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SPATIAL PATTERN OF FISH ASSEMBLAGES ALONG THE RIVER-RESERVOIR GRADIENT CAUSED BY THE THREE GORGE RESERVOIR (TGR)

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Abstract: We analysed spatial pattern in the fish assemblage structure along a longitudinal gradient of the Upper Yangtze River and the Three Gorges Reservoir. We tested the hypothesis that shifts from lotic to lentic environment affect the richness and structure of the fish assemblage. Samplings were carried out from 2005 to 2012 in four zones:(1) Hejiang reach, river upstream from the reservoir; (2) Mudong reach, upper part of the reservoir; (3) Wanzhou reach, middle part of the reservoir, and (4) Zigui reach, lower part of the reservoir. A total of 368706 fish representing 132 native species of 17 families were collected during the study period with Cyprinidae as the dominant group. The results showed that the native species richness decreased while the non-native species increased from river (Hejiang reach) to reservoir (Zigui reach). Patterns in fish assemblage ordination evaluated by correspondence analysis reflected a clear division of the riverine and reservoir zones. Uppermost sampling stations were characterized by species characteristic of flowing waters, whereas in the lowland most lentic species were captured. Further, 22 species, three functional groups (rheophilic, equilibrium, insectivorous) were identified for the upper reach and 16 species, three functional groups (herbivorous, planktivorous, stagnophilic) for the lowland reach by indicator species analysis ($P<0.05$). Therefore, it is evident that impoundment of the Three Gorges Reservoir is the major driving factor to structuring the fish assemblage structure along the longitudinal gradient from river to the reservoir. Different fisheries management actions should be made to conserve or rehabilitate native fish assemblages and control invasive non-native species.

Key words: Fish assemblages; River-reservoir gradient; Indicator species; Three Gorges Reservoir

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Reservoirs are managed ecosystems due to their pronounced environmental gradient; that is, they have limnological properties intermediate between those of rivers and lakes[1]. Reservoirs created by the damming of deep river valleys typically have an elongated morphology and, due to the influence of river inflows, they often show pronounced internal longitudinal gradients in their physicochemical conditions[2—4]. Along such gradient, the upstream region of dams can be divided into three distinct zones: a upstream riverine zone, a transitional zone and a deep lacustrine zone close to the dam[1]. Because of this gradient, local fish assemblages can be organized across space, since each species has different tolerance limits that vary across environmental gradients[5].

The literature demonstrates that river damming and impoundments cause habitat loss, change fish reproductive environments, and cut off migration routes, resulting in a substantial decline of biodiversity[6—8]. The dominance of non-native species in the new en-

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vironment is another concern because reservoirs often shift from native-dominated stream fishes to non-native invasive-dominated fish assemblages[9]. Thus, a detailed understanding of spatial pattern of fish assemblages in a particular reservoir along the river-reservoir gradient is valuable to both fishery management and native species conservation. A manager should, based on local and regional studies, identify any alterations in the structure of the local fish assemblage and take action to avoid irreversible losses of regional biological diversity and/or natural resources as a consequence of river damming[10]. However, most studies have focused on the direct downstream effects on fish assemblages, rather than the upstream impacts[11, 12]. This is because changes produced in the former are sudden, conspicuous and frequently dramatic[13].

The Three Gorges Reservoir (TGR) is the largest impoundments ever created in China. With an area coverage of 1080 km^2, the Three Gorges Reservoir extends for over 600 km upstream on the Yangtze River, including areas with the habitat and spawning grounds of many rare, endemic, and commercial fishes, such as Chinese sucker (*Myxocyprinus asiaticus*), *Coreius guichenoti*, black carp (*Mylopharyngodon piceus*), and grass carp (*Ctenopharyngodon idella*)[14, 15]. Studies reporting initial ecological impacts of the impoundment of TGR on fish assemblage have already been published. However, many of these studies have been limited to the impact examinations on riverine reaches and sole region for the putative changes in species composition and numbers[15—18]. Studies of spatial pattern of fish assemblages along the river-reservoir gradient are scarce and patterns in fish assemblages are rarely considered in management plans.

