Aquat. Living Resour. 19, 349–359 (2006)

DOI: 10.1051/alr:2007005
www.edpsciences.org/alr

Aquatic Living Resources

Community structure of small fishes in a shallow macrophytic lake (Niushan Lake) along the middle reach of the Yangtze River, China

Shaowen Ye[1,2], Zhongjie Li[1,a], Sithan Lek-Ang[3], Guangpeng Feng[4], Sovan Lek[3] and Wenxuan Cao[1]

[1] State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, The Chinese Academy of Sciences, 430072 Wuhan, China
[2] Graduate School of the Chinese Academy of Sciences, 100039 Beijing, China
[3] LADYBIO-UMR 5172, CNRS-University Paul Sabatier, 118 Route de Narbonne, 31062 Toulouse Cedex, France
[4] East China Sea Fisheries Research Institute, The Chinese Academy of Fishery Sciences, 200090 Shanghai, China

Received 22 March 2006; Accepted 2 October 2006

Abstract – This study describes the current status of the small fish community in Niushan Lake in China, and examines the spatial and seasonal variations of the community in relation to key environmental factors. Based on macrophyte cover conditions, the lake was divided into three major habitat types: (1) *Potamogeton maackianus* habitat, (2) *Potamogeton maackianus* and *Myriophyllum spicatum* habitat, and (3) uncovered or less-covered habitat. Fish were sampled quantitatively in the three habitat types by block nets seasonally from September 2002 to August 2003. A total of 10 469 individuals from 27 fish species were caught, among which 20 species were considered as small fishes. *Rhodeus ocellatus*, *Paracheilognathus imberbis*, *Pseudorasbora parva*, *Micropercops swinhonis* and *Cultrichthys erythropterus* were recognized as dominant small fishes according to their abundance and occurrence. It was noted that (1) small fishes predominated the total number of fish species in the lake, which reflected to some degree the size diminution phenomenon of fish resources; (2) many small fishes had plant detritus as their food item, which was consistent with the abundance of macrophyte detritus in the lake and implied the importance of detritus in supporting small fish secondary production. Canonical correspondence analysis suggested that the spatial distributions of most small fishes were associated with complex macrophyte cover conditions. Macrophyte biomass was positively correlated with species richness, diversity index and the catch per unit of effort (CPUE) of the fish community. Water depth had no significant effects on species diversity and distribution of the small fishes. Correspondence analysis revealed a higher occurrence of the small fishes and higher abundance of individuals in summer and autumn. Seasonal length-frequency distributions of several species indicated that more larval and juvenile individuals appeared in spring and summer. This study provides some baseline information which will be essential to long-term monitoring of small fish communities in the Yangtze lakes.

Key words: Small fishes / Freshwater community structure / Habitat utilization / Multivariate statistics / Lake fishery management / Yangtze lakes

Résumé – Structure de la communauté des poissons de petites tailles du lac Niushan connecté au fleuve Yangtze (Chine). Ce travail décrit l'état actuel de la communauté des poissons du lac Niushan (Chine) en examinant la distribution spatiale et les variations saisonnières de la communauté en relation avec les principaux facteurs environnementaux du milieu. Les différentes espèces de macrophytes permettent de diviser les habitats du lac en 3 types : (1) habitat à *Potamogeton maackianus*, (2) habitat à *Potamogeton maackianus* et *Myriophyllum spicatum*, et (3) habitat sans ou peu de macrophyte. Les échantillonnages des poissons des trois types habitats ont été effectués à différentes saisons, de septembre 2002 à août 2003. Au total, 10 469 individus appartenant à 27 espèces de poissons ont été pêchés ; 20 espèces sont considérées comme espèces de petites tailles. Compte-tenu de l'abondance et de l'occurrence des espèces, les espèces dominantes sont : *Rhodeus ocellatus*, *Paracheilognathus imberbis*, *Pseudorasbora parva*, *Micropercops swinhonis* et *Cultrichthys erythropterus*. Il est à noter que (1) les petites espèces prédominent quantitativement en terme de nombre d'espèces péchées, reflétant un certain degré de diminution des tailles des ressources en poisson ; (2) de nombreuses espèces de poissons se nourrissent de détritus de plantes, impliquant une importance de ces détritus végétaux pour la production secondaire au niveau des petites espèces de poissons. L'analyse canonique des correspondances a révélé que la distribution de la majorité des petits poissons est liée à l'abondance des macrophytes.

[a] Corresponding author: zhongjie@ihb.ac.cn

La biomasse des macrophytes est corrélée positivement à la richesse spécifique, à l'indice de diversité et à la prise par unité d'effort CPUE de la communauté des poissons. La profondeur du lac n'a pas d'effet significatif sur la diversité et la distribution des petites espèces de poissons. L'analyse des correspondances a révélé des occurrences plus grandes pour les petites espèces et des abondances sont élevées en été et en automne. Les variations saisonnières des distributions en fréquence de taille des principales espèces montrent que les larves et les juvéniles sont apparus au printemps et en été. Cette étude apporte des informations essentielles pour les aménagements de la communauté des petites espèces de poissons des lacs de la partie médiane du fleuve Yantze.

1 Introduction

There are numerous freshwater lakes distributed along the middle and lower reaches of the Yangtze (Changjiang) River, which cumulatively represent about 30% of the total lake area in China (Liu and He 1992). These temperate Yangtze lakes were formed by flooding of the river in the Late Tertiary, and historically were interconnected with the main river or its branches forming a unique potamo-lacustrine ecosystem complex (Xie and Chen 1996). These lakes are generally shallow (without thermal stratification), and usually have high productivity, abundant vegetation cover and a diverse community of freshwater fishes (40–70 species or even more in some lakes) (Liu 1984; Xie and Chen 1996). Among these freshwater fishes, only the species with high economic value have received research attention with extensive ecological studies taking place in the Yangtze region from the late 1950's (e.g. Jiang 1959; Du 1962; Wu et al. 1963; Anonymous 1976b; Zhu et al. 1976; Xiao and Wang 1988; Liu and He 1992; Zhang et al. 1998a; Tan et al. 2002). In contrast, the small fishes (or forage fishes) which have short life histories and small maximum sizes have received much less attention due to their relatively low commercial importance in the lake fisheries. Consequently, the existing studies concerning the small fishes in the Yangtze lakes are centered chiefly on taxonomy (Zhu 1995) and reproduction, feeding habit, age and growth of a few species (Chen 1959; Hao 1960; Shao and Yi 1991; Yu 1991; Zhang et al. 1998b,c,d; Bian 1999; Xie et al. 2000c). Very few studies have so far been conducted at the community level. In particular, there is little information on the community structure and its relationship to habitat conditions (Xie et al. 2000b; 2001).

In recent years, there has been a shift in the stocking in the Yangtze lakes from common carps to piscivorous fishes (Xie et al. 2000a; Li and Cui 2005), and a trend away from traditional management of fisheries resources towards ecosystem-based management of inland waters (FAO 2003). Consequently, more research is necessary on the composition and abundance of the small fishes in the lakes, and how the community structures vary over space and time, which also has long been a fundamental interest of aquatic ecologists (e.g. Werner et al. 1977; Tonn and Magnuson 1982; Pierce et al. 1994; Rosenzweig 1995; Rotherham and West 2002).

In this study, we describe the community structure of small fishes in Niushan Lake caught using block nets seasonally between 2002 and 2003. Our main purposes were to: (1) provide a whole-lake estimate for species composition, abundance and occurrence of small fishes in shallow vegetated habitats, (2) describe spatial and seasonal distributions of the small fishes in the lake, and potential differences in spatial and trophic resource utilization, and (3) provide baseline information prerequisite to long-term monitoring of small fish communities in the Yangtze lakes.

