





Macroinvertebrate assemblages in streams and rivers of a highly developed region (Lake Taihu Basin, China)

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ABSTRACT: The Lake Taihu Basin, one of the most highly developed regions in China, suffers from severe water pollution and habitat degradation as a result of economic development and urbanization. However, little research has been conducted on the benthic macroinvertebrate assemblages and their environmental relationships. We studied the community structure of benthic macroinvertebrates in this area and explored possible factors regulating their structure, diversity, and distribution. We recorded a total of 104 taxa; Bellamya aeruginosa had the highest frequency of occurrence (71 out of 93 sites), followed by Limnodrilus hoffmeisteri (49) and Corbicula fluminea (42). Oligochaeta was the most abundant taxonomic group, accounting for 89.42% of total macroinvertebrate abundance. Benthic communities were mainly characterized by pollutiontolerant taxa, such as L. hoffmeisteri (Oligochaeta), B. aeruginosa (Gastropoda), and Polypedilum scalaenum (Chironomidae), indicating severe anthropogenic disturbance and habitat degradation. The macroinvertebrate diversity decreased from the western hills to the eastern plains aquatic ecoregions; the Shannon-Wiener and Margalef indices differed significantly between the two ecoregions. The abundances (%) of gathering collectors increased from upstream to downstream, but scrapers showed the opposite trend, consistent with the river continuum concept. Community structure and spatial patterns of macroinvertebrates in the Lake Taihu Basin were strongly correlated with habitat diversity, nutrient loads, and aquatic vegetation coverage. These results provide valuable information for effective management practices of biodiversity conservation in stream and river ecosystems of the Lake Taihu Basin.

KEY WORDS: Anthropogenic disturbance \cdot Habitat degradation \cdot Nutrient enrichment \cdot Ecoregion \cdot Sub-ecoregion \cdot Yangtze River Delta

INTRODUCTION

With rapid urbanization and economic development, China, especially the coastal areas, has attained remarkable economic success. However, this rapid economic growth has resulted in a series of severe

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environmental problems (Fu et al. 2007) such as increases in eutrophication (Qin et al. 2007, Smith 2003), organic pollutants (An & Hu 2006), heavy metals (Zhang et al. 2009), and habitat degradation (Li et al. 2010), which have placed new pressures on national sustainable development. As water quality

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may only partially reflect environmental impact (Birk et al. 2012), more attention should be given to the status of biological communities and conservation biodiversity (Morse et al. 2007) in the management of aquatic ecosystems.

Macroinvertebrates are an important component of stream and river systems and play crucial roles in maintaining the structural and functional integrity of freshwater ecosystems (Wallace & Webster 1996). They alter the geophysical condition of sediments, promote detritus decomposition and nutrient cycling, and facilitate energy transfer among trophic levels (Vanni 2002, Covich et al. 2004). Benthic macroinvertebrates are the most commonly used biological indicators in most aquatic ecosystems due to their variable sensitivity to environmental change (Pignata et al. 2013) and ease of sampling (i.e. low cost). Unfortunately, recent discoveries have shown extinction rates of freshwater fauna to be as much as 5 times greater than that of terrestrial fauna (Ricciardi & Rasmussen 1999). The decline of benthic macroinvertabrates in aquatic systems is largely due to anthropogenic impact in the form of habitat deterioration and nutrient overload. The diversity of the benthic community is progressively simplified due to the decreased number of taxa (Yuan 2010, Cai et al. 2012b). Habitat complexity is one of the key environmental factors influencing macroinvertebrate communities. Complex habitats provide more ecological niches, which make macroinvertebrates highly vulnerable to the loss of their preferred habitat (McGoff et al. 2013). Consequently, habitat deterioration will severely depress the diversity and composition of benthic communities. Thus, identifying the possible factors regulating macroinvertebrate structure, diversity, and distribution can aid the development of more prescriptive conservation and management strategies for freshwater ecosystems in highly developed regions.

The Lake Taihu Basin is one of the most industrialized areas in China. With a population of more than 37 million (2.9% of the total population of China), and as a significant industrial complex, this area contributes 11% to China's gross domestic product (Liu et al. 2013). Cultivated land, which is heavily fertilized each year, covers 15 100 km² of the drainage area, which is >40% of the total area. The plain river network is the main wastewater discharge region of southern Jiangsu Province (Qin et al. 2007); consequently, the freshwater ecosystem of the basin is subject to severe damage. Studies to date have largely focussed on water physico-chemistry (e.g. eutrophication and heavy metals) (Liu et al. 2013)

and aquatic organisms have received little attention despite their importance in ecosystem health (Xiao et al. 2013).

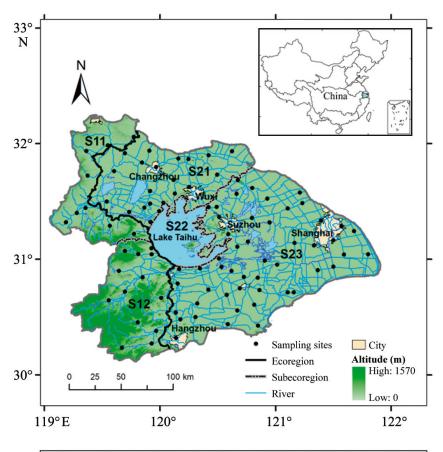
Studies of benthic macroinvertebrate communities in the Basin have been largely focused on Lake Taihu (Cai et al. 2011, 2012a), with very few studies examining the main streams and rivers (Wang et al. 2007, Gao et al. 2011, Wu et al. 2011). Therefore, 3 questions need to be addressed: (1) What is the condition of the benthic macroinvertebrate community structure in the Lake Taihu Basin? (2) Are the macroinvertebrate assemblages in the Lake Taihu Basin similar to other highly developed regions? (3) What are the possible variables regulating their abundance and community structure? To elucidate these questions, the macroinvertebrate communities, water chemistry and habitat characteristics of streams and rivers in the Lake Taihu Basin, as well as the possible factors regulating their structure, diversity and distribution were investigated.

