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Variations of fish composition and diversity related to environmental variables in shallow lakes in the Yangtze River basin

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Abstract – Variations in fish communities of shallow lakes in the Yangtze basins were investigated from September 2007 to September 2009. Six lakes were chosen for comparative study of species composition and diversity in relation to environmental variations. Lake heterogeneity was described with environmental physico-chemical variables, using principal component analysis. Sixteen families, composed of 75 species of fish were found in the studied lakes, Cyprinidae being the dominant group. Fish species were divided by habitat preference and trophic guild: benthopelagic and herbivorous fish were the most common guilds in all lakes. Species diversity and richness were significantly higher in spring, while the evenness, expressed by equitability of Simpson's index, was not significantly different among seasons. Species richness and diversity were significantly higher in vegetated lakes (e.g. Liangzihu Lake) than in non-vegetated lakes (e.g. Biandantang Lake), with the largest area (Liangzihu Lake) harbouring the largest species richness and the greatest diversity. The relationship between environmental variables and fish assemblage were analysed using canonical correspondence analysis (CCA). The dominant gradients describing species composition and abundance among the sampling sites were: total phosphorus, total nitrogen, chlorophyll *a*, transparency and water depth. Our study led to the following conclusions: 1) the water quality was better - i.e. high transparency, low total phosphorus (TP) and total nitrogen (TN) and chlorophyll *a*- in vegetated lakes than in unvegetated lakes; 2) vegetated lakes had higher fish diversity than unvegetated lakes; 3) fish relative abundance (CPUE: number of fish per fishing pass) was significantly related to water chemical parameters. Consequently, the details of the findings are useful and relevant for developing suitable conservation strategies to sustain the integrity of fish communities in these lakes.

Key words: Freshwater fish / Environmental variables / Lake / Fish diversity / CCA / PCA / Yangtze River basin

1 Introduction

As habitat degradation continues to accelerate on a global scale, maintenance of species richness and biodiversity has become a central issue of conservation biology (Jones et al. 2004; Lenihan and Peterson 1998; Rouget et al. 2003; Sinclair et al. 1995). Inland aquatic systems are crucial for the conservation of local and global biodiversity (Moss 2000). In fact, there is a great diversity in the form and function of these aquatic systems, presenting a wide range of habitats (Allan and Flecker 1993; Moss 2000; Williams et al. 2004). This is particularly the case for the fish fauna of shallow waters (Amarasinghe and Welcomme 2002). Indeed, shallow lakes vary considerably in species richness, supporting considerably more species, including more unique and more scarce species than other type of water body (i.e. rivers, streams and ditches) at a regional level (Williams et al. 2004); lakes, therefore, make the greatest contribution to sustaining biodiversity. Unfortunately, most shallow lakes occur in lowland areas, often with high human population densities. As a consequence, their environmental value is being dramatically affected, as demonstrated by numerous studies (De Meester and Declerck 2005; Xie and Chen 1999; Fang et al. 2008).

Conditions in the lakes seem to be a major factor affecting diversity. It is widely accepted that environmental variation plays an important role in the organization of lacustrine fish communities (Jackson and Harvey 1989; Tejerina-Garro et al. 1998; Amarasinghe and Welcomme 2002) However, the most important factors in determining species composition differ between water bodies, ranging from physical habitat, like lake morphology, to water chemistry (Rahel 1984; Jackson and Harvey 1989; Tejerina-Garro et al. 1998; Amarasinghe and Welcomme 2002; Zhao et al. 2006; Petry et al. 2003;

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Teixeira-de Mello et al. 2009). Comparisons of fish community structure in lakes, conducted at the regional scale, have highlighted predictable links between community structure and environmental variations. The investigation of how environmental factors (physico-chemical and biotic) determine the structure of natural assemblages has benefited greatly from the "natural experiments" of comparative studies (e.g., Diamond 1978; Werner et al. 1978). This method can fairly quickly generate and test hypotheses, assess mechanisms, and produce acceptable explanations for community-level problems under a wide variety of conditions (Tonn and Magnuson 1982).

The Yangtze River, also called the Chang Jiang meaning "long river", flows for 6300 km from the Tibetan Mountains to the East China Sea. Its catchment covers 1/5 of the land area of China. The Yangtze River basin accounts for 40% of China's freshwater resources, more than 70% of fishery production, and 40% of the China's GDP (Wong 2007; He et al. 2010). In addition to its social and economic importance, the Yangtze River basin is a centre of immense biological wealth. However, human activities have profoundly degraded the ecosystem of lakes in the Yangtze basin, with consequences such as water quality degradation, threats to biodiversity and algal blooming (Xie and Chen 1999; Fang et al 2008). As lakes are seen as highly productive water bodies, more effort is put into increasing fishery production and less into the conservation of fish biodiversity. Few studies of fish communities were found on this area. Xie et al. (2001) compared small fish community differences between zones with or without submersed macrophytes and found fish communities in submersed macrophytes zones to have significantly higher diversity, density and fish biomass. Ye et al. (2007) examined the spatial and seasonal variations of the fish community relative to two key environmental factors: the macrophyte complex and the water depth. In fact, studies on species richness patterns in these lakes are rare and have been largely ignored by monitoring and protection strategies.

Our aim in the present study was to analyse factors explaining patterns of fish assemblages in different lakes within the Yangtze River basin, based on environmental variations. Two objectives were thus addressed: 1) to describe the fish assemblages present in these lakes by examining the abundance and occurrence of the fish species composition, the assemblage patterns and the influence of environmental variables on the assemblages; 2) to test hypotheses of possible links between changes in the fish community and those in the environment. Consequently, we hope the details of our findings will be useful and relevant to developing suitable conservation strategies to sustain the integrity of fish communities in the area.

