), Wiggins (1996), Dudgeon (1999), Smith (2001), Wang (2002), and Zhou et al. (2003). We converted number of animals collected with each method to individuals (ind)/m^2 and summed them to obtain the density at the respective site. We preserved animals in 10% formalin.

We measured animal wet mass (after blotting) with an electronic balance (Sartorius Intec, Beijing, China), and calculated dry mass (mollusks without shells) according to the ratios of dry:wet mass and tissue:shell mass reported by Yan and Liang (1999). Yan and Liang (1999) collected data from mid-lower Yangtze lakes and treated mollusk samples by removing the shells and then drying shell and tissue separately (Banse and Mosher 1980). We assigned all taxa to functional feeding groups (shredders, collector–gatherers, collector–filterers, scrapers, and predators) according to Morse et al. (1994) and Liang and Wang (1999). We divided the abundances of taxa with several possible

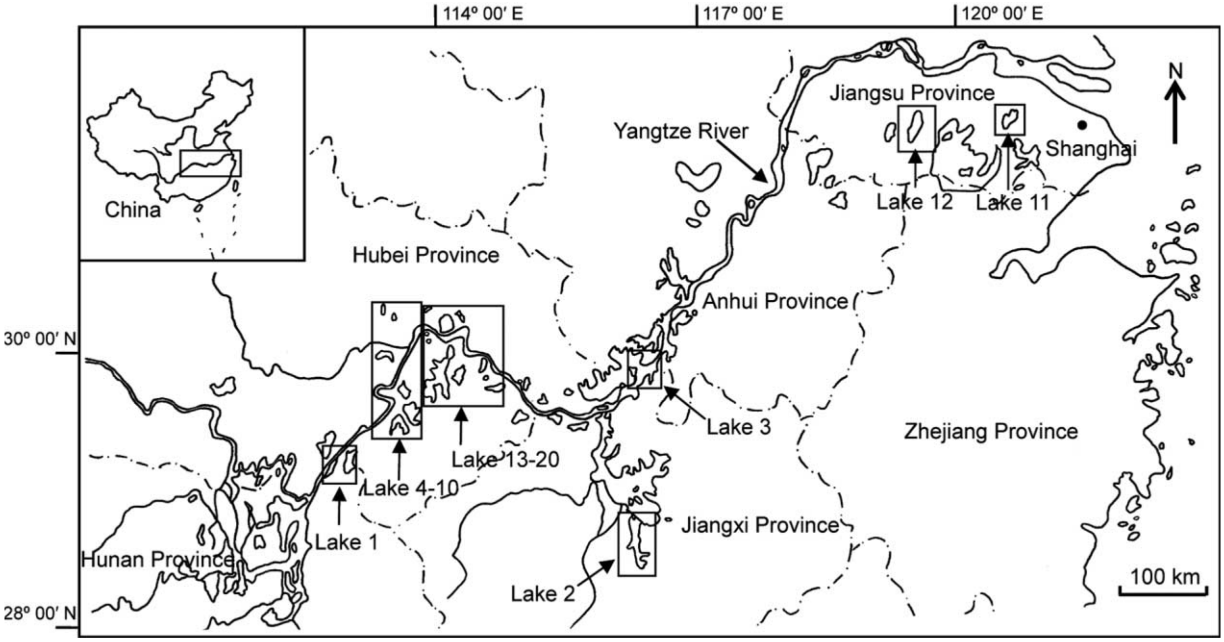

Figure 1. Study lakes along the Yangtze River: Honghu Lake (lake 1, 8 sites), Junshan Lake (lake 2, 7 sites), Longgan Lake (lake 3, 7 sites), Luhu Lake (lake 4, 8 sites), Nanbeizui Lake (lake 5, 6 sites), Niushan Lake (Lake 6, 7 sites), Qiaodun Lake (lake 7, 4 sites, Taojiada Lake (lake 8, 3 sites, Xiaosihai Lake (lake 9, 10 sites, Zhangdu Lake (lake 10, 6 sites), Dianshan Lake (lake 11, 6 sites), Gehu Lake (lake 12, 7 sites), Hongxing Lake (lake 13, 4 sites, Longyang Lake (lake 14, 6 sites), Moshui Lake (lake 15, 5 sites), Nanhu Lake (lake 16, 7 sites), Nantaizi Lake (lake 17, 6 sites), Qingling Lake (lake 18, 3 sites), Sanjiao Lake (lake 19, 3 sites), Sanliqi Lake (lake 20, 4 sites).

feeding activities according to the percentages of their functional designations.