2 Materials and methods

2.1 Study area and habitat characteristics

Niushan Lake (30° 16-22′ N, 114° 27-38′ E), is a 38 km^2 shallow lake located on the south bank of the middle reach of the Yangtze River, within Hubei Province, Central China (Fig. 1). This lake was originally one part of a larger lake, Liangzi Lake, which is connected with the Yangtze River by a channel. Niushan Lake has been separated from Liangzi Lake by a dyke since 1978. The dyke is kept closed in most time of each year (usually from March to October), to prevent the flooding of the Yangtze River into the lake. Morphometric parameters and physicochemical parameters of the lake are given in Table 1. Mean water depth ranges between 2.0 m and 3.5 m, with a maximum depth of 5.0 m (Guan et al. 2005). Summer water temperatures peak in July or August at around 35–37 °C with no thermal stratification, and winter water temperatures dip to 3–5 °C in December or January with no freezing. Most of the shoreline is surrounded by villages and land use in the drainage basin is primarily agricultural.

Niushan Lake was heavily covered with submerged aquatic macrophytes. Before fish sampling, we investigated the composition and distribution of macrophytes in July 2002. The results showed that: (1) *Potamogeton maackianus* was the most dominant macrophyte in the lake, covering about 75% of the lake sediment surface, (2) *Myriophyllum spicatum* was the secondly most dominant macrophyte, covering about 55% of the lake sediment surface, and (3) other species such as *Vallisneria spiralis*, *Najas marina*, *Ceratophyllum demersum* and *Potamogeton malainus* occurred only occasionally and their individual coverage was all less than 5%. Based on the cover condition of the dominant macrophytes, we divided the lake into three major habitat types (coded as H1, H2 and H3 respectively) whose descriptive characteristics and distribution are shown in Table 2 and Fig. 1.

2.2 Fish sampling

Fish were sampled in the three habitat types seasonally from September 2002 to August 2003 using block nets. Autumn sampling was carried out during September and October 2002, winter sampling during December 2002 and January 2003, spring sampling in April 2003 and summer sampling during July and August 2003. Two sampling sites were chosen under each of the three habitat type (H1, H2 and H3) in each

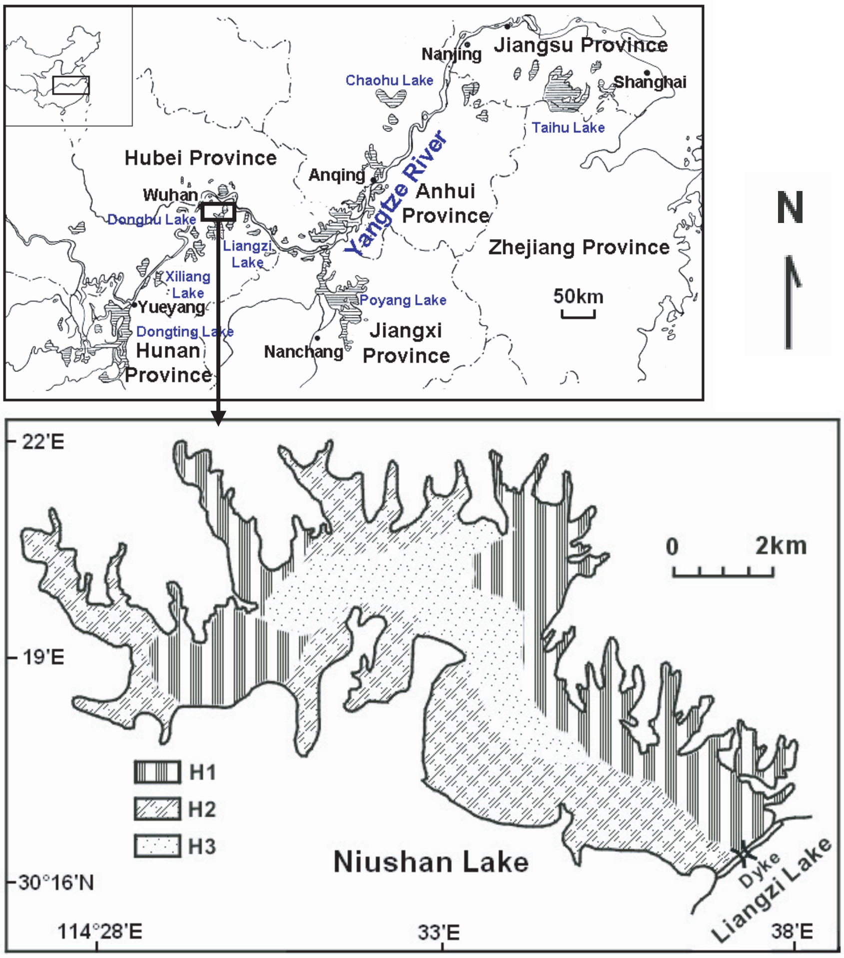

Fig. 1. Geographic location of Niushan Lake and distribution of the three major habitat types H1, H2 and H3 in the lake. See Table 2 for H1, H2 and H3.

Table 1. Morphometric and physicochemical parameters of Niushan lake in April 1999. The physicochemical parameters are the mean values (±SE) computed from 7 measurements across the lake. All data are from Guan et al. (2005).

Area (km^2)	38.0	pH	7.93 ± 0.05
Length (km)	15.8	Conductivity ($\mu S\, cm^{-1}$)	233.6 ± 7.9
Maximum width (km)	3.0	Hardness (German G.D.)	4.93 ± 0.08
Shoreline length (km)	104.5	Alkalinity ($mg\, L^{-1}$)	58.99 ± 0.60
Shoreline development	4.8	Ca^{2+} ($mg\, L^{-1}$)	24.62 ± 0.20
Water temperature (°C)	19.0	Mg^{2+} ($mg\, L^{-1}$)	6.43 ± 0.40
Water depth (m)	2.5 ± 0.1	TN-N ($mg\, L^{-1}$)	0.698 ± 0.020
Secchi depth (cm)	191 ± 17	TP-P ($mg\, L^{-1}$)	0.026 ± 0.001

Table 2. Descriptive characteristics of the three major habitat types in Niushan Lake.

Habitat type	Habitat code	Descriptive characteristics
Potamogeton maackianus habitat	H1	*P. maackianus* was the single dominant submerged macrophyte species. This species grew densely under the water and formed a thick meadow of about 1.0–2.0 m.
P. maackianus and *Myriophyllum spicatum* habitat	H2	The two dominant submerged macrophytes *P. maackianus* and *M. spicatum* grew together. *P. maackianus* grew thickly on the sediment. The long branching stems and feathery leaves of *M. spicatum* created a screen up to the water surface.
Uncovered or less-covered habitat	H3	No submerged macrophyte existed or only *M. spicatum* grew sparsely.

season, for a total of 24 samples on 24 sampling sites throughout the study.

The block nets consisted of a wall of enclosure net (60 m length, 15 mm stretched mesh size) with stones on the bottom side and with floats on the top side. At each sampling site, one block net was deployed at dusk to enclose a defined water area shaped approximately like an equilateral hexagon. The six angles were fixed with bamboo poles, leaving two 3 m openings on opposite sides of the enclosure. Twenty-four hours later, the two openings were simultaneously closed. Attention was paid to minimize disturbance to the enclosed areas. Two hoop nets connected with the block net were then used to collect the enclosed fishes during the next five days. No habitat modification, such as disturbance to macrophyte cover, occurred during the sampling.

2.3 Data collection and treatment

The collected fish were identified, counted, and measured (total length to 1 mm). Submerged macrophyte composition, macrophyte biomass, and water depth were also recorded at each sampling site.

We first constructed a rank-abundance plot to display species abundance data (Magurran 2004), and grouped all the fish species according to their relative abundance (% of total catch) and occurrence frequency. We then classified the species into different trophic guilds based on their main food items (Anonymous 1976a; Zhang 2005), and calculated the proportions of these trophic guilds in total species number and total catch respectively.

Second, we conducted repeated-measures analysis of variance (RM ANOVA) followed by Duncan's multiple comparison test to look for significant differences among the habitat types in the following community indexes: (1) species richness, (2) Shannon-Weiner diversity index, and (3) total CPUE (total catch per sample) of all species. Correlation analysis was run and Pearson *r*-values were calculated to investigate how these community indexes were correlated with macrophyte biomass and water depth.