MATERIALS AND METHODS

Study area

The Lake Taihu Basin (30° 7′ 19″ to 32° 14′ 56″ N and 119° 3′ 1″ to 121° 54′ 26″ E) is situated in the Yangtze River Delta in eastern China and covers an area of approximately 36 900 km² (Fig. 1). It has a water surface area of 6134 km², of which rivers and lakes each comprise around 50%. The dense river network comprises 7% of the total drainage area, with a total tributary length of around 120 000 km (Gao & Gao 2012).

The Lake Taihu Basin, characterized by plains and river networks in the east and hills and streams in the west, can be divided into 2 ecoregions: the western hill aquatic ecoregion (S1) and the eastern plain aquatic ecoregion (S2) (Gao & Gao 2012). Significant differences in land use exist between S1 and S2. Farmland and woodland are the dominant landscapes in S1, accounting for 44.70 and 42.00%, respectively. The relatively low levels of agricultural development in this ecoregion have resulted in fewer pollutants from agricultural sources and less pressure on the aquatic environment. In contrast, cultivated land makes up 50% of the total area of S2, followed by built-up areas (27.36%) and water bodies (17.00%). High levels of urbanization and a high population density in S2 have led to significant agricultural and urban runoff and industrial waste, which are direct causes of water quality deterioration in this area. In



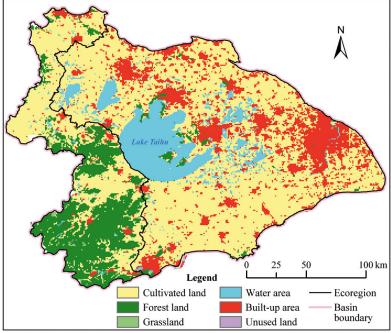


Fig. 1. Location of the sampling sites, aquatic (sub)ecoregions, and land use. S1 (western hill aquatic ecoregion) is comprised of sub-ecoregions S11 and S12, and S2 (eastern plain aquatic ecoregion) is made up of sub-ecoregions S21, S22, and S23. As the objects of this study were rivers and streams, S22 (Lake Taihu) was excluded

addition, rapid development of aquaculture has also accelerated water pollution and eutrophication. For this reason, spatial differentiation in ecology, vegetation, and nutrient levels within each ecoregion are evident, and each ecoregion (S1 or S2) has been divided into 2 (S11 and S12) or 3 (S21, S22 and S23) sub-ecoregions (Fig. 1). As the objects of this study were rivers and streams, S22 (Lake Taihu) was excluded in this study.

Macroinvertebrate sampling

A total of 93 sampling sites were selected across the entire Lake Taihu Basin. Macroinvertebrate samples were collected within a 100 m reach for each site in October 2012. Sampling was conducted with a 30 cm diameter D-frame net with a 500 mm mesh using the multihabitat approach described by Barbour et al. (1999). At each site, 10 sampling units (30 \times 50 cm) were collected to include the major microhabitats (e.g. riffles, pools, banks, submerged and overhanging macrophytes, depositional areas). Determination of major habitat types was made prior to sampling by qualitatively evaluating the sample reach. The 10 sampling units were divided proportionally based on available habitats. All materials collected from a site were pooled and rinsed in the field to remove fine sediments, and all remaining materials were fixed with a 7% buffered formaldehyde solution. In the laboratory, samples were sorted by hand in white enamel pans with the aid of a dissecting microscope. All organisms were preserved in 70% ethanol and identified to the lowest feasible taxonomic level under a dissecting and an upright microscope, using keys by Liu et al. (1979), Morse et al. (1994), Wang (2002), and Tang (2006). Macroinvertebrate abundance was obtained by counting all individuals and expressing the results as ind. m⁻².

Invertebrate taxa were assigned to functional-feeding groups (FFGs) based on invertebrate morphological and behavioral adaptations for acquiring their food (Cummins & Klug 1979, Merritt & Cummins 2008). The FFGs used were categorized as follows: (1) shredders (SH, feed on coarse particulate organic matter >1 mm in size, either live aquatic macrophyte tissue or coarse terrestrial plant litter); (2) scrapers (SC, scrape off and consume the organic matter attached to stones and other substrate surfaces, primarily live plant stems); (3) filtering collectors (FC, sift fine particulates 1000 to 0.45 µm from the flowing column of water); (4) gathering collectors (GC, gather fine particulates of organic matter from the debris and sediments on the stream beds); and (5) predators (PR, feed on other animals, i.e. live prey). The relative abundance (%) of each FFG was calculated from their total abundance in samples from each site.

Measurement of environmental parameters

The pH, conductivity (cond), dissolved oxygen (DO), chlorophyll a (chl a), salinity, and turbidity were measured in under-surface water (collected 0.5 m below the water surface) using a water quality analyzer (YSI 6600 V2); samples were kept at 4°C for further chemical analysis. When the water depth of the stream was less than 0.5 m, water samples were collected from an intermediate depth. The total nitrogen (TN), ammonium (NH₄⁺-N), nitrate (NO₃⁻-N), total phosphorus (TP), orthophosphate (PO₄³⁻-P), total suspended solids (TSS), chemical oxygen demand (COD_{Mn}), and sulfate (SO₄²⁻) were measured in the laboratory based on standard methods (APHA 2012).

To describe the physical properties of the habitat, 6 parameters were chosen: habitat diversity (habitat), channel morphology (channel), aquatic vegetation coverage (vegetation), road density (road), riparian zone land use (land use), and substrate index (SI). The values for habitat, channel, road, and land use were scored in the field and ranged from 0 to 20 (Barbour et al. 1999). The value for vegetation reflected the percentage cover of aquatic vegetation. SI (Weatherhead & James 2001) is a composite index reflecting the heterogeneity of the substrate, and it can be calculated as:

 $SI = 0.07 \times (\% \text{ large boulder}) + 0.06 \times (\% \text{ boulder}) + 0.05 \times (\% \text{ cobble}) + 0.04 \times (\% \text{ pebble}) + 0.03 \times (\% \text{ gravel}) + 0.02 \times (\% \text{ sand}) + 0.01 \times (\% \text{ mud/silt})$

This gives a value ranging from 1 for mud/silt to 7 for large boulders. Prior to the *SI* calculation, the proportion of each particle size class was estimated for each sampling site based on methods described by Kondolf (1997) and Jowett & Richardson (1990). Sub-

strates were classified according to the following criteria: <0.5 mm = mud/silt, 0.5–2 mm = sand, 2–16 mm = gravel, 16–64 mm = pebble, 64–256 mm = cobble, 256–512 mm = boulder, and >512 mm = large boulder.