We used Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) (CANOCO 4.53; Microcomputer Power, Ithaca, New York; Leps and Šmilauer 2003) to analyze the relation between animal assemblages and environments. DCA indicated that a normal model (gradient lengths > 2.0 standard units) would best fit the data. In CCA, we used forward selection and Monte Carlo permutation tests to identify important environmental factors influencing the abundance and distribution of macroinvertebrates. Altogether we analyzed 10 environmental variables and 61 macroinvertebrate taxa in the CCA. Phytoplankton Chl *a* is usually considered a good measure

Table 1. Limnological variables of the study lakes. D_L is calculated as the ratio of shoreline length to lake circumference. D_V is the ratio of 3 mean water depths to maximum water depth. DR is the ratio of √(lake area) to mean water depth.

	Mean	Minimum	Lower quartile	Median	Upper quartile	Maximum	Standard deviation
A = area (km^2)	61.0	0.5	2.4	8.0	65.2	355.0	98.9
D_L = development of lake shoreline	2.7	1.2	1.9	2.1	3.2	6.4	1.4
D_V = development of lake volume	2.1	1.4	1.9	2.0	2.4	2.9	0.4
DR = dynamical ratio of lake	2.0	0.2	0.8	0.9	2.2	8.1	2.2
Z = water depth (m)	2.1	1.2	1.5	1.9	2.6	4.2	0.8
Z_{SD} = Secchi depth (m)	0.9	0.3	0.4	0.5	1.1	3.2	0.8
TN = total N concentration of water (mg/m^3)	3792	536	671	1278	6972	13690	3876
TP = total P concentration of water (mg/m^3)	259	16	37	131	326	1050	223
Chl *a* = phytoplankton chlorophyll *a* concentration (mg/m^3)	36.9	1.1	3.3	21.1	68.8	113.3	39.6
B_{Mac} = wet biomass of submersed macrophytes (g/m^2)	651.6	0.0	0.0	34.3	778.7	6488.3	1455.9

Table 2. Comparison of limnological variables between macrophyte- and phytoplankton-dominated study lakes, with probability levels (p) determined by Student's t-test. See Table 1 for abbreviations. Min = minimum, max = maximum.

Variable	Statistic	Macrophyte-dominated lakes	Phytoplankton-dominated lakes	p
A (km^2)	Mean ± SE	67.2 ± 41.8	39.4 ± 15.9	0.295
	Min–max	1.5–355.0	0.5–146.5	
D_L	Mean ± SE	3.4 ± 0.7	1.9 ± 0.1	0.040
	Min–max	1.2–6.4	1.2–2.2	
D_V	Mean ± SE	2.0 ± 0.1	2.4 ± 0.1	0.040
	Min–max	1.6–2.6	1.9–2.9	
DR	Mean ± SE	2.2 ± 0.9	1.4 ± 0.6	0.463
	Min–max	0.6–8.1	0.2–6.4	
Z (m)	Mean ± SE	1.9 ± 0.2	1.9 ± 0.2	0.853
	Min–max	1.3–2.7	1.2–2.8	
Z_{SD} (m)	Mean ± SE	1.4 ± 0.2	0.4 ± 0.1	0.002
	Min–max	0.9–2.2	0.3–0.5	
TN (mg/m^3)	Mean ± SE	695 ± 39	6980 ± 1127	<0.001
	Min–max	536–918	1638–13690	
TP (mg/m^3)	Mean ± SE	37 ± 5	495 ± 113	0.002
	Min–max	16–56	205–1050	
Chl a (mg/m^3)	Mean ± SE	3.5 ± 0.3	70.2 ± 9.1	<0.001
	Min–max	2.2–5.0	36.8–113.3	
B_{Mac} (g/m^2)	Mean ± SE	1579.0 ± 673.2	0.0 ± 0.0	0.031
	Min–max	506.6–6488.3	0.0–0.0	

of eutrophication, so we conducted a series of regressions of invertebrate variables vs Chl a. Regression analyses and Student's t-tests were done with STATISTICA (version 8.0; StatSoft, Tulsa, Oklahoma). Before statistical analyses, data were $\log_{10}(x + 1)$ transformed to reduce heterogeneity of variances.