2 Material and methods

2.1 Study area

The six lakes (Fig. 1) chosen for our study are located in the central zone of the Yangtze River basin in Hubei, China. This area is in the temperate zone and has a great number of lakes (Hubei alone has over 1300 lakes), therefore providing the necessary conditions to study the insular biogeography of

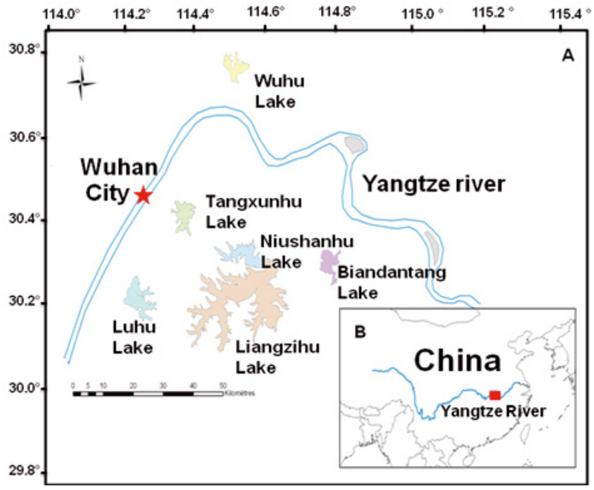

Fig. 1. The six sampled lakes and their locations. (A) The six lakes. (B) China, Yangtze River with the location of the lakes shown indicated by a filled square.

fish assemblages and well suited for comparative studies in aquatic ecology.

In selecting the lakes for this study, we picked those with different macrophyte coverage, surface area and maximum depth, but similar fishery activities. The six lakes chosen are relatively close together and exposed to the same species pool, but differ in surface area and macrophyte coverage. All of the lakes are suburban lakes except Tangxunhu Lake. The lakes present different macrophyte cover: Liangzihu Lake (LZH) and Niushanhu Lake (NSH) have a high coverage (dominated by *Vallisneria natans* (Lour.*) Hara* and *Hydrilla verticillata*) throughout all the year; Luhu Lake (LUH) and Wuhu Lake (WUH) were also covered by macrophytes, but these only appeared in spring and summer. *Potamogeton crispus* Linn. was the dominant macrophyte species in Luhu Lake, but this species senesced and died after summer. The water depth in Wuhu Lake increased sharply (by nearly one metre) in summer, which led to macrophyte death. Biandantang Lake (BDT) and Tangxunhu Lake (TXH) were devoid of macrophytes. The details of lake characteristics and locations are summarized in Table 1.

2.2 Data collection

Habitat descriptions and fish sampling were conducted from September 2007 to September 2009. Within-lake habitat measurements and fish samples were taken at four to twelve locations in each lake, depending on the total surface of the lake and the macrophyte coverage. Sampling started from a random point and then proceeded at evenly distributed intervals along the margins of the water body. We collected data seasonally from each lake. Fish samplings were sometimes repeated the following year because the sampling tools were often destroyed by crabs (*Eriocheir sinensis*) aquaculture in the study lakes. However, only the samplings from intact sampling tools and one dataset for each season in each lake were selected, meaning that about 100 datasets were used in this research.

Table 1. The locations and main characteristics of the studied lakes. TP: total phosphorus; TN: total nitrogen; COD: chemical oxygen demand; DO: dissolved oxygen; Chla: chlorophyll *a*.

Lake	Biandantang	Luhu	Liangzihu	Niushanhu	Tangxunhu	Wuhu
Code	BDT	LUH	LZH	NSH	TXH	WUH
Latitude (°)	30.31	30.22	30.24	30.32	30.43	30.78
Longitude (°)	114.77	114.19	114.53	114.54	114.35	114.51
Area (km^2)	3.5	25	285	38	10	32
Temperature (°C)	21 ± 1.6	23.6 ± 4.0	23.5 ± 3.4	21.9 ± 3.3	23.9 ± 5.2	21.9 ± 5.8
Water depth (m)	1.8 ± 0.4	2.8 ± 0.5	2.9 ± 0.4	2.0 ± 0.3	2.3 ± 0.2	1.8 ± 0.4
Transparency (cm)	56 ± 3	142 ± 66	152 ± 128	71 ± 20	43 ± 29	50 ± 23
TP (mg L^{-1})	0.06 ± 0.01	0.02 ± 0.01	0.02 ± 0.02	0.06 ± 0.03	0.13 ± 0.06	0.08 ± 0.04
TN (mg L^{-1})	1.79 ± 1.06	0.64 ± 0.37	0.48 ± 0.30	0.79 ± 0.51	2.46 ± 0.83	1.12 ± 0.39
COD (mg L^{-1})	1.83 ± 1.47	1.61 ± 0.85	1.33 ± 0.81	2.16 ± 1.32	2.96 ± 0.75	2.28 ± 1.24
DO (mg L^{-1})	7.38 ± 0.91	8.87 ± 0.69	8.73 ± 0.47	8.41 ± 0.99	10.18 ± 2.4	9.25 ± 1.76
Chl*a* (μg L^{-1})	7.49 ± 2.35	7.24 ± 5.00	2.97 ± 3.13	13.03 ± 5.18	52.75 ± 44.73	20.27 ± 16.03
Macrophyte coverages	0%	30%	80%	60%	0%	30%

2.3 Environmental parameter measurements

Eleven environmental characteristics were considered in this research Physical parameters included water body area (AREA), water temperature (WT), water depth (WD), transparency - measured by Secchi depth (TRA) -, and distance to the bank (DIS). Chemical parameters included total phosphorus (TP), total nitrogen (TN), chemical oxygen demand (COD) and dissolved oxygen (DO). In addition, chlorophyll *a* (CHI) and coverage by macrophytes (CRM) per square metre at each sampling station were also taken into account in this study.