Data analysis

The biological indices of Shannon-Wiener (H'), Simpson (1-D), Margalef and Pielou were calculated in terms of abundance using the PAST software package (Paleontological Statistics v.2.17) (Hammer et al. 2001). A principal component analysis (PCA) based on a correlation matrix among samples was used to analyze the physico-chemical data. PCA was performed using CANOCO v.4.5 software (ter Braak & Smilauer 2002). Differences in environmental variables were examined among the 4 sub-ecoregions using 1-way ANOVA at a significance level of p < 0.05.

To examine variation in community structure among the 4 sub-ecoregions, 1-way ANOSIM was employed based on the Bray-Curtis matrix obtained from log(x + 1) transformed abundance data, using the software PRIMER 5.0 (Clarke & Warwick 2001). SIMPER procedures (Clarke 1993) were also applied to determine the typical taxa that contributed most to withingroup similarity. Canonical correspondence analysis (CCA) and redundancy analysis (RDA) were used to identify environmental gradients and their relationships to the benthic community. Detrended correspondence analysis (DCA) was carried out to examine whether CCA (DCA axis 1 length > 3) or RDA (<3) would be appropriate. Manual forward selection was used to determine which environmental variables were significantly related to the benthic community (Monte Carlo test with 9999 permutations, p < 0.1). We selected a significance level of p < 0.1 given the typically high variability in invertebrate data (Yoccoz 1991). The statistical significance of species-environment correlations for the ordination axes were also determined based on 9999 Monte Carlo permutation tests. Data were logarithmically transformed to approximate normality, and taxa occurring at less than 5 sites were excluded for the ANOSIM, CCA, and RDA analyses.

RESULTS

Environmental characterization

ANOVA analyses indicated that the 4 sub-ecoregions differed significantly (p < 0.05) in most physical, chemical, and biological variables, except for

Table 1. Comparison of environmental variables among the 4 sub-ecoregions (western hill aquatic ecoregions S11 and S12, and eastern plain aquatic ecoregions S21 and S23). When 1-way ANOVA indicated significant differences (p < 0.05), each sub-ecoregion differing in the post hoc Tukey tests was given a different letter (a, b, or c). DO = dissolved oxygen; Cond = conductivity; TN = total nitrogen; NH_4^+-N = ammonium; NO_3^--N = nitrate; TP = total phosphorus; $PO_4^{3-}-P$ = orthophosphate; COD_{Mn} = chemical oxygen demand; TSS = total suspended solids; SO_4^{2-} = sulfate; SI = substrate index. 20' refers to a scale with a maximum score of 20. Values are median (range)

	S11 $(n = 9)$	S12 (n = 13)	S21 (n = 21)	S23 $(n = 50)$	F	p
pH	7.88 (7.14–8.73)	7.93 (7.46–8.72)	7.89 (7.54–8.83)	7.88 (7.30–8.41)	0.265	0.850
\overline{DO} (mg l^{-1})	6.0 (2.3–12.0) ^{ab}	7.1 (2.8–11.9) ^a	4.8 (0.7-7.3) ^b	4.8 (0.4–9.4) ^{ab}	4.505	0.005
Cond (µs cm ⁻¹)	0.40 (0.23-1.12) ^{ab}	0.27 (0.15-0.63) ^a	0.64 (0.34-1.08) ^c	$0.60 (0.34 - 0.90)^{bc}$	12.448	< 0.001
TN (mg l ⁻¹)	2.11 (0.98-4.51) ^b	2.15 (1.34-4.11) ^b	4.01 (1.60-8.13) ^a	3.55 (1.08-6.87) ^a	8.462	< 0.001
NH_4^+ -N (mg l^{-1})	$0.02 (0.01-0.60)^{b}$	$0.08 (0-0.99)^{ab}$	1.03 (0-4.51) ^a	$0.65 (0.02-4.36)^{a}$	4.797	0.004
$NO_3^N \text{ (mg l}^{-1}\text{)}$	1.15 (0.06–1.83)	0.88 (0.02-3.24)	1.55 (0.08-3.04)	1.48 (0.02-4.21)	2.340	0.079
TP (mg l^{-1})	0.05 (0.03-0.16) ^{ab}	0.03 (0.02-0.26) ^a	$0.20 (0.04-0.94)^{c}$	$0.16 (0.04 - 0.60)^{bc}$	5.196	0.002
PO_4^{3-} -P (µg l ⁻¹)	22.10 (7.84–36.95)	8.59 (5.01–129.17)	57.79 (3.33–252.11)	45.50 (2.08–247.62)	2.302	0.083
$COD_{Mn} (mg l^{-1})$	3.44 (1.71-6.91)	2.75 (1.19-8.64)	4.50 (2.92-6.04)	4.14 (1.71-6.91)	1.696	0.174
TSS (mg l^{-1})	37 (14-428)	29 (6-278)	75 (34–120)	55 (5-652)	0.174	0.913
Chl a ($\mu g l^{-1}$)	5.6 (2.4-24.0)	7.0 (1.4-25.6)	9.5 (2.8–27.4)	7.6 (1.9–23.3)	2.630	0.055
SO_4^{2-} (mg l ⁻¹)	35.52 (16.16-63.33) ^a	30.59 (14.61–137.37) ^{ab}	94.75 (25.61-246.60) ^b	83.03 (6.54-358.62) ^b	5.362	0.002
$CaCO_3 (mg l^{-1})$	73.84 (57.43-86.15) ^b	65.64 (41.02-98.46) ^b	94.65 (73.84-123.07) ^a	90.25 (53.33-141.54) ^a	11.516	< 0.001
Salinity (%)	0.19 (0.11-0.87) ^{ab}	$0.13 (0.07-0.31)^{b}$	0.32 (0.16-0.53) ^a	$0.30 (0.16-0.57)^a$	7.841	< 0.001
Turbidity (NTU)	29.6 (0.2-667.5)	16.9 (0. 1-1217.6)	94.4 (19.9-236.4)	63.6 (10.0-1139.1)	0.891	0.449
Habitat (20')	10 (1-15) ^a	10 (2-17) ^a	3.29 (1-11) ^b	4 (1–12) ^b	13.315	< 0.001
Channel (20')	10 (2–18) ^a	10 (2-17) ^a	5.71 (1-14) ^b	3 (1-13) ^b	10.987	< 0.001
Vegetation (%)	10 (0-90) ^a	20 (0-70) ^{ab}	6 (0-50) ^b	0 (0-70) ^b	6.246	0.001
Road (20')	9 (6-13) ^a	9 (2-12) ^a	6 (3-12) ^b	5 (1–10) ^b	11.627	< 0.001
Land (20')	9 (4-11) ^a	8 (3-14) ^a	5 (2-9) ^b	4 (1-9) ^b	14.381	< 0.001
SI (1-7)	1.1 (1.0-3.0) ^a	1.5 (1.0-3.9) ^b	1.1 (1.0-1.9) ^a	1.0 (1.0-2.0) ^a	11.427	< 0.001
Simpson	0.62 (0.18-0.88)	0.53 (0-0.83)	0.43 (0-0.82)	0.41 (0-0.87)	2.237	0.089
Shannon-Wiener	1.44 (0.40-2.52) ^a	1.31 (0-2.05) ^{ab}	$0.84 (0-2.07)^{b}$	$0.87 (0-2.31)^{b}$	4.208	0.008
Margalef	2.55 (0.63-4.94) ^a	2.30 (0-4.25) ^a	1.11 (0-2.51) ^b	1.28 (0-3.88) ^b	8.945	< 0.001
Pielou	0.69 (0.25-1)	0.51 (0-0.82)	0.53 (0-0.93)	0.48 (0-0.99)	1.614	0.192