RESULTS

Classified groups of the study lakes

Morphometric, water chemistry, and biological variables (Table 1) varied widely among lakes. According to the standard suggested by Nürnberg (1996) for fixed-boundary classification of lake systems, 50% of lakes were mesotrophic–eutrophic state, and the other 50% were hypereutrophic. Based on the macrophyte–phytoplankton classification scheme of Bachmann et al. (2002), the 10 mesotrophic–eutrophic lakes were macrophyte-dominated lakes characterized by dense macrophyte stands with a wet biomass range of 507.6 to 6488.3 g/m^2, whereas the 10 hypereutrophic lakes were phytoplankton-dominated lakes characterized by high phytoplankton-borne Chl a (with a concentration range = 36.8–113.3 mg/m^3). Lakes differed in their environmental characteristics (Table 2) and were separated along DCA axis 1 (Fig. 2). We analyzed invertebrate data separately for each group of lakes because of the differences in environmental conditions.

Assemblage characteristics of macroinvertebrates in the alternative stable states

We identified a total of 61 macroinvertebrate taxa belonging to 18 families and 51 genera from the lakes. Among them were 8 taxa of oligochaetes, 28 taxa of mollusks, 22 taxa of insects, and 3 taxa of other animals. We identified 54 macroinvertebrate taxa belonging to 17 families and 47

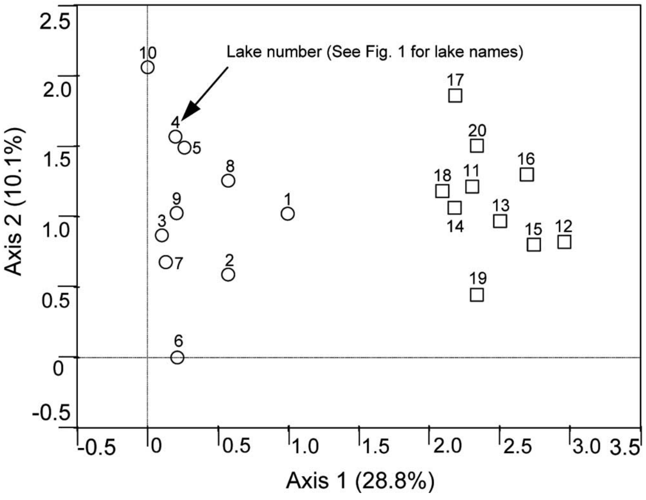

Figure 2. Detrended correspondence analysis ordination plot of lakes based on abundance of macroinvertebrates. Percentage of explained variance is given in the parentheses.

Table 3. Mean (± SE) density (D; individuals/m^2) and biomass (B; g dry mass/m^2; mollusks without shells) of each taxonomic group of macroinvertebrates in study lakes, with percentages in parentheses.

Taxonomic group	Metric	Macrophyte–dominated lakes	Phytoplankton–dominated lakes	All lakes
Total	D	1881 ± 400 (100.0)	2563 ± 1580 (100.0)	2222 ± 1114 (100.0)
	B	1.48 ± 0.24 (100.0)	1.33 ± 0.58 (100.0)	1.41 ± 0.38 (100.0)
Oligochaeta	D	25 ± 4 (1.3)	2033 ± 1512 (79.3)	1029 ± 771 (46.3)
	B	0.10 ± 0.02 (6.8)	0.72 ± 0.45 (54.1)	0.41 ± 0.23 (29.1)
Gastropoda	D	1752 ± 394 (93.1)	5 ± 3 (0.2)	879 ± 278 (39.6)
	B	1.29 ± 0.24 (87.2)	0.21 ± 0.17 (15.8)	0.75 ± 0.21 (53.2)
Bivalvia	D	6 ± 5 (0.3)	0 ± 0 (0.0)	3 ± 1 (0.1)
	B	0.05 ± 0.04 (3.4)	0.00 ± 0.00 (0.0)	0.03 ± 0.01 (2.1)
Insecta	D	92 ± 31 (4.9)	521 ± 123 (20.3)	307 ± 79 (13.8)
	B	0.04 ± 0.02 (2.7)	0.38 ± 0.11 (28.6)	0.21 ± 0.09 (14.9)

genera in the macrophyte-dominated lakes, where density and biomass of total macroinvertebrates ranged from 379 to 3264 ind/m^2 and 0.36 to 5.25 g dry mass [DM]/m^2, respectively. Gastropods constituted the predominant group with 93.1% of total density and 87.2% of total biomass (Table 3). Scrapers were the predominant functional group (Table 4). We identified 21 macroinvertebrate taxa belonging to 8 families and 18 genera in the phytoplankton-dominated lakes, where density and biomass of total macroinvertebrates ranged from 121 to 16,614 ind/m^2 and 0.07 to 6.37 g DM/m^2, respectively. Oligochaetes constituted the predominant group with 79.3% of total density and 54.1% of total biomass (Table 3). Collector–gatherers were the predominant functional group, with 90.8% of total density and 72.9% of total biomass (Table 4).