Therefore, the aims of the present study were to demonstrate spatial patterns of fish assemblages along the river-reservoir gradient and to identify indicator fish species and functional group for each zone. We tested the hypothesis that shifts from lotic to lentic environment affect the richness and structure of the fish assemblage. Through our study, we hope to provide insights into the overall cumulative effect on fish resources of China's massive hydroelectric development plans and management suggestion for the upper Yangtze River fish.

1 Materials and Methods

1.1 Study area and sampling

Fish sampling was conducted at four reaches in the main channel of the upper Yangtze River: Hejiang (28°48′N, 105°50′E), Mudong (29°34′N, 106°50′E), Wanzhou (30°50′N, 108°22′E) and Zigui (39°99′N, 110°69′E) (Fig. 1). Hejiang reach locates in the upper Yangtze River, about 100 km upstream of the backwater of the TGR (175 m ASL). Mudong reach locates in the upper part of the TGR, where is a

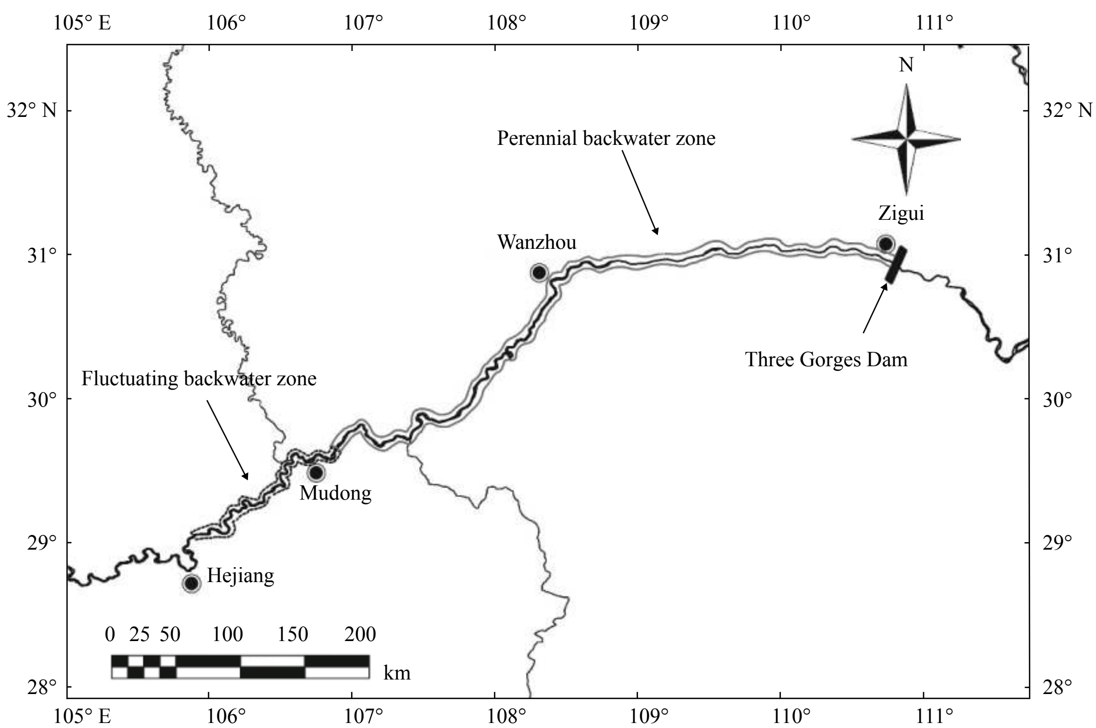


Fig. 1　The Three Gorges Reservoir in the upper Yangtze River with location of sampling stations. Dotted lines represent the fluctuating backwater area and the gray lines represent the perennial backwater area

typical transitional zone. Wanzhou reach locates in the middle part of the TGR, where has been inundated as a lacustrine pool by the first filling in 2003, while Zigui reach locates in lower part of the TGR, just one kilometer away from the Three Gorge Dam (TGD). Both of them locate in the lacustrine zone of TGR.