in pH, TSS, and turbidity (Table 1). Variation of environmental variables between ecoregions was greater than within ecoregions. In general, S11 and S12 had lower nutrient concentrations (e.g. nitrogen and phosphorus) and higher DO, whereas S21 presented the highest nutrient concentrations and pollution levels (e.g. cond and $\rm COD_{Mn}$). S1 values for habitat, channel, vegetation, road, riparian land use, and $\rm SI$ were higher than the corresponding S2 values. Concentrations of the studied nutrients (TN and TP) and chl $\rm a$ showed consistent spatial patterns increasing from west to east, but habitat diversity showed the opposite trend, indicating intensive anthropogenic disturbance in the downstream sections (S21 and S23).

Results of PCA indicated that PC1 and PC2 accounted for 33.1 and 12.2% of the total variance of environmental variables, respectively (Fig. 2). The PC1 primarily described the nutrient loads with negative loadings for TN, TP, PO₄-P, NH₄-N, NO₃-N, F⁻, Cl⁻, SO₄²⁻, CaCO₃, COD_{Mn}, salinity, and cond, while the physical habitat shared positive loadings (e.g. land use, channel morphology, road width) on PC1. The PC2 had a strong positive relationship with TSS

and turbidity. Taken together, results of the PCA suggested that nutrient loads and habitat degradation increased from west to east.

Community composition and diversity

A total of 104 macroinvertebrate taxa were recorded (Table S1 in the Supplement at www.intres.com/articles/suppl/b023p015_supp.pdf), including 10 Gastropoda, 8 Bivalvia, 3 Oligochaeta, 2 Polychaeta, 8 Hirudinea, 8 Crustacea, 30 Chironomidae, 20 Odonata, and 14 other insect taxa. The number of taxa at each station varied between 1 and 24, with an average number of 7.6, and showed a decreasing trend from west to east (Fig. 3). Bellamya aeruginosa was the taxon with the highest frequency of occurrence (71 out of the total 93 sites), and together with Parafossarulus eximius (41) and Semisulcospira cancelata (27), the 3 taxa were important contributors to the total abundance of Gastropoda. Limnodrilus hoffmeisteri and Branchiura sowerbyi best represented Oligochaeta within the basin, with frequen-

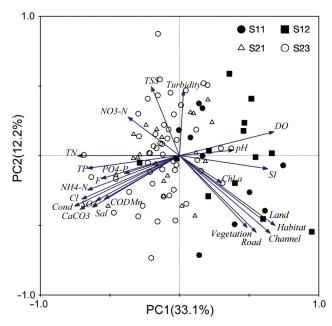
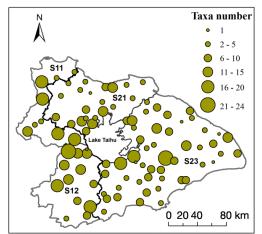


Fig. 2. Principal component analysis (PCA) plot of the first 2 principal components of 23 environmental factors. Values on the axes indicate the percentages of total variation accounted for by each axis

cies of occurrence of 49 and 41, respectively. Compared with the high occurrences of the former 2 taxa, Rhyacodrilus sinicus was found only once within S23. The frequency of occurrence for Corbicula fluminea (42) was the highest of the Bivalvia. Other Bivalvia (Anodonta woodiana elliptica, A. w. pacifica, Acuticosta chinensis, Unio douglasiae, and Limnoperna fortunei) also had frequencies of occurrence greater than 10. Exopalaemon modestus and Neocaridina denticulata were the 2 main taxa of Crustacea and were found in 37 and 26 stations, respectively. The Chironomidae Polypedilum scalaenum and Chirono-

mus plumosus are pollution-tolerant taxa and had frequencies of 12 and 11, respectively.