Macroinvertebrate assemblages in relation to environments

The density and biomass of macroinvertebrates in the lakes were mostly governed by phytoplankton Chl *a*, wet biomass of submersed macrophytes (B_{Mac}), Secchi depth (Z_{SD}), and by the development of lake shoreline (D_L) (Fig. 3A, B). Environmental factors strongly correlated with the first axis were Chl *a*, B_{Mac}, and Z_{SD}. The 2nd CCA axis was correlated with D_L. Thus, Chl *a* and B_{Mac} were the key factors structuring macroinvertebrate assemblages.

Macroinvertebrate patterns along the eutrophication gradient

As eutrophication increased, the number of macroinvertebrate taxa decreased (Fig. 4). We observed 3 types of response patterns of density and biomass of total macroinvertebrates and main functional feeding groups to eutrophication: 1) collector–gatherers (mainly Tubificidae and Chironomidae) and predators (e.g., *Tanypus*) increased (Figs 5A, C, 6A, C, 7); 2) scrapers (e.g. Bithyniidae) decreased (Figs 5B, 6B, 7); and 3) total macroinvertebrates first decreased and then increased (Figs 5D, 6D, 7).

Phytoplankton Chl *a* was inversely correlated with macrophyte biomass at lower levels of Chl *a* concentration

Table 4. Mean (± SE) density (D; individuals/m^2), biomass (B; g dry mass/m^2; mollusks without shells) of each functional feeding group of macroinvertebrates in study lakes, with percentages in parentheses.

Functional feeding group	Metric	Macrophyte-dominated lakes	Phytoplankton-dominated lakes	All lakes
Shredders	D	3 ± 1 (0.2)	1 ± 1 (0.0)	2 ± 1 (0.1)
	B	0.00 ± 0.00 (0.0)	0.01 ± 0.01 (0.8)	0.01 ± 0.01 (0.7)
Collector–filterers	D	7 ± 5 (0.4)	0 ± 0 (0.0)	3 ± 2 (0.1)
	B	0.05 ± 0.04 (3.4)	0.00 ± 0.00 (0.0)	0.02 ± 0.02 (1.4)
Collector–gatherers	D	83 ± 20 (4.4)	2326 ± 1558 (90.8)	1204 ± 835 (54.2)
	B	0.13 ± 0.03 (8.8)	0.97 ± 0.57 (72.9)	0.55 ± 0.29 (39.0)
Scrapers	D	1752 ± 394 (93.1)	5 ± 3 (0.2)	879 ± 201 (39.6)
	B	1.29 ± 0.24 (87.2)	0.21 ± 0.17 (15.8)	0.75 ± 0.20 (53.2)
Predators	D	36 ± 15 (1.9)	231 ± 50 (9.0)	134 ± 28 (6.0)
	B	0.01 ± 0.01 (0.7)	0.14 ± 0.04 (10.5)	0.08 ± 0.02 (5.7)