Third, we used canonical correspondence analysis (CCA) (Ter Braak 1986) to associate the spatial distribution of fishes with habitat conditions (first with the three habitat types, and then with macrophyte biomass and water depth). CCA is a direct gradient analysis that simultaneously relates two multivariate data sets and is commonly used to quantify the relationship between species and environmental variables. The advantages of CCA for ecological studies of communities were reviewed by Palmer (1993). On the other hand, we employed correspondence analysis (CA) to visualize seasonal distribution of the fish community. CA is a type of ordination that calculates site and species "scores" based on reciprocal averaging. It provides a method for representing data in a euclidean space so that the results can be visually examined for structure (Manly 1994).

Statistical analyses were carried out under the version 2.0.1 of R (Ihaka and Gentleman 1996). For the CCA and the CA, the values of fish abundance, macrophyte biomass and depth at each sampling site were log $(x + 1)$ transformed to stabilize variances.

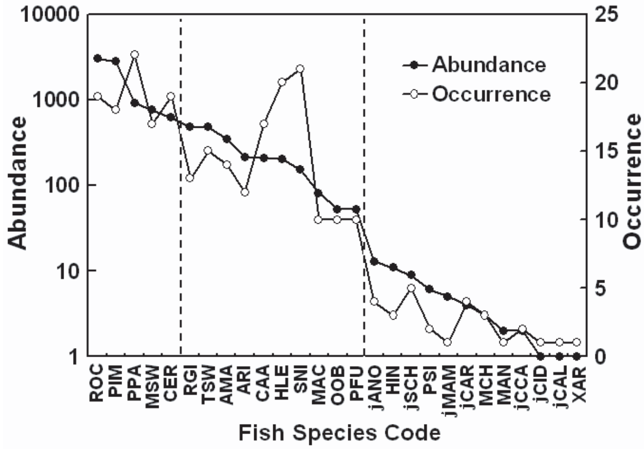

Fig. 2. Rank-abundance (total number of individuals sampled) and occurrence (number of the samples in which the species was present) of the 27 fish species caught in Niushan Lake throughout the study. Species abundance represented in log scale to avoid undue influence of the most abundant species on the figure. See Table 3 for species codes.

3 Results

3.1 Abundance and occurrence

A total of 10 469 individuals from 27 fish species (listed in Table 3) was caught throughout the study. Species rank-abundance and occurrence diagram (Fig. 2) displayed that the 27 species were classified into three groups, according to their relative abundance and occurrence frequency (Table 3):

Dominant species included *Rhodeus ocellatus, Paracheilognathus imberbis, Pseudorasbora parva*, *Micropercops swinhonis*, and *Cultrichthys erythropterus*. These five species were characterized by high relative abundance (all above 5% of the total 10 469 individuals) and high occurrence frequency (from 63.0% to 70.4% of the 24 samples). They amounted to 77.7% of the total catch of the sampled individuals.

Frequent species included *Rhinogobius giurinus, Toxabramis swinhonis, Acheilognathus macropterus*, *Abbottina rivularis, Carassius auratus auratus*, *Hemiculter leucisculus*, *Sarcocheilichthys nigripinnis*, *Macrognathus aculeatus*, *Odontobutis obscura*, and *Pelteobagrus fulvidraco.* These ten species displayed moderate relative abundance (between 0.5% and 4.6%) but a wide range of occurrence frequency, varying from 37.0% to 77.8%. They amounted to 21.7% of the total catch of individuals.

Rare species included *Aristichthys nobilis*, *Hyporhamphus intermedius*, *Siniperca chuatsi*, *Pseudobrama simoni*, *Megalobrama amblycephala, Channa argus*, *Macropodus chinenis*, *Misgurnus anguilliccaudatus*, *Cyprinus carpio*, *Ctenopharyngodon idellus, Culter alburnus*, and *Xenocypris argentea*, with a relative abundance below 0.15% of the total 10 469 individuals and an occurrence frequency below 20%. These 12 species contributed only 0.6% of the total catch of individuals.

Table 3. List of the 27 fish species caught in Niushan Lake from September 2002 to August 2003, with their common name, relative abundance, occurrence frequency, mean TL, TL range and code used in the analyses. The species in bold type were dominant small fishes. *: Large-bodied species whose juveniles were only caught.

Family	Scientific name	Common name	Code	Relative abundance (%)	Occurrence frequency (%)	Mean TL ±SE (mm)	TL range (mm)
Cyprinidae	1. *Ctenopharyngodon idellus**	Grass carp	jCID	0.01	4.2	226	–
	2. *Toxabramis swinhonis*	–	TSW	4.54	62.5	81 ± 0.8	32-116
	3. *Hemiculter leucisculus*	Sharpbelly	HLE	1.97	83.3	98 ± 2.2	26-197
	4. *Cultrichthys erythropterus*	**Redfin culter**	**CER**	**5.88**	**79.2**	**130 ± 1.7**	**39–239**
	5. *Culter alburnus**	Topmouth culter	jCAL	0.01	4.2	225	–
	6. *Megalobrama amblycephala **	Wuchang bream	jMAM	0.05	4.2	138 ± 6.9	122–159
	7. *Xenocypris argentea*	Freshwater yellow tail	XAR	0.01	4.2	102	–
	8. *Pseudobrama simoni*	–	PSI	0.06	8.3	64 ± 2.1	56–71
	9. *Aristichthys nobilis**	Bighead carp	jANO	0.12	16.7	139 ± 15.7	73–264
	10. *Pseudorasbora parva*	**Stone moroko**	**PPA**	**8.80**	**91.7**	**54 ± 0.5**	**24–118**
	11. *Sarcocheilichthys nigripinnis*	Blackfin minnow	SNI	1.44	87.5	79 ± 1.1	41–118
	12. *Abbottina rivularis*	Chinese false gudgeon	ARI	2.06	50.0	61 ± 0.7	33–103
	13. *Acheilognathus macropterus*	Bitterling	AMA	3.34	58.3	56 ± 0.8	41–78
	14. *Paracheilognathus imberbis*	**Bitterling**	**PIM**	**26.70**	**75.0**	**45 ± 0.6**	**19–70**
	15. *Rhodeus ocellatus*	**Bitterling**	**ROC**	**29.11**	**79.2**	**38 ± 0.4**	**24–52**
	16. *Cyprinus carpio**	Common carp	jCCA	0.02	8.3	159 ± 6.9	138–179
	17. *Carassius auratus auratus*	Crucian carp	CAA	2.02	70.8	69 ± 7.8	41–166
Cobitidae	18. *Misgurnus anguillicaudatus*	Oriental weatherfish	MAN	0.02	4.2	66 ± 4.5	61–70
Bagridae	19. *Pelteobagrus fulvidraco*	Yellow catfish	PFU	0.50	41.7	95 ± 3.4	56–204
Hemiramphidae	20. *Hyporhamphus intermedius*	Halfbeak	HIN	0.11	12.5	118 ± 3.0	105–134
Serranidae	21. *Siniperca chuatsi**	Mandarin fish	jSCH	0.09	20.8	88 ± 10.9	46–170
Eleotiidae	22. *Odontobutis obscura*	Dark sleeper	OOB	0.51	41.7	143 ± 4.8	66–209
	23. *Micropercops swinhonis*	**Swinhon's sleeper**	**MSW**	**7.25**	**70.8**	**38 ± 0.5**	**21–52**
Gobiidae	24. *Rhinogobius giurinus*	–	RGI	4.55	54.2	35 ± 0.9	19–56
Belontiidae	25. *Macropodus chinenis*	Roundtail paradise fish	MCH	0.03	12.5	48 ± 6.2	36–57
Channidae	26. *Channa argus**	Chinese snakehead	jCAR	0.04	16.7	133 ± 11.2	94–176
Mastacembelidae	27. *Macrognathus aculeatus*	Spiny eel	MAC	0.77	41.7	163 ± 2.4	105–218

3.2 Population composition

The 27 fish species belonged to 10 families, of which Cyprinidae was the predominant family (17 species, 63.0% of the total species number; Table 3). Among the 27 species, 20 were considered as small fishes because their first maturity ages are less than two years (Anonymous 1976a) and maximum sizes are small (<240 mm TL in this study; Table 3). Only juveniles of the seven large-bodied fish species *C. idellus*, *C. alburnus*, *M. amblycephala*, *A. nobilis*, *C. carpio*, *S. chuatsi*, and *C. argus* were caught in the study.