Total abundance of macroinvertebrate varied greatly between 1.33 and 39 080 ind. m⁻², with an average of 1159 ind. m⁻². A relatively even abundance distribution was observed and an extremely high abundance was recorded at some stations (mainly located in urban rivers) in the northeastern regions of S2 (Fig. 3) due to the high abundance of Oligochaeta (Fig. S1 in the Supplement). The most abundant taxonomic group was Oligochaeta, accounting for 89.42% of the total macroinvertebrate abundance (Fig. S1) followed by Gastropoda (7.57%), Crustacea (1.17%), Bivalvia (0.74%), and Chironomidae (0.65%). Of all the 104 taxa, L. hoffmeisteri contributed 86.3% of the total macroinvertebrate abundance and 96.56% of the total Oligochaeta abundance. Additionally, B. sowerbyi accounted for 3.4 % of the total Oligochaeta abundance, and these 2 taxa together accounted for most of the Oligochaeta abundance. Gastropoda was the most widely distributed taxonomic group, with B. aeruginosa representing 70.8% of the total Gastropoda abundance. P. eximius (8.8%), S. cancelata (6.4%), Parafossarulus striatulus (5.5%), and Alocinma longicornis (3.6%) were also important taxa of Gastropoda. Bivalvia were mainly distributed at the station around Lake Taihu, but could not be found in many stations in the west of S1 and in the east of S2. C. fluminea and L. fortunei were the most abundant Bivalvia, representing 51.8 and 21.7% of total Bivalvia abundance, respectively. Crustacea were common at the sites around Lake Taihu, and E. modestus and N. denticulata each accounted for half of the abundance. Odonata mainly appeared in the upstream parts of the basin, and Polychaeta were more common downstream (Fig. S2 in the Supplement).



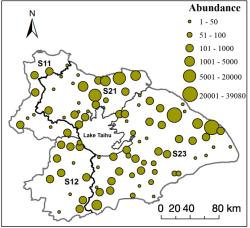


Fig. 3. Spatial patterns of taxa number (taxa sample site-1) and total abundance of benthic macroinvertebrates (ind. m-2)

The 4 diversity indices showed similar spatial patterns, with higher values in the west (S1) and lower values in the east (S2) (Fig. S3 in the Supplement). The mean Shannon-Wiener values for S11 and S12 were 1.44 and 1.31, whereas for S21 and S23 they were 0.84 and 0.87. The Margalef richness index for S11 (2.55) and S12 (2.30) were also much higher than those for S21 (1.11) and S23 (1.28). One-way ANOVA analyses (significance at p < 0.05) indicated that the 4 sub-ecoregions differed significantly in Shannon-Wiener and Margalef indices, but not for Simpson and Pielou indices (Table 1). The Simpson values for S11 (0.62) and S12 (0.53) were much higher than those for S21 (0.43) and S23 (0.41). The evenness of the macroinvertebrate assemblage showed a similar pattern. Specifically, the values for the Pielou index in S11 (0.69) and S12 (0.51) were higher than those for S21 (0.53) and S23 (0.48). Furthermore, values of the 4 diversity indices were relatively low, showing low biodiversity of benthic macroinvertebrates in the basin.

Distribution of macroinvertebrate FFGs

The 104 taxa were categorized as follows: 10 SH, 13 SC, 18 FC, 23 GC, and 40 PR. SC dominated the benthic communities and accounted for 50% of the total abundance, followed by GC (25%), FC (13%), and SH (11%) (Fig. S4 in the Supplement). Although PR had the most taxa, it represented less than 2% of the abundance of the invertebrate community. Specifically, *B. aeruginosa* also contributed 70% to the total abundance of SC. Thus, SC were the most widely distributed and made up the largest proportion. *L. hoffmeisteri* contributed 96% to the total abundance of GC, the distribution of which was in accord with that of *L. hoffmeisteri*.

FFG had different distribution patterns in different sub-ecoregions. Specifically, SC represented 45.1% of the total abundance in S11. The percentages of GC and FC were smaller (24.2 and 20.4%, respectively), and SH and PR accounted for 7.0 and 3.3% of the abundance. SC was also the main functional group in S12 and made up 60.0% of the abundance, followed by FC (15.1%) and SH (14.5%), but GC (6.93%) and PR (3.53%) were rarely found in this sub-ecoregion. On the contrary, GC were the most dominant FFG in S21 and S23, accounting for 82.0 and 82.4% abundance, respectively. Overall, the highest percentages of SC were in upland stream sections while GC dominated further downstream.

Multivariate analyses

One-way ANOSIM indicated that there were significant differences in macroinvertebrate community structure between S11 and S23 (p = 0.040), and between S12 and S21 (p =0.026) (Table 2). Although there was no significant difference between S11 and S12 in macroinvertebrate community structure, the dominant taxa of these 2 sub-ecoregions were quite different. S21 and S23 were mainly characterized by Gastropoda and Oligochaeta, and their contributions in these 2 areas were very similar (Table 3).

DCA revealed that a unimodal model (i.e. CCA) would be more appropriate for the whole data set (DCA axis 1 length = 12.12). The CCA identified 5 environmental variables highly correlated with the macroinvertebrate community. The first and second canonical axes explained 8.2% (eigenvalue of 0.261) and 3.4% (0.111) of the variation in the taxa data, respectively (Table 4). Monte Carlo permutation tests revealed significant species-environment correlations for the first 2 axes (p < 0.05). The first axis was positively correlated with habitat diversity and SI (intra-set correlations of 0.69 and 0.66, respectively), and negatively correlated with TN (r = -0.53). This axis mainly reflected habitat diversity, substrate, and nutrient gradient. Axis 2 showed a positive correlation with turbidity (r = 0.43).