The fish investigations were conducted each year from 2005 to 2012 (except Mudong in 2005 and Zigui from 2005 to 2007). Fish sampling methods were followed in Zhu and Chang (2008) and Yang, *et al.* (2012)[17, 19]. All the native species sampled in the four sites were classified into 12 functional groups based on habitat preference, trophic and life-history characteristics. Flow preference and trophic characterization was for adult stages following Ding (1994) with modifications based on unpublished data[20]; the life-history classification follows Cao, *et al.* (2007) and Froese and Pauly (2011)[21, 22].

1.2 Multivariate analyses

Species abundance-by-site matrices from 2005 to 2012 were analyzed by correspondence analysis (CA) using CANOCO (Version 4.5). CA is an indirect gradient technique that simultaneously ordinates sample and species scores obtained by reciprocal averaging[23]. Species abundances were log (x + 1) transformed before analysis. In our analyses, we down-weighted rare species and selected Hill's scaling option. Only the first two canonical axes from these multivariate analyses were retained for interpretation. To determine if assemblage structure differed significantly among sites, the non-parametric Kruskal-Wallis test was performed using sample scores from the first two CA axes as dependent variables and site as a categorical variable.

Indicator species analysis (ISA) was also conducted in PC-ORD 5.0 to identify particular species and functional groups that best discerned along the river-reservoir gradient[24]. ISA measures the relative abundance and exclusivity of a particular species or functional group in a region. The ISA was used to supplement the MRPP as an additional measure of taxonomic and functional group distinction among a priori selected study regions[25]. Species indicator values range from 100 for a perfect regional indicator to 0 for a poor regional indicator. The significance of species indicator values was obtained from Monte Carlo simulations with 5000 randomizations.

2 Results

2.1 Fish richness

A total of 363598 specimens were captured, belonging to 132 native species and 17 families (Tab. 1). Cyprinidae had the greatest number of species (77), followed by Cobitidae (17), Bagridae (10) and Homalopteridae (4). Among them, 109, 96, 93 and 79 native species were collected from Hejiang, Mudong, Wanzhou and Zigui, respectively. Further, 17 non-native species were captured: *Protosalanx hyalocranius*, *Salangichthys tangkahkeii*, *Hemisalanx brachyrostralis*, *Acipenser schrenckii*, *Polyodon spathala*, *Huso duricus×Acipenser schrencki*, *Tinca tinca*, *Megalobrama amblycephala*, *Cirrhinus molitorella*, *Ictalurus punctatus*, *Micropterus salmoides*, *Tilapia* sp., *Lucioperca lucioperca*, *Clarias leather*, *Colossoma brachypomus*, *Ameiurus melas* and *Gambusia affinis*. The non-native species amounted to 0.04%, 0.02%, 0.30% and 6.07% of the total number of individual fish in Hejiang, Mudong, Wanzhou and Zigui, respectively. Among them, the non-native species (*P. hyalocranius*, *I. punctatus*, *M. amblycephala*, *Tilapia* sp.) amounted to 96.8% of the total number of non-native species when considering all sampled zones. The results showed that interannual number of native species decreased while the non-native species increased from river (Hejiang reach) to reservoir (Zigui reach) (Fig. 2).