2.4 Fish sampling and measurements

To capture fish, one multimesh gill-net and one trap-net were set together at each site. The multimesh gill-net method followed that used by Appelberg (2000). The total length of each net was 20 m using mesh sizes between 5 and 55 mm knot to knot. The mesh sizes followed a geometric series, with a ratio of about 1.25 between mesh sizes, and were assembled in the following order: 43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35 and 30 mm. Using randomly selected mesh sizes, the nets were set in the water at 6:00~7:00 p.m. and were hauled out at 6 : 00 ~ 7 : 00 a.m. the following day. Fish collected were immediately identified to the species level, counted, weighed to the nearest gram, measured (total length, to the nearest mm) and then classified into habitat and trophic guild. The habitat and trophic guild of each species was based on our previous research and on FishBase data (Froese and Pauly 2010). The relative abundance of each species at each sampling was expressed in terms of catchper-unit effort (CPUE, mean number of individuals per fishing pass). In order to record all the fish species, for the analysis of fish species composition, we also investigated the fish species from fishery catches.

2.5 Statistical analysis

Lake environmental variations were analysed using principal component analysis (PCA) with the physico-chemical data.

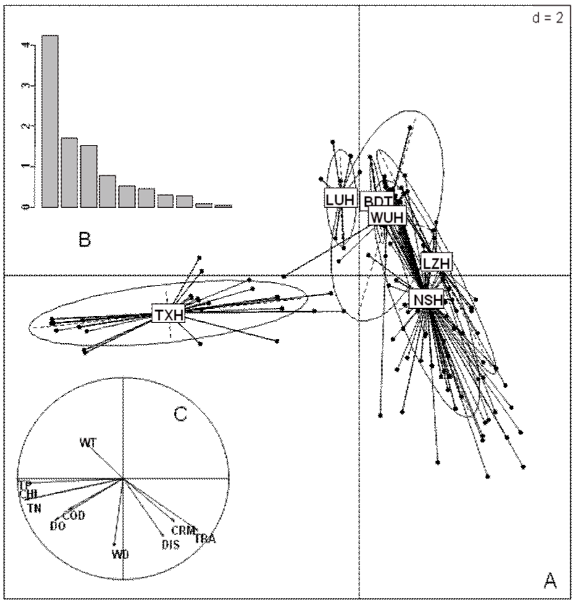

Fig. 2. Results of principal component analysis (PCA) on environmental variables measured for each lake. The first two principal components described 42 and 17% of the total hydrological variation, respectively. (A) Each lake is presented as an ellipsoid. For lake identifications see Material and Methods. (B) Barplot showing eigenvalues in the PCA (C) Vector plot showing the correlation of environmental variables in the F1 - F2 plane.

Geometrically, PCA is a rigid rotation of the original data matrix, and can be defined as a projection of samples onto a new set of axes. The maximum variance is projected or "extracted" along the first axis, the maximum variation uncorrelated with axis-1 is projected on the second axis, the maximum variation uncorrelated with the first and second axis is projected on the third axis, and so on. PCA is now used routinely by ecologists (Townsend et al. 1997; Grossman et al. 1998; Lamouroux et al. 1999; Brosse et al. 1999, 2001) to simplify large data sets while reducing information loss, and to assess intercorrelation among variables of interest (Grossman et al. 1991).

Three diversity indices were chosen for diversity comparisons among different lakes and different seasons, these were: species richness, Simpson's inverse index and equitability of Simpson index. Simpson's inverse index was calculated by the formula: $D = 1/\Sigma\ p_i^2$, where p_i is the proportional abundance of species i. Equitability of Simpson inde was calculated by dividing Simpson's inverse index by S, where S is the species richness. This index allows species richness to be removed, in order to consider only the distribution of the different species; it is, thus, used to express the evenness of a community. The differences of diversity among the four seasons and the six lakes were tested by Kruskal-Wallis and multiple comparison tests. The Kruskal-Wallis test is a nonparametric (distribution free) test used to compare three or more groups of sample data and the multiple comparison tests are a group of tests made following a one or two-factor ANOVA or a Kruskal-Wallis test.

The relationships of fish community structure with environmental factors were analysed using canonical correspondence analysis (CCA). CCA is a direct gradient analysis method that concomitantly analyses the species and environmental data and produces two types of site score. Weighted average site scores were used in this study. For detail on the merits and shortcomings of CCA in relation to other ordination methods, see Palmer (1993) and McCune (2002). The species occurring in only a single lake were omitted from the analysis. Before the analysis started, data on relative species abundances were log-transformed ($\ln(x + 1)$) to reduce the weight of a few dominant species. The environmental variables were $\log 10(x + 1)$-transformed to approximate normal distributions, but normal distribution was not achieved for all of the variables. A Monte Carlo permutation test (999 permutations) was performed to test the significance of the relationships between environmental variables and species composition among study sites (i.e. the significance of the sum of all eigenvalues). The Monte Carlo method is for testing whether a set of data is consistent with a null hypothesis. It is appropriate for a situation where the theoretical distribution of the test statistic is unknown. The test procedure is to use Monte Carlo methods to generate 999 further data sets of the same size as the true data, under the conditions defined by the null hypothesis. The value for the test statistic is calculated for each of these data sets and the distribution of these values is examined. If the value of the test statistic for the actual data is similar to the values obtained from the artificial data sets, then the null hypothesis is accepted, whereas if it is more extreme than the observed value, the hypothesis is rejected.

PCA and CCA ordinations were carried out in the R software using the "ade4" package (Dray and Dufour 2007).