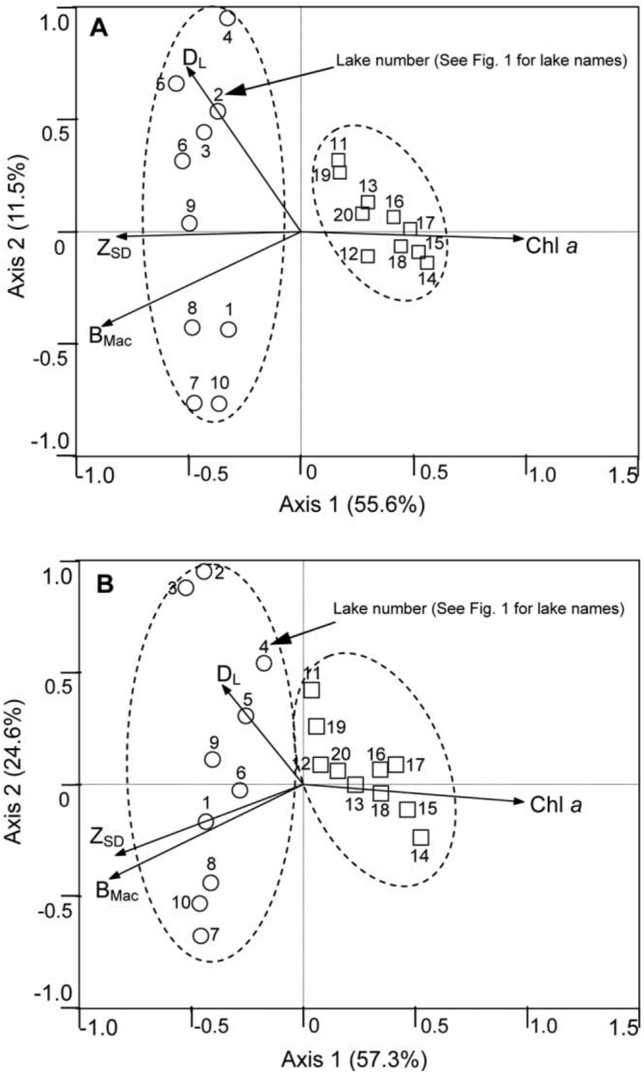

Figure 3. Canonical correspondence analysis biplots of sites and environmental variables influencing macroinvertebrate density (A) and biomass (B) in the study lakes. Percentage of explained variance is given in parentheses. Chl *a* = phytoplankton chlorophyll *a* concentration, B_{Mac} = wet biomass of submersed macrophytes, Z_{SD} = Secchi depth, D_L = development of lake shoreline.

(Fig. 8). No submersed macrophytes were found in lakes where Chl *a* reached a level >30 mg/m^3. This shift generated a sufficiently large perturbation to push scrapers out of one state and into another.

DISCUSSION

In floodplain lakes, one of the most serious problems caused by eutrophication is the disappearance of submerged macrophytes and the switch to a turbid, phytoplankton-dominated state (Scheffer et al. 1993, 2001, Hilt et al. 2006). In our study lakes, some Chl *a* data were missing along the gradient, so the critical thresholds of Chl *a* for the loss of macrophytes could not be ideally defined, but the decreasing trend of B_{Mac} along Chl *a* suggests that aquatic macrophytes disappear abruptly at a moderate Chl *a* level. Wang et al. (2014) used a larger data set consisting of 76 lake-years of data collected from the same geographic area. They found well defined alternative states of macrophytes along the TP gradient and defined a range of moderate TP values (20–80 mg/m^3) as the threshold for the clear to turbid regime shift (Wang et al. 2014). When we regressed B_{Mac} against Chl *a* based on the data set from Wang et al. (2014), we found a folded B_{Mac}–Chl *a* relationship. The threshold Chl *a* for the abrupt loss of macrophytes was ~30 mg/m^3, a level corresponding to the lowest Chl *a* for the lakes without macrophytes. This finding supports our idea that aquatic macrophytes disappear abruptly at a moderate Chl *a*. The abrupt loss of macrophytes was accompanied by a change in the dominant groups of macroinvertebrates from epiphytic animals (e.g., Bithyniidae) in the macrophyte-dominated lakes to pollution-tolerant animals (e.g., Tubificidae, *Tanypus*) in the phytoplankton-dominated lakes along the eutrophication gradient.

Macroinvertebrate diversity declined with increasing eutrophication in Yangtze-disconnected lakes. A similar trend has been reported in other studies (Crowns et al. 1992, Gong and Xie 2001). According to Simpson's (1964) theory of spatial heterogeneity, a more complex and diverse fauna is found in more heterogeneous and complex physical and chemical environments. Aquatic macrophytes provide structural support, increase niche space (Rosine 1955, Rooke 1984, Jeppesen et al. 1998), and offer refuges from predators (Thorp and Bergey 1981, Hargeby et al. 1994). Macrophytes play a critical role in the maintenance of macroinvertebrate diversity (Brönmark 1989, Jeppesen et al. 1998). With increasing eutrophication, phytoplankton concentration in-

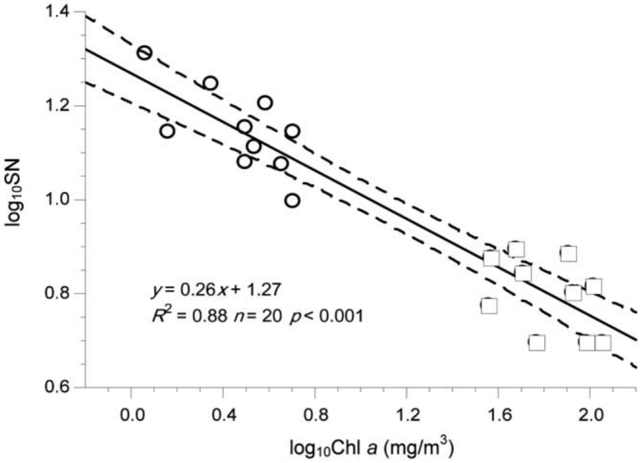

Figure 4. Regression between phytoplankton chlorophyll *a* concentration ($\log_{10}$Chl *a*) and number of species ($\log_{10}$SN) of macroinvertebrates in study lakes. Dashed lines indicate 95% confidential limits.