2.2 Spatial pattern of fish assemblage composition

Ordination showed major spatial pattern of fish assemblage composition along the river-reservoir gradient based on the fish abundance. The first CA axis (eigenvalue = 0.390) ordinated samplings in two main groups (riverine and reservoir samplings) with significant differences between score values (Kruskal-Wallis test, P<0.01) (Fig. 3). For the second CA axis (eigenvalue=0.118), significant difference was found only between Wanzhou reach and Zigui reach (Kruskal-Wallis test, P<0.01). Samplings with high Axis I scores were composed of species associated with reservoirs (e.g. *Xenocypris argentea*, *Hemiculter bleekeri* and *Parabramis pekinensis*), while samplings with low Axis I scores contained species more characteristic of flowing waters (e.g. *Jinshaia sinensis*, *Rhinogobio ventralis*, and *Rhinogobio cylindricus*, *Coreius guichenoti*).

According to the Indicator Species Analysis (ISA), 38 out of the 132 examined species showed significant indicator values (P<0.01, Tab. 2). The species with high indicator values of Hejiang reach are *Lepturichthys fimbriata*, *Leptobotia rubrilabris* and *Jinshaia sinensis*. Indicative species of Mudong reach are *Rhinogobio cylindricus*, *Ancherythroculter nigrocauda*, *Pseudogobio vaillanti* and *Siniperca kneri*. For Wanzhou reach, there are *Acrossocheilus monticolus*, *Culter mongolicus mongolicus* and *Hemiculter*

Tab. 1 List of species among sampling reaches.

Scientific name	Family	Abbreviation	HJ	MD	WZ	ZG
Anguilla japonica Temminck *et* Schlegel	Anguillidae	*Ajap*	*		*	
Zacco platypus (Temminck *et* Schlegel)	Cyprinidae	*Zpla*	*	*	*	*
Opsariichthys bidens Günther	Cyprinidae	*Obid*	*	*	*	*
Aphyocypris chinensis Günther	Cyprinidae	*Achi*	*			
Mylopharyngodon piceus (Richardson)	Cyprinidae	*Mpic*	*	*	*	*
Ctenopharyngodon idellus (Cuvier *et* Valenciennes)	Cyprinidae	*Cide*	*	*	*	*
Phoxinus oxycephalus Sauvage *et* Dabry	Cyprinidae	*Poxy*				*
Squaliobarbus curriculus (Richardson)	Cyprinidae	*Scur*	*	*	*	*
Elopichthys bambusa (Richardson)	Cyprinidae	*Ebam*		*	*	*
Pseudolaubuca sinensis Bleeker	Cyprinidae	*Psin*	*	*	*	*