3 Results

3.1 Environmental variations in the studied lakes

Physico-chemical parameters of the six studied lakes were analysed by PCA (Fig. 2) to identify the differences / similarities between the lakes. The first two principal components described 42% and 17% of the total hydrological variation, respectively. The six lakes were mostly differentiated by the first PCA axis. Hydrological variables had high loadings on the first component, such as: chlorophyll *a* (0.923), total phosphorus (0.886), total nitrogen (0.886) and transparency (–0.806). Thus, the first component represents a contrast between the lakes presenting eutrophication and those with macrophyte vegetation.

The comparison between the six lakes is shown (Fig. 2a). Tangxunhu Lake (TXH) was very different from other lakes, as this is an urban lake with high total phosphorus, total nitrogen, chlorophyll *a* and chemical oxygen demand. The other five lakes are suburban lakes. Among these, Liangzihu Lake (LZH) and Niushanhu Lake (NSH) were found to be close to each other and far from Tangxunhu Lake. The macrophyte coverage of these two lakes was relative higher than for the other lakes, and they had lower TP, TN, COD, chlorophyll *a* and higher transparency (Table 1). The remaining three lakes were located in the intermediate position between Tangxunhu Lake and Liangzihu Lake + Niushanhu Lake (Fig. 1a). Their similarities were the absence of macrophytes, in Biandantang Lake (BDT), or temporary macrophyte coverage in spring and summer (as at the end of summer, most of the macrophytes had senesced and died), in Luhu Lake (LUH) and Wuhu Lake (WUH).

3.2 Fish composition of shallow lakes in the Yangtze River basin

All together, 75 species of fish were found across the six lakes. A maximum number of 64 species was found in Liangzihu Lake, while a minimum of only 37 species was found in Biandantang Lake. The fish identified belonged to 16 families, of which Cyprinidae had the greatest species richness; 43 species from this family being found. The largest number of species from this family was found in Liangzihu Lake. The members of other families had relatively low species richness, ranging from 1 to 5 species per family. In total, 17 791 individual fish were caught during the sampling period. Six species represented less than 0.5% of the total catches. The six most abundant species were *Toxabramis swinhonis, Hemiculter leucisculus, Rhodeus ocellatus, Pseudorasbora parva, Rhinogobius giurinus* and *Squalidus nitens*, which accounted for 74% of fish collected. Eight species were found to have more than 25% occurrence frequency: *H. leucisculus, T. swinhonis, P. parva, R. giurinus, S. nitens, Carassius carassius, Culterichthys erythropterus, and R. ocellatus. H. leucisculus* was the most frequent of all fish species found (Table 2).

Divided by habitat, benthopelagic fish was the most common type in all the lakes. It is worth mentioning that 31 species of benthopelagic fish were found in Niushanhu Lake, which represents 54% of the total number of species in this lake (Table 3). Only five species of pelagic fish were found in the lakes. The number of demersal fish species varied from 8 to 18 in the studied lakes. A larger number of demersal fish species were found in macrophyte lakes, such as Liangzihu Lake, Niushanhu Lake and Luhu Lake.

Based on their trophic level, we divided all captured fish into three groups: carnivorous, herbivorous and benthivorous. A total of 16 carnivorous fish species were identified, 15 of which were found in Liangzihu Lake, the highest number of

Table 2. Total number (N), relative abundance (RA), relative occurrence (RO), fish total length range (TL) and species composition of fish sampled in each lake from September 2007 to September 2009. X indicates the presence of fish species in each lake. BDT: Biandantang Lake; LUH: Luhu Lake; LZH: Liangzihu Lake; NSH: Niushanhu Lake; TXH: Tangxunhu Lake; WUH: Wuhu Lake.