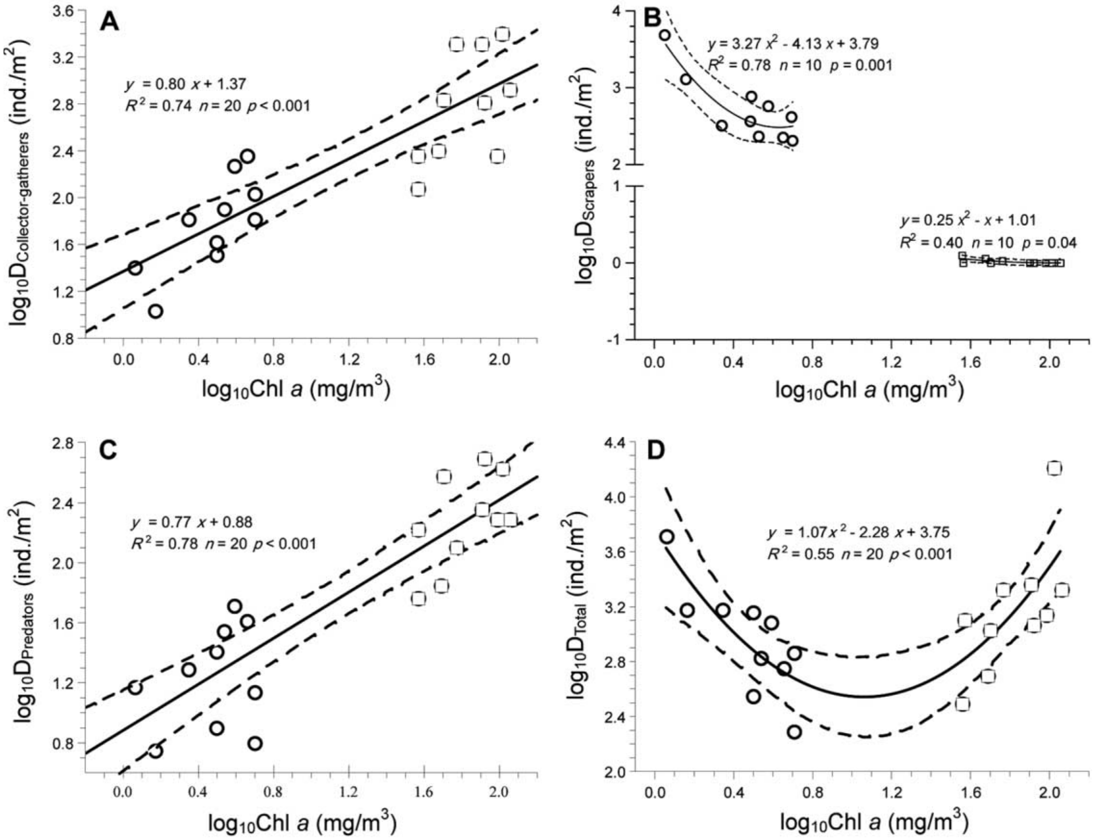

Figure 5. Regressions of densities (D) of collector–gatherers (A), scrapers (B), predators (C), and total macroinvertebrates (D) on phytoplankton chlorophyll *a* concentration ($\log_{10}$Chl *a*). Dashed lines indicate the 95% confidential limits. Ind. = individuals.

creases. This increase is accompanied by a decrease in the euphotic depth, which inhibits the growth of submersed macrophytes (Jupp and Spence 1977, Hough et al. 1989, Dodds 2002). Thus, the disappearance of macrophytes will lead to low spatial heterogeneity and a further decline of macroinvertebrate diversity.

The density of total macroinvertebrates in the study lakes initially decreased, and then increased along the eutrophication gradient. This pattern has not been documented elsewhere. Decreasing density of plant-associated scrapers along with loss of submersed macrophytes was the underlying cause of the initial decrease in total density. Wang et al. (2006) also pointed out the strong dependence of scrapers on the abundance of submersed macrophytes in a study focused on plant-associated gastropod (as scrapers) assemblages in Yangtze shallow lakes. The monotonic decreasing response of scrapers to loss of macrophytes implies that a minimum coverage of macrophytes is necessary for the development of scrapers. Previous studies probably did not detect such a pattern because invertebrates colonizing aquatic plants were not taken into account during sampling (Bazzanti and Seminara 1986, Gong and Xie 2001, Moss et al. 2003, Timm et al. 2006). Moreover, most previous studies were local-scale surveys of eutrophic–hypereutrophic lakes (Wiederholm 1984, Xiong et al. 2003, Jiang et al. 2011), where macroinvertebrates show monotonic decreasing or increasing responses to eutrophication. We found this pattern along the gradient of eutrophication because we included epiphytic animals and undertook a regional-scale systematic investigation.