On the CCA plot, stations in S11 and S12 were plotted mainly on the positive side, whereas stations bin S21 and S23 were clustered on the negative side of the plot. These placements indicated different environmental conditions along Axis 1 for the ecoregions (Fig. 4a). Moreover, S11 and S12 had higher values of SI and habitat diversity than S21 and S23, whereas S21 and S23 had higher TN concentrations. The CCA also revealed relationships among 32 benthic taxa and environment variables (Fig. 4b). Two Oligochaeta taxa (L. hoffmeisteri and B. sowerbyi) and 2 Polychaeta taxa (Nephtys oligobranchia and Nereis japonica) occurred at sites with high TN

Table 2. One-way ANOSIM showing significance levels in macroinvertebrate community structure among the 4 subecoregions (see Fig. 1). Upper triangular matrix shows the dissimilarity (%), and lower triangular matrix shows the R statistic; $^*p < 0.05$

	S11	S12	S21	S23
S11		79.7	82.3	80.42
S12	0.055		81.33	78.19
S21	0.123	0.132*		75.31
S23	0.194*	0.097	0.017	

Table 3. Characteristic species for each sub-ecoregion (see Fig. 1) identified by SIMPER procedure, their contributions (contr., %) to within-group similarity (up to a cumulative percentage of 80 %), and average abundance (abun., ind. m⁻²) in each sub-ecoregion were calculated

Taxa		S11 Contr.	Abun.	12 Contr.	S2 Abun.		Sí Abun.	23 Contr.
Oligochaeta Branchiura sowerbyi Limnodrilus hoffmeisteri	1.5	6.1	3.0	7.3	99.0 1289.3	11.1 20.0	1318.4	18.2
Crustacea Neocaridina denticulata sinensis Exopalaemon modestus	9.6	12.4	17.8 1.8	6.9 4.3			5.0	5.9
Chironomidae Cricotopus sylvestris Ploypedilum scalaenum	0.9 5.8	3.7 4.1						
Gastropoda Bellamya aeruginosa Parafossarulus eximius Radix swinhoei Semisulcospira cancelata Stenothyra glabra	42.1 3.6	39.5 8.1	45.6 7.3 14.0 2.1	31.9 8.0 13.2 5.1	70.9 14.1	43.2 7.8	67.9 7.0	47.4 8.9
Bivalvia Corbicula fluminea Total	1.5 65.0	6.2 80.0	13.5 105.1	7.2 83.9	1473.2	82.1	1398.3	80.4

and low habitat diversity, whereas *Aciagrion* sp. (Odonata) was found at sites with low TN and high habitat diversity. *L. fortunei* (Bivalvia) occurred at sites with high turbidity. One Chironomidae taxa (*Procladius* sp.) and 2 Gastropoda taxa (*Radix swinhoei* and *Stenothyra glabra*) were found at sites with high *SI*.

In consideration of the significant spatial difference, the macroinvertebrate communities of the 2 ecoregions were analyzed separately (Fig. 5). When the 2 ecoregions were analyzed separately, DCA indicated that CCA and RDA would be more appropriate for S1 (DCA axis 1 length = 6.05) and S2 (DCA axis 1

Table 4. Summarized results of canonical correspondence analysis and macroinvertebrate abundance data of 93 stations (taxa occurring at less than 5 sites were excluded). Intra-set correlations between the first 4 canonical axes and the environmental variables are presented

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues Species–environment correlations	0.261 0.822	0.111 0.627	0.067 0.512	$0.033 \\ 0.468$	3.202
Cumulative percentage variance of species data of species—environment relationship Sum of all canonical eigenvalues	8.2 52.4	11.6 74.7	13.7 88.2	14.7 94.8	0.498
Intra-set correlations Total nitrogen Chl a Turbidity Habitat SI	-0.53 0.16 0.04 0.69 0.66	0.14 0.04 0.43 -0.24 0.23	0.29 -0.06 -0.28 -0.02 0.14	-0.10 0.37 -0.19 -0.07 0.16	

length = 2.9), respectively. The CCA identified 3 environmental variables (vegetation, channel, and SI) that were significantly correlated with the benthic community of the S1 ecoregion. The first 3 CCA axes explained 10.2% (eigenvalue of 0.368), 6.9%~(0.249) and 5.5%(0.180) of species data variance, respectively. As for the S2 ecoregion, RDA indicated that 5 environmental variables (vegetation, land use, TP, turbidity, and COD_{Mn}) were highly correlated with macroinvertebrate communities. The first 2 CCA axes explained

14.5 and 5.5% of species data variance, with eigenvalues of 0.145 and 0.055, respectively.

DISCUSSION

Benthic macroinvertebrate characteristics

A total of 104 macrozoobenthic taxa were recorded in this study. Compared with previous studies, 113 macroinvertebrate taxa were detected by Wang et al. (2007) in this region. It must be pointed out that

when Wang et al. (2007) sampled upstream in the Changzhou area, the sampling sites were mainly located in streams, so more aquatic insects were found. This study found more taxa than Gao et al. (2011) and Wu et al. (2011) due to inclusion more rivers and streams in the basin and higher sampling efforts.

Macroinvertebrate FFG proportions were likely affected by anthropogenic alteration of riparian vegetation (Compin & Céréghino 2007). In this study, the percentages of GC increased from upstream to downstream, reflecting that GC were able to find sufficient

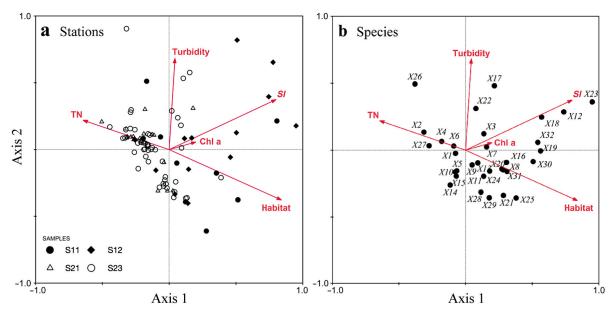


Fig. 4. Canonical correspondence analysis of macroinvertebrate taxa and environmental variables showing (a) station scores and (b) species scores. TN = total nitrogen, SI = substrate index, X1 = Bellamya aeruginosa, X2 = Limnodrilus hoffmeisteri, X3 = Corbicula fluminea, X4 = Branchiura sowerbyi, X5 = Parafossarulus eximius, X6 = Exopalaemon modestus, X7 = Semisulcospira cancelata, X8 = Neocaridina denticulata sinensis, X9 = Anodonta woodiana elliptica, X10 = Acuticosta chinensis, X11 = Parafossarulus striatulus, X12 = Radix swinhoei, X13 = Unio douglasiae, X14 = Alocinma longicornis, X15 = Anodonta woodiana pacifica, X16 = Glossiphonia complanata, X17 = Limnoperna fortunei, X18 = Stenothyra glabra, X19 = Ploypedilum scalaenum, X20 = Chironomus plumosus, X21 = Glossiphonia sp., X22 = Dicrotendipus lobifer, X23 = Procladius sp., X24 = Macrobrachium nipponense, X25 = Aciagrion sp., X26 = Nephtys oligobranchia, X27 = Nereis japonica, X28 = Helobdella fusca, X29 = Cricotopus sylvestris, X30 = Glyptotendipes tokunagai, X31 = Hippeutis cantori, X32 = Physa sp.