Species	Family	Abbr.	N	RA (%)	RO (%)	TL (mm)	BDT	LUH	LZH	NSH	TXH	WUH
Misgurnus anguillicaudatus	Cobitidae	Mang	16	0.1	2.5	78–147			X	X	X	X
Abbottina rivularis	Cyprinidae	Ariv	308	1.7	20.9	40–110			X	X	X	X
Acheilognathus chankaensis	Cyprinidae	Ntai	216	1.2	13.6	55–98			X	X	X	
Acheilognathus macropterus	Cyprinidae	Amac	56	0.3	6.3	32–104			X	X	X	X
Aristichthys nobilis	Cyprinidae	Anob	26	0.1	3.2	150–478				X	X	X
Carassius carassius	Cyprinidae	Caur	379	2.1	30.1	32–294	X	X	X	X	X	X
Cirrhinus molitorella	Cyprinidae	Cmol	170	0.9	2.8	171–264						X
Culter alburnus	Cyprinidae	Calb	11	0.1	2.8	121–406	X	X		X	X	X
Culter dabry	Cyprinidae	Cdab	85	0.5	12.6	50–298	X	X		X	X	X
Culter mongolicus	Cyprinidae	Cmon	81	0.5	21.0	134–380	X	X	X	X		X
Culterichthys erythropterus	Cyprinidae	Cery	696	3.8	27.6	28–285			X	X	X	X
Cyprinus carpio	Cyprinidae	Ccar	20	0.1	6.3	93–390				X	X	X
Distoechodon hupeinensis	Cyprinidae	Dhup	423	2.3	12.9	19–220			X	X	X	X
Elopichthys bambusa	Cyprinidae	Ebam	1	0.01	0.4	148						X
Hemiculter leucisculus	Cyprinidae	Hleu	2703	15.0	49.3	26–246	X	X	X	X	X	X
Hemibarbus maculatus	Cyprinidae	Hmac	7	0.04	1.8	159–280					X	
Hemiculter bleekeri	Cyprinidae	Hble	40	0.2	4.9	94–216			X	X	X	X
Hypophthalmichthys	Cyprinidae	Hmol	4	0.02	1.4	111–493	X	X		X		X
Megalobrama amblycephala	Cyprinidae	Mamb	1	0.01	0.4	148						X
Panacheilognathus imberbis	Cyprinidae	Pimb	460	2.5	17.8	16–85	X	X	X	X		X
Paracanthobrama guichenoti	Cyprinidae	Pgui	13	0.07	2.8	104–254					X	X
Pseudobrama simoni	Cyprinidae	Psim	65	0.4	1.4	69–177						X
Pseudorasbora parva	Cyprinidae	Ppar	1802	10.0	40.9	27–130	X	X	X	X	X	X
Rhodeus fangi	Cyprinidae	Rfan	148	0.8	7.7	27–49			X	X		
Rhodeus ocellatus	Cyprinidae	Roce	1994	11.1	25.2	13–90	X	X	X	X	X	X
Sarcocheilichthys nigripinnis	Cyprinidae	Snig	163	0.9	16.1	28–115			X	X	X	X
Squalidus argentatus	Cyprinidae	Sarg	261	1.5	17.5	40–140			X	X	X	X
Squalidus nitens	Cyprinidae	Snit	1032	5.7	31.5	35–105	X	X	X	X	X	X
Xenocypris davidi	Cyprinidae	Xdav	17	0.1	3.5	147–320	X	X			X	X
Macropodus chinensis	Belontiidae	Mchi	2	0.01	0.4	30–60				X		
Hypseleotris swinhonis	Eleotridae	Hswi	530	2.9	16. 8	22–79			X	X		X
Odontobutis obscurus	Eleotridae	Oobs	15	0.1	4.6	75–157	X	X	X	X		X
Rhinogobius giurinus	Gobiidae	Rgiu	1112	6.1	37.8	16–102	X	X	X	X	X	X
Hyporhamphus intermedius	Hemiramphidae	Hint	186	1.0	10.5	41–179	X	X	X	X	X	X
Mastacembelus sinensis	Mastacembelidae	Msin	22	0.1	4.6	125–245					X	
Neosalanx taihuensis	Salangidae	Acha	216	1.2	4.2	44–122				X	X	
Siniperca chuatsi	Serranidae	Schu	5	0.03	1.8	163–390	X	X		X	X	
Pelteobagrus fulvidraco	Siluridae	Pful	27	0.2	5.9	48–221			X	X		X
TOTAL			17791	100	100		16	16	23	30	27	32

Table 3. Fish assemblage composition in each lake, grouped by habitat and trophic guild. *N* is the number of species. BDT: Biandantang Lake; LUH: Luhu Lake; LZH: Liangzihu Lake; NSH: Niushanhu Lake; TXH: Tangxunhu Lake; WUH: Wuhu Lake.

Lake		Habitat Guild								Trophic Guild					
	Total	Pelagic		Pelagic-neritic		Benthopelagic			Demersal	Carnivorous		Herbivorouc		Benthivorous	
BDT	42			10	26	20	46	10	26		10	19	26	16	22
LZH	63			14	19	28	39	18	25	15	21	25	35	23	32
LUH	40			10	25	16	40	11	28		23	14	35	17	43
NSH	57			10	18	31	54	13	23	11	15	28	39	18	25
TXH	40			10	25	19	48	10	25	10	14	15	21	15	21
WUH	40				22	18	44	10	27	9	13	16	22	15	21
TOTAL	75	5	7	14	19	36	48	20	27	16	21	33	44	26	35

carnivorous fish species among all the lakes (Table 3). *Pseudobagrus nitidus* only appeared in Liangzihu Lake, while *Leiocassis longirostris*, as an aquaculture species, was only found in Niushanhu Lake. Herbivorous fish were the most frequent in all the lakes. A total of 33 herbivorous fish species were identified. Niushanhu Lake had the largest number of herbivorous fish species - up to 28 species - while only 15 were found in Wuhu Lake and Tangxunhu Lake. In total, 26 species of benthivorous fish species were found, the largest number of which were found in Liangzihu Lake (23 benthivorous species).

3.3 Spatial and temporal changes of fish diversity

3.3.1 Seasonal variability

The seasonal changes in fish diversity are shown (Fig. 3). Species richness (Fig. 3a) and diversity (inverse Simpson index, Fig. 3b) were significantly different among the four seasons, but the evenness (expressed by equitability of Simpson index, Fig. 3c) showed no significant difference among seasons (Kruskal-Wallis test). Subsequent multiple comparison tests showed that species richness was significantly higher in spring than in autumn, and that there were no significant differences between other seasons (Fig. 3a). Species diversity was also significantly higher in spring than in autumn and summer (Fig. 3b).