The 27 species ranged from 19 to 239 mm TL (Table 3). Sixteen species (59.3% of the total species number) were below 100 mm, mean TL, nine species (33.3%) between 100 and 165 mm, and the other two species (7.4%) above 200 mm. In fact, the two species with mean TL above 200 mm both belong to large-bodied fishes and only one juvenile individual of them was caught in the study.

Based on main food items of the 27 fish species, they were classified into five trophic guilds: detritivore, omnivore, carnivore, planktivore, and herbivore (Table 4). Figure 3 showed that the trophic guild with the highest proportion in total species number was the omnivore (37.0%, 10 species), followed by the carnivore (29.6%, 8 species) and the detritivore (22.3%, 6 species); the trophic guild with the highest proportion in total catch was the detritivore (61.2%) owing to the abundant detritivorous bitterlings (*R. ocellatus*, *P. imberbis* and *A. macropterus*), followed by the omnivore (19.8%) and the carnivore (18.8%). Detritivorous or partially detritivorous small fishes (e.g. some omnivorous small fishes also have plant detritus as their main food item; Table 4) seemed to have a high proportion in both total species number and total catch in the current Niushan Lake.

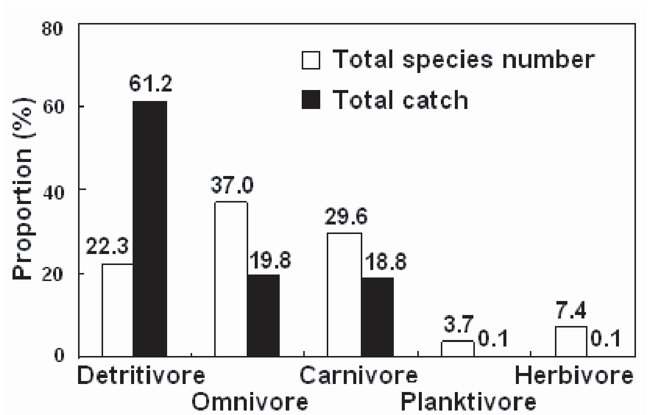

Fig. 3. Proportions of the five trophic fish guilds in total species number and total catch.

Table 4. Main food items and trophic guilds of the 27 fish species. Species were listed in alphabetical order. The species in bold type were dominant small fishes. Diet data are from Anonymous (1976a) and Zhang (2005).

Species	Code	Main food items	Trophic guild
Abbottina rivularis	ARI	Zoobenthos, Micro-crustaceans, Insect larvae, Plant detritus	Omnivore
Acheilognathus macropterus	AMA	Plant detritus, Algae	Detritivore
Aristichthys nobilis	jANO	Zooplankton, Algae	Planktivore
Carassius auratus auratus	CAA	Plant detritus, Micro-crustaceans	Detritivore
Channa argus	jCAR	Fishes	Carnivore
Ctenopharyngodon idellus	jCID	Aquatic plants	Herbivore
Culter alburnus	jCAL	Fishes	Carnivore
Cultrichthys erythropterus	**CER**	**Small fishes, Shrimps**	**Carnivore**
Cyprinus carpio	jCCA	Zoobenthos, Insects, Plant detritus	Omnivore
Hemiculter leucisculus	HLE	Insect larvae, Micro-crustaceans, Algae, Plant detritus	Omnivore
Hyporhamphus intermedius	HIN	Insect larvae, Micro-crustaceans, Alage	Omnivore
Macrognathus aculeatus	MAC	Insect larvae, Plant detritus, Shrimps	Omnivore
Macropodus chinenis	MCH	Insect larvae, Algae,	Omnivore
Megalobrama amblycephala	jMAM	Aquatic plants	Herbivore
Micropercops swinhonis	**MSW**	**Insect larvae, Micro-crustaceans, Small fishes**	**Carnivore**
Misgurnus anguillicaudatus	MAN	Insect larvae, Micro-crustaceans, Plant detritus, Algae	Omnivore
Odontobutis obscura	OOB	Small fishes, Shrimps	Carnivore
Paracheilognathus imberbis	**PIM**	**Plant detritus, Algae**	**Detritivore**
Pelteobagrus fulvidraco	PFU	Small fishes, Zoobenthos, Shrimps	Carnivore
Pseudobrama simoni	PSI	Plant detritus	Detritivore
Pseudorasbora parva	**PPA**	**Zooplankton, Micro-crustaceans, Algae, Plant detritus**	**Omnivore**
Rhinogobius giurinus	RGI	Insect larvae, Micro-crustaceans, Small fishes	Carnivore
Rhodeus ocellatus	**ROC**	**Plant detritus, Algae**	**Detritivore**
Sarcocheilichthys nigripinnis	SNI	Insect larvae, Plant detritus, Shrimps	Omnivore
Siniperca chuatsi	jSCH	Fishes	Carnivore
Toxabramis swinhonis	TSW	Insect larvae, Micro-crustaceans, Algae, Plant detritus	Omnivore
Xenocypris argentea	XAR	Plant detritus	Detritivore

Table 5. Mean values (±SE) of species richness, Shannon-Weiner diversity index and total CPUE of all species in the three habitat type (H1, H2 and H3), with the *p*-values of analysis of variance and the results of Duncan's multiple comparison tests. Means with different letters are significantly different from each other at the 0.05 level. Pearson's correlation coefficients (*r*) and corresponding *p*-values between species richness, diversity index, total CPUE and macrophyte biomass or water depth were also given.

	Habitat				Macrophyte biomass		Water depth	
	H1	H2	H3	*p*	Pearson's *r*	*p*	Pearson's *r*	*p*
Species richness	^{a}12.13 ±1.17	^{a}13.25 ±0.80	^{b}7.75 ±1.01	0.002	0.673	<0.001	−0.265	0.211
Diversity index	^{a}2.18 ±0.16	^{a}2.37 ±0.21	^{b}1.74 ±0.10	0.026	0.370	0.083	0.219	0.315
Total CPUE	^{a}433.5 ±68.9	^{b}746.8 ±104.6	^{c}128.4 ±31.0	0.005	0.435	0.036	−0.177	0.140

3.3 Spatial variation

Species richness, Shannon-Weiner diversity index, and total CPUE of all species varied significantly among the three habitat types (H1, H2 and H3) (Table 5). They were always higher in H1 and H2 than in H3 where no macrophyte existed or only a few grew sparsely. H1 and H2 were both macrophytic habitats, dominated by different macrophyte species (Table 2). Species richness and diversity index were similar between H1 and H2, while total CPUE was higher in H2 than in H1.

The correlation analysis results (Table 5) suggested that species richness and total CPUE were positively correlated with macrophyte biomass significantly; diversity index was also positively correlated with macrophyte biomass but not significantly. Despite water depth was not significantly correlated with species richness, diversity index and total CPUE, it played somewhat negatively effects on species richness and total CPUE, and somewhat positively effects on diversity index.

The 12 rare fish species were not included in the CCA to avoid unduly influencing the analysis (Ter Braak 1986; Pennington 1996). All the 12 species were caught with very low abundance (≤13 individuals), and the removal of them had no distinct influence on the associations between the rest 15 small fishes and habitat conditions. The CCA on the 15 species to the three habitat types was statistically significant (p = 0.011) and the two axes accounted for 64.8% and 35.2% of the variability in the fish-habitat relationship. The CCA on the 15 species to macrophyte biomass and water depth was also statistically significant (p = 0.024) and the two axes accounted