food in urban streams (Suren & McMurtrie 2005, Compin & Céréghino 2007). Wang et al. (2012) reported that the relative abundance of GC was significantly higher in disturbed streams. Similar patterns have also been found in other regions of China

(Jiang et al. 2011), consistent with the river continuum concept (RCC) (Vannote et al. 1980) that longitudinal distributions of FFGs follow longitudinal patterns in basal resources. In addition, *Limnodrilus hoffmeisteri* was the most dominant GC, and its dis-

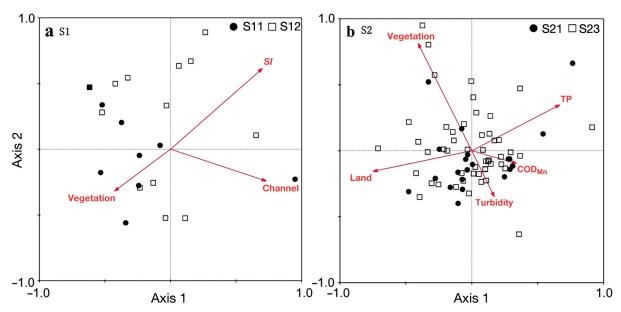


Fig. 5. (a) Canonical correspondence analysis biplot of western hill aquatic ecoregion S1 and (b) redundancy analysis biplot of eastern plain aquatic ecoregion S2. SI = substrate index, TP = total phosphate, COD_{Mn} = chemical oxygen demand

tribution also supports the idea that taxa in highorder rivers are more tolerant to disturbance and organic pollution than those in low-order rivers (Jiang et al. 2011). In contrast, SC were more abundant in headwaters, and decreased gradually with increasing stream size, the distribution of which also followed the predictions of the RCC.

Multivariate analyses indicated distinct spatial patterns in benthic community structure, coinciding with locations from west to east and reflecting associated environmental conditions. Macroinvertebrate assemblages in the basin were mainly dominated by Oligochaeta (e.g. L. hoffmeisteri and Branchiura sowerbyi), Gastropoda (e.g. Bellamya aeruginosa) and Chironomidae (e.g. Chironomus plumosus and Polypedilum scalaenum). Generally, these taxa are able to live in stressful environments and are known to occur in highly degraded systems (Wang et al. 2012). Accordingly, L. hoffmeisteri and B. sowerbyi, the most representative Oligochaeta within the basin, were widely spread and occurred abundantly in some sites. These 2 Oligochaeta taxa are reported to be able to tolerate extremely oxygen-deficient environments (Takamura et al. 2009). Five Gastropoda taxa were also characteristic taxa, among which B. aeruginosa was the most frequent (Table 3). Bellamya spp. have been reported to be insensitive to pollution and able to inhabit moderately to highly polluted water bodies (Cao & Jiang 1998). For example, Bellamya purificata is not only able to live normally in conditions with extremely high total nitrogen content (2.77%), but also in areas with extremely high biomass (428 g m⁻²) (Cao & Jiang 1998). Chironomus spp. larvae are widely distributed in the basin, and the high densities of these taxa has been regarded as an excellent bio-indicator of freshwater pollution (Hooper et al. 2003). The low taxon richness and dominance of pollution-tolerant taxa indicates serious environmental pollution in the basin. Compared with the highly developed Lake Taihu Basin, the Qiantang River Basin, with high forest cover and less anthropogenic impact, contains more Odonata and EPT (Ephemeroptera, Plecoptera, and Trichoptera) (Wang et al. 2012). These taxa are known to be sensitive to external influence (Jowett et al. 1991) and are mainly found in the upstream parts of the basin. This may be ascribed to more anthropogenic disturbance in the eastern plain areas than the western hill areas. Corbicula fluminea was found mainly in sites with high turbidity and low nutrient loads. This taxon is reported to be sensitive to environmental changes, and low DO levels might strongly influence its survival (Saloom & Duncan 2005).

The macroinvertebrate diversity indices showed a pattern of high values in the west and low values in the east. In particular, the Shannon-Wiener and Margalef indices for the western hill aquatic ecoregion (S1) were much higher than that for the eastern plain aquatic ecoregion (S2). This may be ascribed to the different urbanization and anthropogenic disturbance levels in the 2 ecoregions.

Primary factors governing the benthic macroinvertebrate assemblages

Our results suggest that the most important factors regulating assemblage structure are habitat heterogeneity, organic enrichment, and aquatic vegetation coverage. Habitat heterogeneity is known to be one of the determinate factors of benthic macroinvertebrate community structure (Shostell & Williams 2007). In this study, the habitat heterogeneity in S1, a mostly hilly and mountainous region, was relatively higher than that in S2, where the landscape consists mainly of plains and dense river networks. The macroinvertebrate community in S1 was also more abundant and diverse. Macroinvertebrate biodiversity is mainly determined by the numbers of taxa and individuals, and higher diversity can be detected in complex habitats because of more living space or surface area (Shostell & Williams 2007). Therefore, the more structurally complex the habitat, the more diverse macroinvertebrate community can be (McGoff et al. 2013). Substrate grain size and heterogeneity also affected the diversity of benthic assemblages (Allen & Vaughn 2010). In this study, Radix swinhoei and Stenothyra glabra were mainly found in sites with high SI values, because of their habit of climbing on hard substrate. Moreover, turbidity is generally considered a surrogate measure for sediment loading, and has been found to be closely related to the abundance and diversity of benthic macroinvertebrates (Hall & Killen 2005).