Total dry mass of invertebrates followed the same trend along the eutrophication gradient as total density, a result that is inconsistent with the patterns of wet mass reported in previous studies (Wollheim and Lovvorn 1995, Gong and Xie 2001, Timm et al. 2006). This discrepancy may be partially explained by methodological differences in the measurement of biomass. In previous studies the wet mass of mollusks was measured including their shells, whereas we measured dry mass without shells.

The decrease of density and biomass of total macroinvertebrates at the initial stage of eutrophication may be explained by the gradual disappearance of aquatic macrophytes because they provide food sources and more habitable surface area for epiphytic animals (Newman 1991, Jeppesen et al. 1998). In particular, macrophytes provide appropriate substrates for the oviposition of snails (Brönmark 1989, Wang et al. 2006). The increases in density and biomass in the late stage of eutrophication results from a steep increase of pollution-tolerant taxa. In eutrophic water bodies, intensive decomposition leads to a lack of dis-

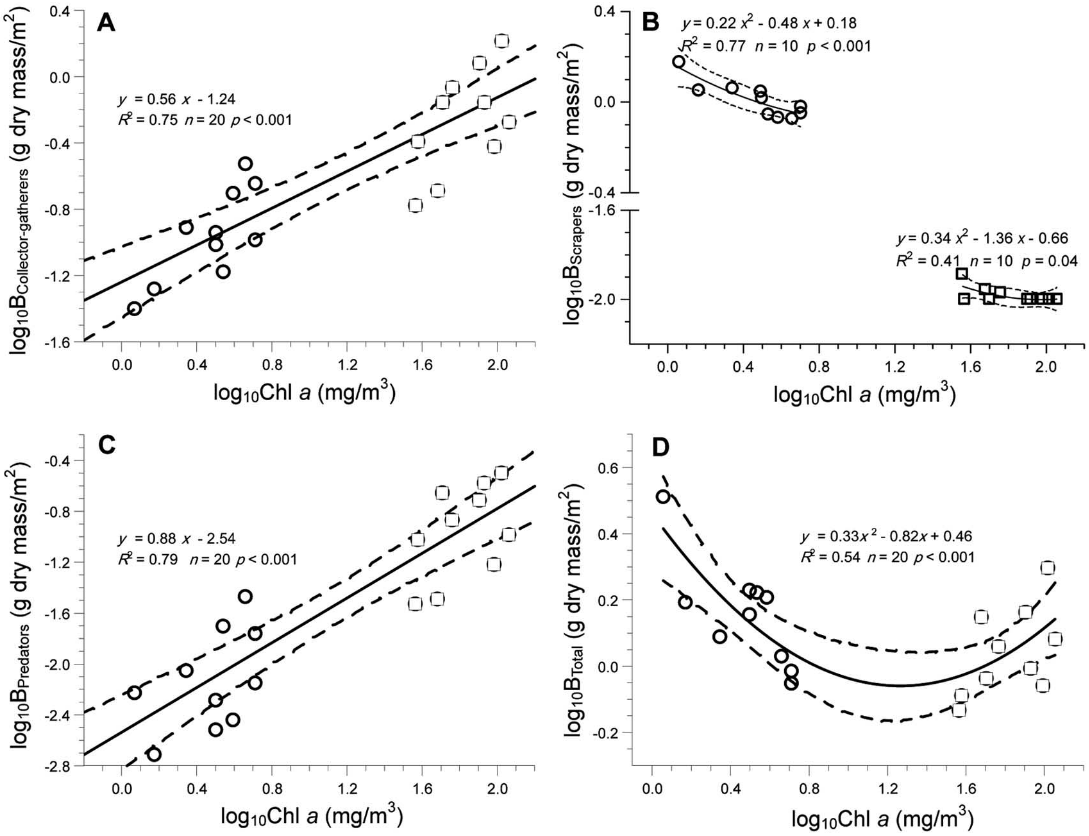

Figure 6. Regressions of biomass (B) of collector–gatherers (A), scrapers (B), predators (C), and total macroinvertebrates (D) on phytoplankton chlorophyll *a* concentration ($\log_{10}$Chl *a*). Dashed lines indicate the 95% confidential limits. Ind. = individuals.

solved O_2, which results in the replacement of pollution-sensitive taxa by pollution-tolerant ones (Rosenberg and Resh 1993, Jiang et al. 2011). The bottom of the studied hypertrophic water bodies always consisted of a thick layer of fine organic sludge, which forms a suitable habitat only for pollution-tolerant taxa (e.g., Tubificidae, *Tanypus*), belonging to the collector–gatherers feeding type (Strayer 1985, Brinkhurst and Gelder 1991).