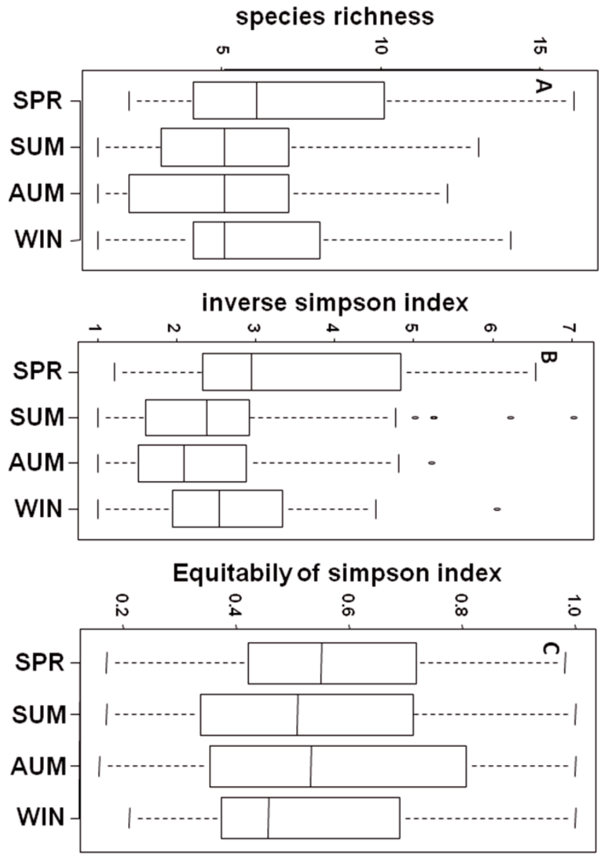

Fig. 3. Seasonal changes in the fish community. (A) Species richness comparisons among the four seasons; (B) Simpson's Inverse Index comparisons among the four seasons; (C) Equitability of Simpson index comparisons among the four seasons. SPR: spring; SUM: summer; AUM: autumn; WIN: winter.

3.3.2 Fish diversity comparisons among lakes

Fish species richness, diversity and evenness comparisons were found significantly different among the six lakes (Fig. 4). Biandantang Lake had the lowest value both in species richness and diversity (Fig. 4a, 4b). When examined with multiple comparison tests, species richness was found significantly lower in Biandantang Lake than in Luhu Lake and Liangzihu Lake; the difference of species richness was also significant between Liangzihu Lake and Niushanhu Lake (Fig. 4a). Fish diversity was higher in Liangzihu and Luhu lakes than in the other lakes. Biandantang Lake and Tangxunhu Lake had the lowest value of diversity, which was significantly different from Luhu Lake and Liangzihu Lake (Fig. 4b). Niushanhu Lake had the highest value of evenness, which was significantly higher than in Tangxunhu Lake (Fig. 4c).

3.3.3 Environment and fish community

The most important variables (Table 4, Fig. 5) describing the species composition among the study sites were chlorophyll *a* TP, and TN for axis 1 (*X*-axis); and transparency, water depth and area for axis 2 (*Y*-axis). In ecological terms, axis 1 showed gradients in species composition related to water chemistry variables Species composition varied along a gradient from small, eutrophic lakes (high TN and TP) to larger lakes with low TN, TP and chlorophyll *a*; axis 1 described mainly the relationships of spatial and temporal variation with the assemblage composition. The first two CCA axes had eigenvalues of 0.19 and 0.13, explaining 28% and 19% of variation in the relationship between species composition and environmental factors, respectively. The overall Monte Carlo randomization test showed a significant result for the sum of all eigenvalues (999 permutations, $p < 0.01$).

Based on the CCA scores, three clusters of fish were identified (Fig. 5). Cluster I (upper part of Fig. 5) was positively related to TN, TP, chlorophyll *a* and COD, dominated by *Neosalanx taihuensis, Hemibarbus maculatus, Cyprinus carpio, Culter dabry* and *Xenocypris davidi*; Cluster II (left part of Fig. 5) was mostly related to limnological characteristics parameters (e.g. lake surface area and water depth) dominated by *Squalidus nitens, Squalidus argentatus, Abbottina rivularis* and *Acheilognathus chankaensis*; Cluster III (low-right part of Fig. 5) was positively related to transparency, macrophyte coverage, negatively related to TN, TP, chlorophyll *a* and COD, and dominated by *Rhodeus fangi, Hypseleotris swinhonis* and *Rhinogobius giurinus*. Cluster III can be subdivided into two groups (groups a and b). Cluster III was made up of the most frequent species in the lakes, and concentrated in the middle-left part of Fig. 5; Cluster III was positively related to macrophyte coverage and transparency.

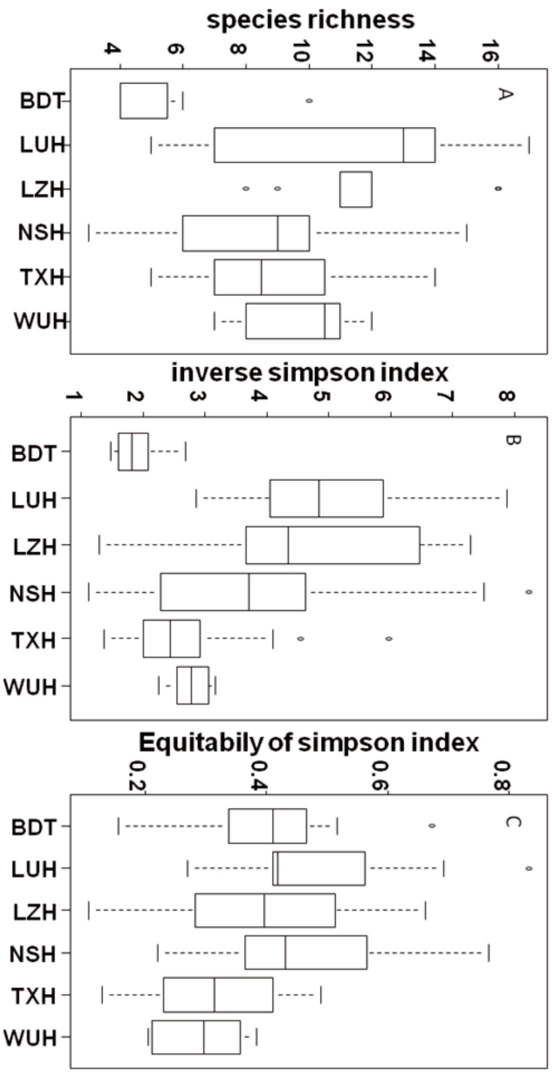

Fig. 4. Comparisons of fish community diversity among the six lakes. (A). Species richness comparisons among the six lakes; (B). Simpson's Inverse Index comparisons among the six lakes; (C). Equitability of Simpson index comparisons among the six lakes. BDT: Biandantang Lake; LUH: Luhu Lake; LZH: Liangzihu Lake; NSH: Niushanhu Lake; TXH: Tangxunhu Lake; WUH: Wuhan Lake.