Our results also indicated that the composition of the macroinvertebrate community was inversely related to the level of nutrient enrichment (as indicated by measurements of the water column TP, ${\rm COD_{Mn}}$, and chl a), which is congruent with other studies (Donohue et al. 2009, Yuan 2010, Pokorny et al. 2012). Moreover, great impacts of nutrient loads on benthic community structure were previously reported in this region (Gao et al. 2011, Wu et al. 2011). Nutrient loads could influence macroinvertebrate community structure as a consequence of increased food availability where nutrients stimulate primary

production. The intermediate productivity hypothesis (IPH) predicts that species diversity is maximized at some intermediate level of productivity, at which competition for food is reduced and the coexistence of potentially competing species is promoted (Widdicombe & Austen 2001). The most resistant taxa would tend to increase significantly, excluding the most sensitive ones, and the community would eventually have fewer taxa but a greater number of individuals. It would also increase eutrophic processes and organic enrichment resulting in the reduction of DO, which may become limiting to the survival of some sensitive taxa.

Aquatic vegetation also has an important role in structuring macroinvertebrate assemblages via providing living space (Angradi et al. 2001) or selecting species traits related to population dynamics and feeding habits (Céréghino et al. 2008). In addition, the roots of some macrophytes might provide benthic macroinvertebrates with DO (Takamura et al. 2009). The river channels in S2 have undergone high levels of regulation and channelization, which might also explain the low biodiversity in this ecoregion. This result is in agreement with the findings of Kennedy & Turner (2011), who reported that river regulation and channelization can reduce macroinvertebrate diversity and density. Regulated and channelized river channels isolate rivers from surrounding riparian areas by severing linkages between the aquatic and riparian communities and breaking the integrity of ecological structure to a certain extent. Thus, river channelization processes and structural heterogeneity were identified as important factors affecting the abundance and species richness of resident macroinvertebrate assemblages (Lepori et al. 2005).

There was a distinct geographical difference between the adjacent S1 and S2 ecoregions, and their benthic macroinvertebrate communities reflected significant differences between them. Specifically, the most sensitive factors for macroinvertebrate assemblages in S1 were habitat conditions and aquatic vegetation coverage, whereas the benthic macroinvertebrate assemblages in S2 were mutually influenced by nutrient enrichment, habitat heterogeneity, and turbidity. Previous studies have indicated that natural geologic and geographic features could be important factors influencing macroinvertebrate community structure across large-scale regional distances (Li et al. 2001, Weigel et al. 2003). Geographic differentiation between the 2 ecoregions might affect human activity and land use patterns, which, in turn, magnify regional distinctions (Allan 2004). With less impacts of urbanization, S1 had relatively better

environmental conditions, lower nutrient concentrations and more diverse habitat. More taxa were found in S1, including several sensitive taxa. The urbanization level in S2 showed an increasing trend from west to east, and there was also increasing trends for nutrient loads and habitat degradation from west to east. The major cities, with denser human populations, are mainly distributed in the northeastern areas (Fig. 1). Urban rivers are more regulated and channelized, and result in less aquatic vegetation. Accordingly, macroinvertebrate assemblages are subject to severe anthropogenic pressures and water pollution, as illustrated by the lower diversity and dominance of pollution-tolerant taxa. The number of taxa found at each station and the macroinvertebrate diversity indices in S2 decreased gradually from west to east, while the abundance of Oligochaeta showed the opposite trend. Extremely high abundance of Oligochaeta was found in several urban rivers sites. High abundance of Oligochaeta, especially L. hoffmeisteri and B. sowerbyi, are regarded as excellent bio-indicators of highly polluted ecosystems (Takamura et al. 2009).

The percentage variation of benthic fauna explained by CCA was low, which is often the case with ecological data, and the cumulative percentage variance of species data was 14.7% of all 4 axes (Økland 1999). Moreover, the environmental variables used in this paper are mainly physico-chemical parameters of water and limited habitat data. We did not include sediment data such as sediment organic matter content, and connectivity of rivers and lakes. All these factors would significantly affect the composition of benthic macroinvertebrates. For instance, hydrological connectivity can strongly influence macroinvertebrate assemblages (Gallardo et al. 2008, Leigh & Sheldon 2009). In this study, Nephtys oligobranchia and Nereis japonica were only found in those rivers connected with the Yangtze River or coastal rivers, which may be related to the dispersal process and salinity.

Synthesis and implications for benthic biodiversity conservation

Our results indicated that the Lake Taihu Basin macroinvertebrate assemblage was mainly characterized by pollution-tolerant taxa, and the macroinvertebrate diversity was relatively low, indicating severe anthropogenic disturbance and habitat degradation. The Shannon-Wiener and Margalef indices showed a significant difference between the western

hill aquatic ecoregion and the eastern plain aquatic ecoregion. The results also revealed the detrimental impacts of anthropogenic disturbance (such as increased nutrient concentration, degraded habitat and aquatic vegetation) on macroinvertebrate assemblages. At present, nutrient enrichment and habitat degradation appear to be the most pervasive anthropogenic stresses on freshwater ecosystems in China, resulting from industrial and agricultural development (Fang et al. 2006). Understanding the relationships between nutrient concentrations and the macroinvertebrate assemblages is important for biodiversity restoration, and controlling the inflow of nutrients would help accelerate the restoration process. The restoration of aquatic macrophytes could be achieved through increasing habitat heterogeneity. Macrophytes can also remove nutrients from the water, and can be harvested to eliminate them from the ecosystem (Takamura et al. 2003). It is of vital importance to reduce channelization and maintain connectivity between the aquatic and terrestrial environments (Kennedy & Turner 2011). Ecological restoration will have little beneficial effect on macroinvertebrate biodiversity if the restoration schemes do not account for river regulation and channelization, which affect structural heterogeneity relevant to the benthic macroinvertebrates (Lepori et al. 2005). Our results provide valuable information for the conservation and management of biodiversity in developed and developing areas. We propose that particular attention should be paid to nutrient reduction and restoration of habitat heterogeneity.

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