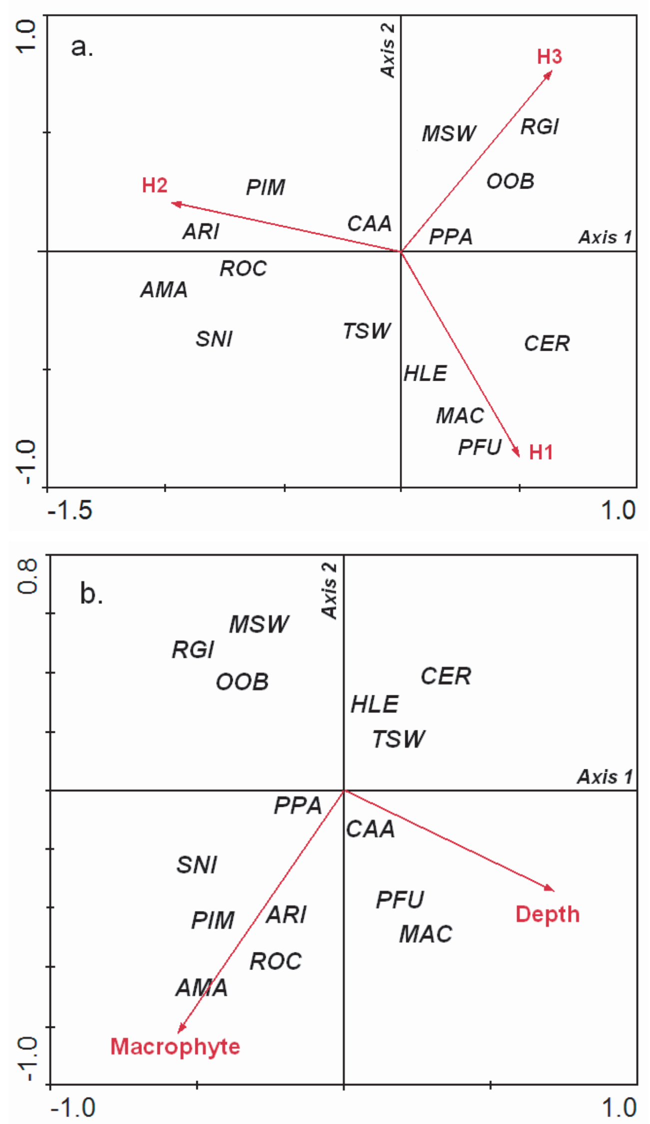

Fig. 4. F1×F2 plane of canonical correspondence analysis (CCA) showing fish species distributions in relation to habitat conditions in Niushan Lake. a) CCA on the 15 small fishes to the three habitat types H1, H2 and H3; b) CCA on the 15 small fishes to macrophyte biomass and water depth. AMA: *A. macropterus*, ARI: *A. rivularis*, CAA: *C. auratus auratus*, CER: *C. erythropterus*, HLE: *H. leucisculus*, MAC: *M. aculeatus*, MSW: *M. swinhonis*, OOB: *O. obscura*, PFU: *P. fulvidraco*, PIM: *P. imberbis*, PPA: *P. parva*, RGI: *R. giurinus*, ROC: *R. ocellatus*, SNI: *S. nigripinnis*, TSW: *T. swinhonis*.

for 59.3% and 40.7% of the variability in the fish-habitat relationship.

The CCA results (Figs. 4a,b) can be used to identify the associations between the 15 small fishes with habitat conditions: (1) *C. erythropterus*, *H. leucisculus*, *T. swinhonis*, *M. aculeatus* and *P. fulvidraco* preferred the *P. maackianus* habitat (H1). The former three species were associated with low macrophyte biomass and little influence of water depth, while the latter two species with high macrophyte biomass and deep water. (2) *A. macropterus*, *P. Imberbis*, *R. ocellatus*, *A. Rivularis* and *S. nigripinnis* preferred the densely-vegetated habitat of coexisting

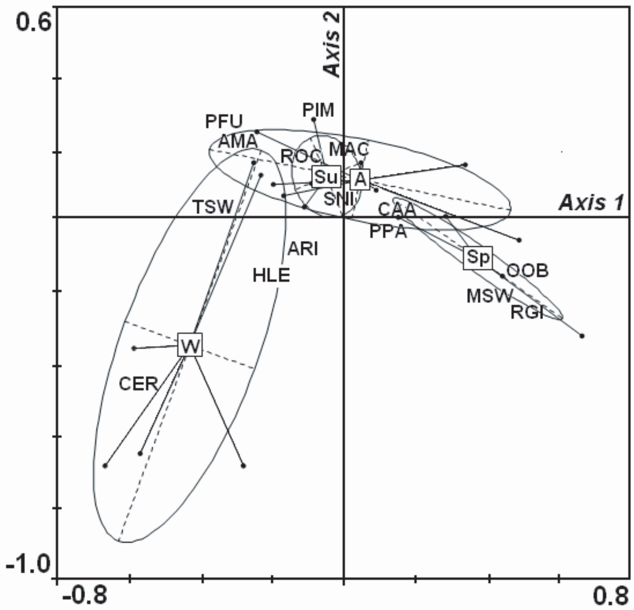

Fig. 5. F1 × F2 plane of correspondence analysis (CA) of the 15 small fish abundances across the 24 seasonal sampling sites (represented as dots on the plane) in Niushan Lake. A: Autumn, W: Winter, Sp: Spring, Su: Summer. AMA: *A. macropterus*, ARI: *A. rivularis*, CAA: *C. auratus auratus*, CER: *C. erythropterus*, HLE: *H. leucisculus*, MAC: *M. aculeatus*, MSW: *M. swinhonis*, OOB: *O. obscura*, PFU: *P. fulvidraco*, PIM: *P. imberbis*, PPA: *P. parva*, RGI: *R. giurinus*, ROC: *R. ocellatus*, SNI: *S. nigripinnis*, TSW: *T. swinhonis*.

P. maackianus and *M. spicatum* (H2), with only a weak influence of water depth on their distributions. (3) *M. swinhonis*, *O. obscura* and *R. giurinus* were restricted to shallow uncovered or less-covered areas (H3). (4) *P. parva* and *C. auratus auratus* were abundant in all the three habitat types and showed no spatial pattern of distribution.

3.4 Seasonal variation

The CA of the 15 small fish abundances across all the 24 sites (6 sites in each season) visualized seasonal characteristics of the fish community. The CA was statistically significant ($p = 0.041$) and the first two axes accounted for 68.9% of the variability (44.6% and 24.3% respectively). Distribution of the sampling sites regarding the four seasons on the CA F1 × F2 plane (Fig. 5) indicated that the community structure showed the opposition between summer and autumn (with high temperature), and winter and spring (negative coordinate) with low temperature. On the other hand, it can be inferred from the associations between species and seasonal sites that most of the 15 species were more common during summer and autumn while less during winter and spring. Moreover, we can see the relative stability of the community in summer and spring (small circle) comparing to autumn and especially winter.

Population size structures of six small fish species *R. ocellatus*, *P. imberbis*, *A. macropterus*, *P. parva*, *T. swinhonis* and *C. erythropterus* were measured in the four seasons. All the