4 Discussion and conclusion

As environments are modified by anthropogenic pressures, the species composition of fish communities has been found to change (Cowx 1994), i.e. decreasing biodiversity in lakes (Xie and Chen 1999; Fang et al. 2008), and increases in omnivorous fish as river system habitats deteriorate (Karr 1981; Roth et al. 1996; Schleiger 2000). Studies of fish communities that focus on the relationships between fish and their habitats are of particular importance because of their value in quantifying the effects of habitat supply limits, which by some means control the size and dynamics of fish communities (Barbour and Brown 1974; Amarasinghe and Welcomme 2001; Zhao et al. 2006). Among ecosystems that support a higher biodiversity, wetlands occupy only about 1% of the earth's surface, but provide a habitat for about 20% of the world's species (Dugan 1993).

Table 4. Summary of the canonical correspondence analysis on environmental parameters measured for all lakes. Monte Carlo test run for the sum of all eigenvalues was significant (999 permutations, $p < 0.01$).

	X-Axis	*Y*-Axis	r^2	*p*	
AREA	−0.624	−0.463	0.196	0.001	***
WT	0.341	−0.284	0.115	0.002	**
WD	0.428	0.502	0.183	0.001	***
TRA	−0.7	0.587	0.512	0.001	***
DIS	−0.186	0.208	0.101	0.007	**
TP	0.794	−0.079	0.505	0.001	***
TN	0.762	−0.238	0.519	0.001	***
COD	0.474	0.298	0.273	0.001	***
DO	0.261	−0.309	0.189	0.001	***
CHI	0.868	−0.261	0.471	0.001	***
CRM	−0.517	0.175	0.180	0.001	***

Statistical significance: $p < 0.001$ ***; $p < 0.01$ **; $p < 0.05$ *

4.1 Fish community structure and patterns in shallow lakes of the Yangtze basin

Fish species richness was relatively high in this area (varying from 40 to 64 species in our study lakes) compared with lakes in other regions (average of 35 species) in China (Zhao et al. 2006) and lakes in other temperate regions, i.e. 25 species in the temperate regions of Europe and Asia; 67 species in the temperate region of South America (Teixeira-de Mello et al. 2009; Tonn and Magnuson 1982; Persson et al. 1992; Fischer and Eckmann 1997), and the dominant fish in our studied lakes were herbivorous.

The dominance of herbivorous fish in the study lakes can be explained by equilibrium-based mechanisms. It is well known that equilibrium-based mechanisms are inseparably linked to niche structure in communities (Tonn and Magnuson 1982). In saturated communities, species richness is proposed to be a function of the resource availability, tolerable niche overlap and minimum niche size along a resource gradient (Menge and Sutherland 1976; Connell 1978). If the tolerable niche overlap and minimum niche size are relatively constant (Roughgarden 1974; Werner 1977), species richness should depend mainly on habitat complexity. Similarly, more productive habitats allow greater dietary specialization and should support more species (MacArthur 1972). Herbivorous fish species such as *Parabramis pekinensis*, *Xenocypris argentea* and *Ctenopharyngodon idellus* feed mainly on plants or plant debris, while other herbivorous fish such as *Aristichthys nobilis, Hemibarbus maculatus* and *Hemibarbus labeo* feed mainly on plankton. As a result, it does not matter whether macrophytes or phytoplankton are the main primary producer in these lakes, in both cases there is a rich food source for herbivorous fish and they could thus become the dominant fish species in all the investigated lakes.