Pseudolaubuca engraulis (Nichols)	Cyprinidae	*Peng*	*	*	*	*
Sinibrama taeniatus (Nichols)	Cyprinidae	*Stae*	*		*	
Ancherythroculter kurematsui (Kimura)	Cyprinidae	*Akur*	*	*	*	*
Ancherythroculter wangi (Tchang)	Cyprinidae	*Awan*	*	*		
Ancherythroculter nigrocauda Yih *et* Woo	Cyprinidae	*Anig*	*	*	*	*
Hemiculterella sauvagei Warpachowski	Cyprinidae	*Hsau*		*		
Hemiculter leucisculus (Basilewsky)	Cyprinidae	*Hleu*	*	*	*	*
Hemiculter tchangi Fang	Cyprinidae	*Htch*	*	*	*	*
Hemiculter bleekeri Warpachowski	Cyprinidae	*Hwar*	*	*	*	*
Cultrichthys erythropterus (Basilewsky)	Cyprinidae	*Cery*	*	*	*	*
Culter alburnus Basilewsky	Cyprinidae	*Calb*	*	*	*	*
Culter mongolicus (Basilewsky)	Cyprinidae	*Cmon*	*	*	*	*
Culter oxycephalus Bleeker	Cyprinidae	*Coxy*		*	*	*
Culter dabryi Bleeker	Cyprinidae	*Cdab*		*	*	*
Culter oxycephaloides Kreyenberg *et* Pappenheim	Cyprinidae	*Coxc*		*		
Parabramis pekinensis (Basilewsky)	Cyprinidae	*Ppek*	*	*	*	*
Megalobrama pellegrini (Tchang)	Cyprinidae	*Mpel*	*	*	*	
Xenocypris argentea Günther	Cyprinidae	*Xarg*		*		*
Xenocypris davidi Bleeker	Cyprinidae	*Xdav*	*	*	*	*
Xenocypris fangi Tchang	Cyprinidae	*Xfan*			*	
Xenocypris microlepis Bleeker	Cyprinidae	*Xmic*	*		*	
Pseudobrama simoni (Bleeker)	Cyprinidae	*Psim*	*	*	*	*
Aristichthys nobilis (Richardson)	Cyprinidae	*Anob*	*	*	*	*
Hypophthalmichthys molitrix (Cuvier *et* Valenciennes)	Cyprinidae	*Hmol*	*	*	*	*
Hemibarbus labeo (Pallas)	Cyprinidae	*Hlab*	*	*	*	*
Hemibarbus maculatus Bleeker	Cyprinidae	*Hmac*	*	*	*	*
Pseudorasbora parva (Temminck *et* Schlegel)	Cyprinidae	*Ppar*	*	*	*	*
Sarcocheilichthys sinensis Bleeker	Cyprinidae	*Ssin*	*	*	*	*
Sarcocheilichthys nigripinnis (Günther)	Cyprinidae	*Snig*	*	*	*	*
Gnathopogon herzensteini (Günther)	Cyprinidae	*Gher*	*			
Gnathopogon imberbis (Sauvage *et* Dabry)	Cyprinidae	*Gimb*	*	*		
Squalidus argentatus (Sauvage *et* Dabry)	Cyprinidae	*Sarg*	*	*	*	*
Squalidus wolterstorffi	Cyprinidae	*Swol*			*	
Coreius heterodon (Bleeker)	Cyprinidae	*Chet*	*	*	*	*
Coreius guichenoti (Sauvage *et* Dabry)	Cyprinidae	*Cgui*	*	*	*	
Rhinogobio typus Bleeker	Cyprinidae	*Rtyp*	*	*	*	*
Rhinogobio cylindricus Günther	Cyprinidae	*Rcyl*	*	*	*	*