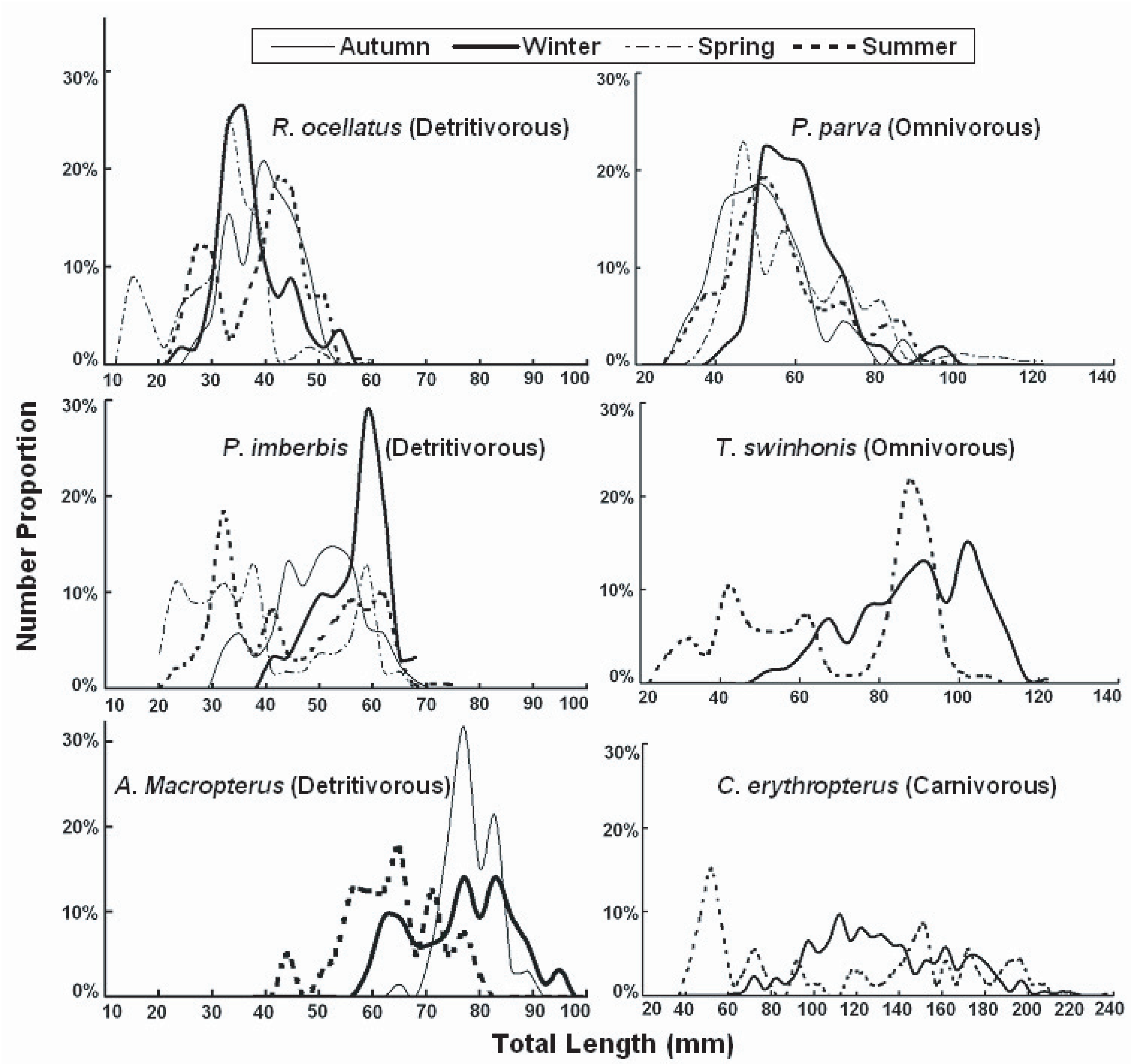

Fig. 6. Seasonal length-frequency distributions of six small fish populations in Niushan Lake.

six small fishes are major forages for piscivorous fishes in the lakes within the Yangtze region. There appeared to be a distinct seasonal pattern of increased frequency of larger sizes as the season progressed (Fig. 6). It was indicated that more larval and juvenile individuals occurred in spring and summer than in autumn and winter.

4 Discussion

4.1 Current status of small fishes in Niushan Lake

The 27 fish species sampled in Niushan Lake are all native and common in the lakes along the middle and lower reaches of the Yangtze River. Twenty of them are small fishes defined as age at first maturity less than two years (Anonymous 1976a) and a maximum size less than 240 mm. The other seven fish were larger species of which only the juvenile stages were caught using our sampling protocol. Another 8 small fish species and 10 large fish species have been found in Niushan Lake commercial fishery and from other sampling programmes (i.e. electrofishing, gillnetting, and diets of cormorants). Using the combined records, the fish community in Niushan Lake during the study period (2002–2003) consisted of 45 fish species. Twenty-eight small fish species accounted for over 60% of the total number of species. Similar predominance of small fishes among whole fish communities was also reported in other Yangtze lakes, such as Bao'an Lake (Fang et al. 1995), Donghu lake (Huang and Xie 1996), and Honghu Lake (Song et al. 1999). This phenomenon has been considered as a kind of indication of size diminution of fish resources in these lakes (Cao et al. 1991; Xie and Chen 1996). On the other hand, *R. ocellatus*, *P. imberbis*, *P. parva*, *M. swinhonis*, and *C. erythropterus* were recognized as the dominant small fishes in Niushan Lake in terms of both abundance and occurrence.

Most of the species caught were detritivorous or partially detritivorous. *X. argentea* and *P. simoni* are two typical detritivorous detritus feeders with highly specialized thick lips and long gut for ingesting and digesting plant debris (Zhu 1960). The bitterlings (*A. macropterus*, *P. imberbis* and *R. ocellatus*) and the crucian carp *C. auratus auratus* have a relatively generalized feeding habitat. In the shallow macrophytic Yangtze lakes, they commonly feed on low quality food, mainly macrophyte detritus, supplemented by planktonic algae, cladocerans, chironomid larvae and other food items (Chen 1959; Anonymous 1976a; Bian 1999; Zhang 2005). *P. parva, S. nigripinnis*, *A. rivularis*, and *M. aculeatus* prefer zooplankton and insect larvae, a small quantity of macrophyte detritus also occurs frequently in the contents of their digestive tracts (Anonymous 1976a; Xie et al. 2000c; Zhang 2005). In Niushan Lake, accumulations of macrophyte detritus are derived mainly from the net primary production of the two dominant submerged macrophytes, *P. maackianus* and *M. spicatum*. A layer of macrophyte detritus was commonly found on the sediment. Detritus originating from the macrophytes supports significant portion of small fish biomass. Plant detritus has also been shown to be an important energy source by Catella and Petrere (1996) in the fish community of a Brazil floodplain lake, by Havens et al. (1996) in a subtropical lake ecosystem in USA, and by Liu (2006) in the zoobenthos community of Yangtze lakes.

4.2 Spatial and seasonal variations of the small fish community

Aquatic vegetation often plays a significant role in structuring fish communities (Dibble et al. 1996; Xie et al. 2001; Rotherham and West 2002). The majority of fish species were found under the complex macrophyte cover conditions (i.e. densely-vegetated habitats of coexisting *P. maackianus* and *M. spicatum* or *P. maackianus*). Only a few benthic species *M. swinhonis*, *O. obscura* and *R. giurinus* inhabited uncovered or less-covered areas. These species appeared less dependent on macrophyte cover. Yin (1995) has suggested that these species can reduce their dependence on the macrophytic bottom through color and form adaptations and tend to remain motionless, thereby decreasing encounter rates with predators and making themselves less conspicuous.

The positive association between the distribution of small fishes and the submerged macrophytes is likely due to the benefits offered by the macrophyte cover: (1) *Increased foraging opportunities.* Although these small fishes do not feed directly on *P. maackianus* and *M. spicatum* like herbivorous carps, they are supplied with abundant macroinvertebrate prey (e.g. mollusk and shrimp), periphyton (epiphytic algae), and detritus from the macrophytes (Liu 1999; Bian 1999). (2) *Reduced predation risk*. Structural complexity created by *P. maackianus* and *M. spicatum* (both with a year-round presence in Niushan Lake) could influence the ability of piscivorous predators to capture the small fishes, in the form of refuge provided by the thick *P. maackianus* meadow and the long branching stems and feathery leaves of *M. spicatum*. (3) *Spawning sites.* Many of the small fishes deposit their adhesive or semi-adhesive eggs on the fine leafy submerged macrophytes, where oxygen content in the water and hydrochemical environment are favorable for the eggs to hatch out (Petr 2000).

C. erythropterus, *H. leucisculu* and *T. swinhonis* are three pelagic species in the lake. Their extension into the coexisting *P.maackianus* and *M. spicatum* habitat (H2) was limited, perhaps due to the visual and swimming barriers created by the very long (up to water surface) stems of *M. spicatum*. The detritivorous bitterlings *A. macropterus*, *R. ocellatus* and *P. imberbis* co-occurred in the H2. Their high spatial overlap implied that the limitation of detritus resources in the lake was rare. Moreover, there is a difference in the timing of reproduction among the three species (Anonymous 1976a), possibly as a mechanism to reduce potential trophic competition in the critical period (May 1974) following yolk sac absorption. Both *P. parva* and *C. auratus auratus* are very adaptable, with high physiological tolerance for environmental disturbance or a wide range of water quality conditions (Zhang 2005). They spawn repeatedly over a long period and have a broad dietary spectrum (Chen 1959; Zhang et al. 1998c,d). These characteristics provide the evidences for their ubiquitous distribution among the three habitat types in the lake.