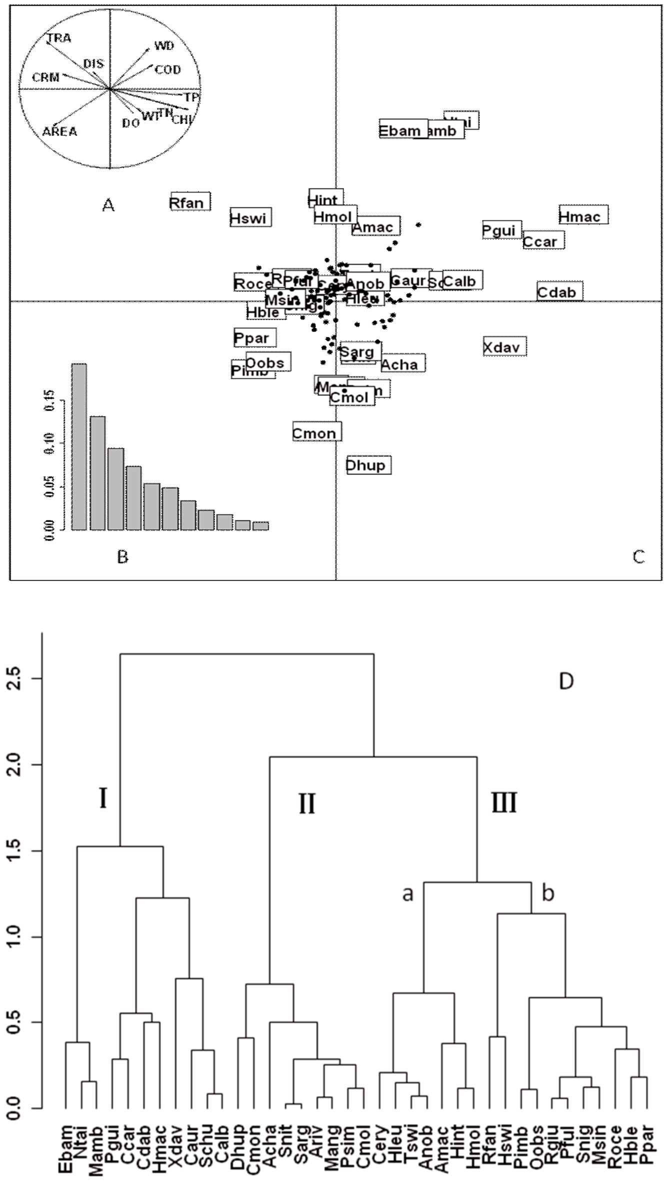

Fig. 5. Results of CCA analysis performed on the fish-environmental data matrices. (A) Canonical weights of each environmental variable. (B) Barplot showing eigenvalues in the CCA The first two CCA axes explain 28% and 19% of variance, respectively. (C) Canonical weights of each species (black dots are the sampling stations). (D) Clusters of fish based on CCA scores. For fish species and environmental variable identifications, see Table 2 and Material and Methods.

4.2 Environment and fish community

In this research, we found fish community structures and diversity were co-affected by limnological characteristics (lake area, water depth), macrophyte coverage and some physico-chemical parameters. Different fish species were related to different environmental parameters.

Grouped by CCA scores, three clusters of fish were identified as being highly related to different environmental variables. The first of these clusters was dominated by *Hemibarbus maculatus, Carassius auratus* and *Culter dabry*. This group of fish was positively related to TN, TP and chlorophyll *a*. Most of these species are tolerant of environmental changes, presenting high growth rates in the presence of high levels of algae or in eutrophic lakes. As these tolerant species have a high resistance to environmental stress, it is assumed that the raising of their population density could be used as an indicator to reflect any worsening of environmental conditions (Karr 1981; Fausch et al. 1984; Roth et al. 1996; Schleiger 2000).

The second group of fish was dominated by *Squalidus nitens, Squalidus argentatus, Abbottina rivularis* and *Acheilognathus chankaensis,* and was related to limnological characteristics parameters (i.e. lake area and water depth) High density (CPUE) of these fish would be found in shallow habitats and large lakes. Furthermore, most of the species in this cluster were common and widespread in the studied lakes.

The third group of fish species seems to be sensitive to environmental changes (e.g. *Rhodeus fangi*). They were negatively related to TN, TP and chlorophyll *a*, and positively related to transparency and macrophyte coverage. The cluster can be subdivided into two groups (Fig. 5). One group is made up of the most frequent species in the lakes, concentrated in the central part of Figure 5, such as *Toxabramis swinhonis* and *Hemiculter leucisculus.* This group is less sensitive to the environment compared with the other group of fish in this cluster. The second group brings together sensitive species from the lakes. Most of these species are only found in clear waters with high macrophyte coverage. This group of fish, dominated by *Rhodeus fangi, Hypseleotris* and *Odontobutis obscurus*, can probably be used as indicators in these lakes.

All the lakes are exposed to the same species pool and are relatively close to each other (Fig. 1), but the patterns of fish community were found to be different among them. Fish species richness, diversity and evenness were relatively higher in vegetated lakes (i.e. Liangzihu Lake, Luhu Lake and Niushanhu Lake) than in unvegetated lakes (i.e. Biandantang Lake and Tangxunhu Lake). Based on our investigations, the environments of the lakes were shown to be significantly different. The relationships between the environment and fish communities are valuable for lake management. Several decades ago, all of the shallow lakes in the Yangtze basins were highly covered by macrophytes (Xie and Chen 1999; Fang et al. 2008). However, due to water pollution and intensive fishery activities, some lakes are now found to be completely devoid of macrophytes (Xie and Chen 1999; Fang et al. 2008) We have shown that as the coverage of macrophytes decreases, the water conditions deteriorate (i.e. increasing TN, TP and COD, decreasing transparency).

Some previous studies have shown a significant effect of macrophytes on fish communities in Yangtze basin shallow lakes. They found that this type of habitat along with structural complexity of macrophytes harboured high fish diversity (Xie et al. 2002; Ye et al. 2006). In this study, the fish community was also linked to macrophytes. Our study confirmed the following conclusions: 1) the water quality was better (i.e. high transparency, low TN, TP and chlorophyll *a*) in vegetated lakes than in unvegetated lakes; 2) vegetated lakes had higher fish diversity than unvegetated lakes; 3) relative fish abundance (CPUE) was significantly related to the macrophyte coverage.

4.3 Management suggestions

We suggest that a good method for restoring water quality would be to replant macrophytes in these lakes. The choice of macrophyte species used for restoration should be based on their biological characteristics. Species with a long life-span (e.g. *Vallisneria natans* (Lour.) Hara and *Hydrilla verticillata*) would be most suitable, while species that senesce and die at the end of the summer, like *Potamogeton crispus* Linn. (which widely distributed in Luhu Lake) should be introduced into these lakes with caution.

It is worth mentioning that two non-native species (*Cirrhinus molitorella* and *Leiocassis longirostris*) were found during our samplings. *Cirrhinus molitorella* (only found in Luhu Lake) had probably escaped from nearby fish ponds and does not pose a serious problem as an invasive species at present because it is a sub-tropical species that requires high water temperatures to survive in winter. However, the ecological risk of *Leiocassis longirostris* (escaped from cages in Niushanhu Lake) is under estimated. We strongly suggest that more caution should be taken with the ecological security when introducing an alien species to lakes and nearby water bodies.

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