Continued Tab.1

Scientific name	Family	Abbreviation	HJ	MD	WZ	ZG
Rhinogobio ventralis (Sauvage *et* Dabry)	Cyprinidae	*Rven*	*	*	*	
Platysmacheilus nudiventris Lo, Yao *et* Chen	Cyprinidae	*Pnud*	*	*		
Abbottina rivularis (Basilewsky)	Cyprinidae	*Ariv*	*	*	*	*
Abbottina obtusirostris Wu et Wang	Cyprinidae	*Aobt*	*		*	
Microphysogobio kiatingensis (Wu)	Cyprinidae	*Mkia*	*	*	*	*
Pseudogobio vaillanti (Sauvage)	Cyprinidae	*Pvai*		*		
Saurogobio dumerili Bleeker	Cyprinidae	*Sdum*			*	
Saurogobio dabryi Bleeker	Cyprinidae	*Sdab*	*	*	*	*
Saurogobio gymnocheilus Lo, Yao *et* Chen	Cyprinidae	*Sgym*	*	*	*	*
Gobiobotia (*Gobiobotia*) *filifer* (Garman)	Cyprinidae	*Gfil*	*	*	*	*
Xenophysogobio boulengeri Tchang	Cyprinidae	*Xbou*	*	*		
Xenophysogobio nudicorpa (Huang *et* Zhang)	Cyprinidae	*Xnud*	*			
Rhodeus sinensis Günther	Cyprinidae	*Rsin*	*	*	*	*
Rhodeus ocellatus (Kner)	Cyprinidae	*Roce*	*	*	*	*
Acheilognathus macropterus (Bleeker)	Cyprinidae	*Amac*	*	*	*	*
Acheilognathus omeiensis (Shih *et* Tchang)	Cyprinidae	*Aome*	*		*	
Acheilognathus chankaensis (Dybowski)	Cyprinidae	*Acha*		*	*	*
Spinibarbus sinensis (Bleeker)	Cyprinidae	*Ssie*	*	*	*	*
Acrossocheilus monticolus (Günther)	Cyprinidae	*Amon*	*	*	*	
Acrossocheilus yunnanensis (Regan)	Cyprinidae	*Ayun*	*			
Onychostoma sima (Sauvage *et* Dabry)	Cyprinidae	*Osim*	*	*	*	*
Tor (*Folifer*) *brevifilis brevifilis* (Peters)	Cyprinidae	*Tbre*	*			
Bangana rendahli (Kimura)	Cyprinidae	*Bren*			*	
Pseudogyrinocheilus procheilus (Sauvage *et* Dabry)	Cyprinidae	*Ppro*	*	*	*	*
Garra pingi pingi (Tchang)	Cyprinidae	*Gpin*	*			*
Schizothorax (*Schizothorax*) *wangchiachii* (Fang)	Cyprinidae	*Swan*	*			*
Schizothorax (*Schizothorax*) *prenanti* (Tchang)	Cyprinidae	*Spre*			*	
Schizothorax (*Schizothorax*) *chongi* (Fang)	Cyprinidae	*Scho*	*			
Procypris rabaudi (Tchang)	Cyprinidae	*Prab*	*	*	*	*
Cyprinus (*Cyprinus*) *carpio* Linnaeus	Cyprinidae	*Ccar*	*	*	*	*
Carassius auratus (Linnaeus)	Cyprinidae	*Caur*	*	*	*	*
Myxocyprinus asiaticus(Bleeker)	Catostomidae	*Masi*	*	*	*	*
Yunnanilus sichuanensis Ding	Cobitidae	*Ysic*	*			
Paracobitis variegatus (Sauvage *et* Dabry)	Cobitidae	*Pvar*	*	*		*
Paracobitis potanini (Günther)	Cobitidae	*Ppot*	*			
Paracobitis wujiangensis Ding *et* Deng	Cobitidae	*Pwuj*	*		*	
Triplophysa (*Triplophysa*) *angeli* (Fang)	Cobitidae	*Tang*	*			
Botia superciliaris Günther	Cobitidae	*Bsup*	*	*	*	*
Botia reevesae Chang	Cobitidae	*Bree*	*	*		*
Parabotia fasciata Dabry	Cobitidae	*Pfas*	*	*	*	*
Parabotia bimaculata Chen	Cobitidae	*Pbim*		*		
Leptobotia elongata (Bleeker)	Cobitidae	*Lelo*	*	*	*	*
Leptobotia taeniops (Sauvage)	Cobitidae	*Ltae*	*	*	*	*
Leptobotia pellegrini Fang	Cobitidae	*Lpel*	*	*	*	
Leptobotia microphthalma Fu *et* Ye	Cobitidae	*Lmic*		*		
Leptobotia rubrilabris (Dabry)	Cobitidae	*Lrub*	*	*		
Cobitis sinensis Sauvage *et* Dabry	Cobitidae	*Csin*	*	*		*