Water depth was generally an important factor influencing spatial patterns of fish communities in North American and European deep lakes (Keast 1978; Laffaille et al. 2001). Different from those lakes, water depth had no significant influence on species diversity and distribution of small fishes in Niushan Lake. Generally, habitat factors affected fish habitat choice through physiochemical factors such as temperature, oxygen, and habitat complexity (Tonn and Magnuson 1982; Pierce et al. 1994). Because of the shallowness of water in Niushan lake, the variations in water depth were relatively small and depth had little effect on the physiochemical factors (Guan et al. 2005), resulting in the lack of water depth effects.

The structure of the small fish community varied among seasons. Most of the 15 species were more common during summer and autumn than during winter and spring, perhaps due to their reproductive habits, seasonal activity, and overwintering mortality (Yin 1995; Zhang 2005). The higher abundance of individuals in summer and autumn was also consistent with seasonal dynamics of their food resources such as phytoplankton, zooplankton and zoobenthos (Cuan et al. 2005). We observed more larval and juvenile individuals in spring or summer from the seasonal length-frequency distributions for several species, which is consistent with their breeding time of these species between April and August in the lake.

4.3 Implications for lake fishery management

In the past several decades, fish species of small size have flourished and dominated fish communities in many Yangtze lakes, like the current Niushan Lake, mainly due to habitat fragmentation or modification, reckless overfishing on commercial species, and unchecked elimination of piscivorous species (Cao et al. 1991; Xie and Chen 1996). These small fishes usually have low market values and potentially compete for resources with other large or medium commercial fishes. Thus, developing methods to utilize the lower quality fish resources as well as to control their abundance within a proper range has become an important objective of the Yangtze lake fishery management. While these small fishes are not targeted directly by the local fishery, they are forages of many native high quality piscivorous fishes such as mandarin fish *S. chuatsi*

(Jiang 1959), Chinese snakehead *C. argus* (Du 1962), and topmouth culter *C. alburnus* (Zhu et al. 1976). Artificial stocking of the native piscivorous fishes therefore is viewed as a promising strategy for controlling the excess small fish resources in the Yangtze lakes (Xie et al. 2000a; Li and Cui 2005). Furthermore, studies on North American and European lakes suggested that stocking piscivorous fishes into lakes may improve water quality through the trophic-cascading effects (Carpenter and Kitchell 1988; Van Liere and Gulati 1992).

An understanding of the food organisms of the piscivorous fishes is important for the successful management of piscivorous fisheries. Most small fishes in the Yangtze lakes spawn between April and August, and more larval and juvenile individuals of several species in our study were observed in spring or summer. The availability of small fish as prey for piscivorous predator can be effected by prey size structure and predator's size-selective feeding (Pierce et al. 2001). Therefore, we suggested that the favorable seasons for stocking juvenile piscivorous fishes should be late spring or early summer when the small fishes with suitable size are most abundant in the lakes.

The results of the present study suggest that macrophyte cover may play an important role in determining the structure of small fish community, such as species composition, diversity and distribution. Maintenance of macrophyte cover is essential for high diversity and abundance of small fishes, and hence fishery yield of piscivorous fishes. On the other hand, it is also essential to regulate the level of macrophyte abundance, as other studies indicated that dense vegetation could result in low feeding efficiency and poor growth of both small fishes and piscivorous fishes (Colle and Shireman 1980; Miranda and Pugh 1997; Xie et al. 2005). Further studies are needed in future to investigate the effects of macrophyte cover on predator-prey interactions of fish, and to assess ecosystem consequences of the stocking of piscivorous fishes into the Yangtze lakes.

Acknowledgements. We express our thanks to Mr. Xinnian Chen, Bin Zhang and Yushun Chen for their assistance in the field sampling. We appreciate the helpful comments of the three anonymous referees and the editor on early versions of this paper. The study was financially supported by the Key Technologies R & D Programme of China (No. 2002AA601021 and No. 2004BA526B05) and the State Key Laboratory of Freshwater Ecology and Biotechnology (No. 2005FB02).

References

Anonymous, Department of Ichthyology, Institute of Hydrobiology, CAS, 1976a, Fishes of the Yangtze River. Beijing, Science Press (in Chinese).

Anonymous, Section of Fish Ecology, the 4th Laboratory, Institute of Hydrobiology, CAS, 1976b, Study on the fish yield of Lake Donghu, Wuchang, with comments on the subject of rational stocking. Acta Hydrobiol. Sinica 6, 16–26 (in Chinese).

Bian S.J., 1999, Preliminary studies on the feeding habits and digestive system of five species of minnow Cyprinidae fishes in Liangzi Lake. Master Dissertation. Wuhan: Fisheries College, Huazhong Agricultural University, Wuhan (in Chinese).

Cao W.X., Zhang G.H., Ma J., Yu D.H., 1991, Preliminary studies on the phenomenon of size diminution of the fish resources in Lake Honghu. In: Honghu Research Group, Institute of Hydrobiology, CAS (Ed.) Studies on comprehensive exploitation of aquatic biological productivity and improvement of ecological environment in Lake Honghu. Beijing, China Ocean Press, pp. 148–152 (in Chinese).

Carpenter S.R., Kitchell J.F., 1988, Consumer control of lake productivity. Bioscience 38, 764–769.

Catella A.C., Petrere M. Jr., 1996, Feeding patterns in a fish community of Baia da Onca, a floodplain lake of the Aquidauana River, Pantanal, Brazil. Fish. Manage. Ecol. 3, 229–237.

Chen P.X., 1959, An ecological study of *Carassius auratus* in Lake Liangzi. Acta Hydrobiol. Sinica 4, 411–419 (in Chinese with English abstract).

Colle D.E., Shireman J.V., 1980, Coefficients of condition for largemouth bass, bluegill, and redear sunfish in hydrilla-infected lakes. Trans. Am. Fish. Soc. 109, 521–531.

Dibble E.D., Killgore K.J., Harrel S.L., 1996, Assessment of fish-plant interactions. Am. Fish. Soc. Symp. 16, 357–372.

Du J.R., 1962, On the biology of the Chinese snake-head, *Ophiocephalus argus*, in Liangzi Lake. Acta Hydrobiol. Sinica 2, 54–65 (in Chinese with English abstract).

Fang R.L., Zhang T.L., Liu H.Q., 1995, Characteristic of fish fauna of Bao'an Lake and its fishery utilization. In: Liang Y.L., Liu H.Q. (Eds.) Resources, environment and fishery ecological management of macrophytic lakes. Beijing, Science Press, pp. 205–210 (in Chinese with English abstract).

FAO Fisheries Department, 2003, The ecosystem approach to fisheries. FAO Technical Guidelines for Responsible Fisheries. No. 4, Suppl. 2. Rome, FAO.

Guan Z.H., Liu R.Q., Wang J., Feng W.S., Wang H.Z., Xu Q.Q., Xie Z.C., Liang Y.L., 2005, Resource and environmental characteristics of small and medium lakes. In: Cui Y.B. and Li Z.J. (Eds.) Fishery resources and conservation of environment in lakes of the Changjiang River basin. Beijing, Science Press, pp. 9–89 (in Chinese).

Hao T.H., 1960, An ecological study of a fresh water goby *Odontobutis obscura* (Temm. et Schl.) in Liangzi Lake of Hubei. Acta Hydrobiol. Sinica 2, 145–158 (in Chinese with English abstract).

Havens K.E., Bull L.A., Warren G.L., Crisman T.L., Phlips E.J., Smith J.P., 1996, Food web structure in a subtropical lake ecosystem. Oikos 75, 20–32.

Huang G.T., Xie P., 1996, Changes in the structure of fish community with the analysis on the possible reasons in Lake Donghu, Wuhan. Acta Hydrobiol. Sinica 20 (Suppl.), 38–46 (in Chinese with English abstract).

Ihaka R., Gentleman R., 1996, R: a language for data analysis and graphics. J. Comput. Graph. Stat. 5, 299–314.

Jiang Y.G., 1959, On the biology of mandarin fish, *Siniperca chuatsi* of Liangzi Lake. Acta Hydrobiol. Sinica 3, 375–385 (in Chinese with English abstract).

Keast A., 1978, Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fish. 3, 7–31.

Laffaille P., Brosse S., Gabas S., Lek S., 2001, Fish spatial distribution in the littoral zone of Lake Pareloup (France) during summer. Arch. Hydrobiol. 153, 129–144.