Among the nutrient–macroinvertebrate relationships shown in Figs 4, 5, and 6, only density and biomass of scrapers presented 2 plateaus along the eutrophication gradient. The response pattern of scrapers, which mainly consisted of gastropods associated with macrophytes, closely followed the response pattern of macrophytes. At higher eutrophication levels, collector–gatherers increased because of the gradually increasing dominance of soft silt, rich in organic matter, and the increase of predators may be the result of reduction in macrophytes because plants can provide refuges and impede predation (Allan and Castillo 2007).

Conclusions

Human activities generate a significant eutrophication threat to floodplain lakes, which can shift lakes from the clear to the turbid state, and our results indicate that the structure of macroinvertebrate assemblages will also change accordingly. Our comparisons of macroinvertebrate assemblages in the 2 types of lakes indicated that lake eutrophication is accompanied by decline in invertebrate diversity, dis-

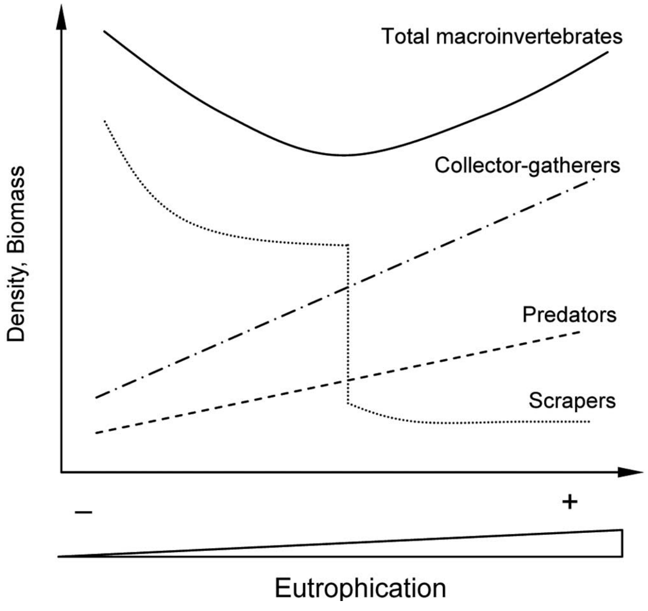

Figure 7. Tendency diagrams to illustrate responses of density and biomass of different functional feeding groups to the regime shifts caused by eutrophication in the Yangtze lakes.

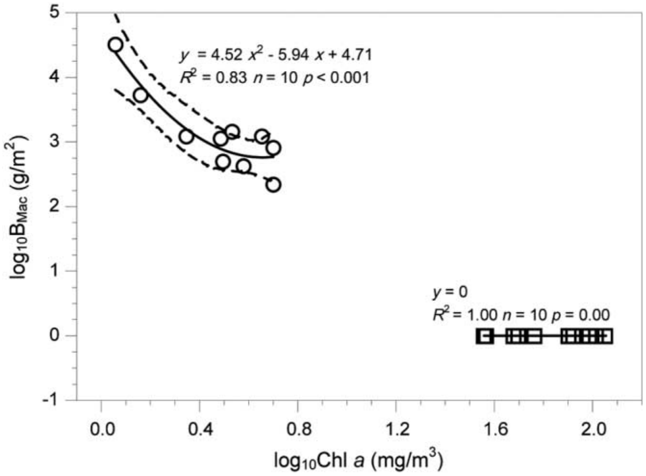

Figure 8. Regression between phytoplankton chlorophyll a concentration ($\log_{10}$Chl a) and macrophyte biomass ($\log_{10}B_{Mac}$) in study lakes. Dashed lines indicate the 95% confidence limits.

appearance of pollutant-sensitive taxa, and aggregation of pollutant-tolerant taxa. Along the eutrophication gradient, macrophyte cover dropped sharply from a high to a very low level. This pattern was mirrored by the abundance of scrapers, which depend on macrophytes, and thus, reflects the eutrophication level. Thus, a clear-water state with abundant submersed macrophytes and a specific biomass or coverage of macrophytes is important for the development of gastropod assemblages and for the maintenance of high diversity in the benthos. To reach a stable clear-water and macrophyte-dominated equilibrium of the lake ecosystem, we suggest that the nutrient concentration should be reduced enough to maintain the survival of dense stands of aquatic plants.

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