Li Z.J., Cui Y.B., 2005, Approaches of fishery reconstruction and ecosystem restoration in the lakes. In: Cui Y., Li Z.J. (Eds.) Fishery resources and conservation of environment in lakes of the Changjiang River basin. Beijing, Science Press, pp. 58 (in Chinese).

Liu J.K., 1984, Lakes of the middle and lower basins of the Changjiang (China). In: Taub F.B. (Ed.) Ecosystems of the world 23: Lakes and reservoirs. Amsterdam, Elsevier, pp. 331–355.

Liu J.K., 1999, Advanced hydrobiology. Beijing, Science Press (in Chinese).

Liu J.K., He B.W., 1992, Cultivation of the Chinese freshwater fishes (3rd edition). Beijing, Science Press (in Chinese).

Liu X.Q., 2006, Food composition and food webs of zoobenthos in Yangtze lakes. PhD Dissertation. Wuhan: Institute of Hydrobiology, the Chinese Academy of Sciences (in Chinese with English abstract).

Magurran A.E., 2004, Measuring biological diversity. Maldan, MA, Blackwell Science.

Manly B.F.J., 1994, Multivariate statistical methods: a primer (2nd edition). London, Chapman and Hall.

May R.C., 1974, Larval mortality in marine fishes and the critical period concept. In: Blaxter J.H.S. (Ed.) The early life history of fish. New York, Springer-Verlag, pp. 3–19.

Miranda L.E., Pugh L.L., 1997, Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. N. Am. J. Fish. Manage. 17, 601–609.

Palmer M.W., 1993, Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74, 2215–2230.

Pennington M., 1996, Estimating the mean and variance from highly skewed marine survey data. Fish. Bull. 94, 498–505.

Petr T., 2000, Interactions between fish and aquatic macrophytes in inland waters. A review. FAO Fisheries Tech. Pap. No. 396. Rome, FAO.

Pierce C.L., Rasmussen J.B., Leggett W.L., 1994, Littoral fish communities in southern Quebec lakes: relationships with limnological and prey resource variables. Can. J. Fish. Aquat. Sci. 51, 1128–1138.

Pierce C.L., Sexton M.D., Pelham M.E., Liao H., 2001, Dynamics of the littoral fish assemblage in Spirit Lake, Iowa, and implications for prey availability for piscivores. N. Am. J. Fish. Manage. 21, 884–896.

Rosenzweig M.L., 1995, Species diversity in space and time. Cambridge, Cambridge University Press.

Rotherham D., West R.J., 2002, Do different seagrass species support distinct fish communities in south-eastern Australia? Fish. Manage. Ecol. 9, 235–248.

Shao W., Yi B.L., 1991, Reproduction and growth of *Macropodus chinenis* and its predacity on mosquito larvae. Oceanol. Limnol. Sinica 22, 181–186 (in Chinese with English abstract).

Song T.X., Zhang G.H., Chang J.B., Miao Z.G., Deng Z.L., 1999, Fish diversity in Honghu Lake. Chinese J. Appl. Ecol. 10, 86–90 (in Chinese with English abstract).

Tan X.C., Xia L.Q., Kenichi T., Xie P., Chang J.B., 2002, Hydroacoustic surveys on temporal and spatial distributions of stocked carps in the East Lake. Acta Hydrobiol. Sinica 26, 585–590 (in Chinese with English abstract).

Ter Braak C.J.F., 1986, Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.

Tonn W.M., Magnuson J.J., 1982, Patterns in the species composition and richness of fish assemblages in northern wisconsin lakes. Ecology 63, 1149–1166.

Van Liere L., Gulati R.D., 1992. Restoration and recovery of shallow eutrophic lake ecosystems in the Netherlands: epilogue. Hydrobiologia 233, 283–287.

Werner E.E., Hall D.J., Laughlin D.R., Wagner D.J., Wilsmann L.A., Funk F.C., 1977, Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34, 360–370.

Wu X.W., Yang G.R., Le P.Q., Huang H.J., 1963, Commercial fauna of China (Freshwater Fish). Beijing, Science Press (in Chinese).

Xiao Y.X., Wang X.S., 1988, The fish population structure and potential production in Jinji Lake. J. Fish. China 12, 267–275 (in Chinese with English abstract).

Xie P., Chen Y.Y., 1996, "Evil Quartet" of inland waters in China – impact of human activities on the loss of biodiversity. Acta Hydrobiol. Sinica 20 (Suppl.), 6–23 (in Chinese).

Xie S.G., Cui Y.B., Li Z.J., 2000a, Ecological studies on lake fisheries on piscivorous fishes: theory and methods. Acta Hydrobiol. Sinica 24, 72–81 (in Chinese).

Xie S.G., Cui Y.B., Zhang T.L., Fang R.L., Li Z.J., 2000b, The spatial pattern of the small fish community in the Biandantang Lake – a small shallow lake along the middle reach of the Yangtze River, China. Environ. Biol. Fishes 57, 179–190.

Xie S.G., Cui Y.B., Zhang T.L., Li Z.J., 2000c, Seasonal patterns in feeding ecology of three small fishes in the Biandantang Lake, China. J. Fish Biol. 57, 867–880.

Xie S.G., Cui Y.B., Li Z.J., 2001, Small fish communities in two regions of the Liangzi Lake, China, with or without submersed macrophytes. Appl. Ichthyol. 17, 89–92.

Xie S.G., Li Z.J., Cui Y.B., Murphy B.R., 2005, Distribution, feeding and body condition of four small fish species in the near-shore and central areas of Liangzi Lake, China. Environ. Biol. Fish. 74, 379–387.

Yin M.C., 1995, Fish ecology. Beijing, China Agriculture Press (in Chinese).

Yu D.H., 1991, Studies on the biology of *Culter erythropterus* Basil. in Lake Honghu. In: Honghu Research Group, Institute of Hydrobiology, CAS (Ed.) Studies on comprehensive exploitation of aquatic biological productivity and improvement of ecological environment in Lake Honghu. Beijing, China Ocean Press, pp. 172–178 (in Chinese).

Zhang G.H., Deng Z.L., Xu Y.G., Miao Z.G., Chang J.B., Song T.X., 1998a, Survey on the numbers and catches of weirs in Honghu Lake. J. Lake Sci. 10, 68–74 (in Chinese with English abstract).

Zhang T.L., Cui Y.B., Fang R.L., Xie S.G., Li Z.J., 1998b, Population biology of topmouth gudgeon (*Pseudorasbora parva*) in Bao'an Lake – I. Age and growth. Acta Hydrobiol. Sinica 22 (Suppl.), 139–146 (in Chinese with English abstract).

Zhang T.L., Cui Y.B., Fang R.L., Xie S.G., Li Z.J., 1998c, Population biology of topmouth gudgeon (*Pseudorasbora parva*) in Bao'an Lake – II. Reproduction. Acta Hydrobiol. Sinica 22 (Suppl.), 147–154 (in Chinese with English abstract).

Zhang T.L., Cui Y.B., Fang R.L., Xie S.G., Li Z.J., 1998d, Population biology of topmouth gudgeon (*Pseudorasbora parva*) in Bao'an Lake – III. Food habits. Acta Hydrobiol. Sinica 22 (Suppl.), 155–164 (in Chinese with English abstract).

Zhang T.L., 2005, Life-history strategies, trophic patterns and community structure in the fishes of Lake Biandantang. PhD Dissertation. Wuhan: Institute of Hydrobiology, the Chinese Academy of Sciences (in Chinese with English abstract).

Zhu J.H., 1960, The biology of *Xenocypris davidi* of Liangzi Lake. Acta Hydrobiol. Sinica 2, 159–170 (in Chinese with English abstract).

Zhu S.Q. 1995, Synopsis of freshwater fisher of China. Nanjing, Jiangsu Science and Technology Publishing House (in Chinese).

Zhu Z.R., Lin Y.T., Fang R.L., 1976, On the food habit of *Erythroculter mongolicus* and *E. ilishaeformis* in Lake Donghu, Wuchang, and the problem of their population control. Acta Hydrobiol. Sinica 6, 36–52 (in Chinese).