Continued Tab.1

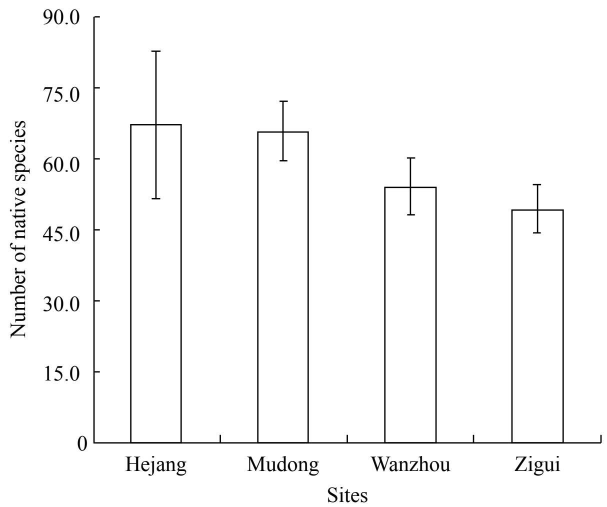
Scientific name	Family	Abbreviation	HJ	MD	WZ	ZG
Misgurnus anguillicaudatus (Cantor)	Cobitidae	*Mang*	*	*	*	*
Paramisgurnus dabryanus Sauvage	Cobitidae	*Pdab*	*		*	
Lepturichthys fimbriata (Günther)	Homalopteridae	*Lfim*	*	*		*
Jinshaia sinensis (Sauvage *et* Dabry)	Homalopteridae	*Jsin*	*	*		*
Sinogastromyzon sichangensis Chang	Homalopteridae	*Ssic*	*			
Sinogastromyzon szechuanensis Fang	Homalopteridae	*Ssze*	*	*	*	
Pelteobagrus fulvidraco (Richardson)	Bagridae	*Pful*	*	*	*	*
Pelteobagrus eupogon (Boulenger)	Bagridae	*Peup*	*	*	*	*
Pelteobagrus vachelli (Richardson)	Bagridae	*Pvac*	*	*	*	*
Pelteobagrus nitidus (Sauvage *et* Dabry)	Bagridae	*Pnit*	*	*	*	*
Leiocassis longirostris Günther	Bagridae	*Llon*	*	*	*	*
Leiocassis crassilabris Günther	Bagridae	*Lcra*	*	*	*	*
Pseudobagrus truncatus (Regan)	Bagridae	*Ptru*	*	*	*	*
Pseudobagrus emarginatus (Regan)	Bagridae	*Pema*	*	*		
Pseudobagrus pratti (Günther)	Bagridae	*Ppra*	*			
Mystus macropterus (Bleeker)	Bagridae	*Mmac*	*	*	*	
Silurus asotus Linnaeus	Siluridae	*Saso*	*	*	*	*
Silurus meridionalis Chen	Siluridae	*Smer*	*	*	*	*
Liobagrus marginatus (Bleeker)	Amblycipitidae	*Lmag*	*			
Liobagrus nigricauda Regan	Amblycipitidae	*Lnig*	*			
Liobagrus marginatoides (Wu)	Amblycipitidae	*Lmar*	*			
Glyptothorax fokiensis (Rendahl)	Sisoridae	*Gfok*	*	*	*	
Glyptothorax sinensis (Regan)	Sisoridae	*Gsin*	*	*	*	
Clarias fusus (Lácepède)	Clariidae	*Cfus*				*
Oryzias latipes (Temminck *et* Schlegel)	Oryziatidae	*Olat*				*
Hyporamphus intermedius (Cantor)	Hemiramphidae	*Hint*		*	*	*
Monopterus albus (Zuiew)	Synbranchidae	*Malb*			*	*
Siniperca chuatsi (Basilewsky)	Serranidae	*Schu*	*	*	*	*
Siniperca kneri Garman	Serranidae	*Skne*		*	*	
Siniperca scherzeri Steindachner	Serranidae	*Ssch*	*	*		
Micropercops swinhonis (Günther)	Eleotridae	*Mswi*	*	*	*	*
Mugilogobius myxodermus (Herre)	Gobiidae	*Mmyx*	*			
Rhinogobius giurinus (Rutter)	Gobiidae	*Rgiu*	*	*	*	*
Rhinogobius brunneus (Temminck *et* Schlegel)	Gobiidae	*Rbru*	*			
Rhinogobius cliffordpopei (Nichols)	Gobiidae	*Rcli*			*	
Macropodus chinensis (Bloch)	Belontiidae	*Mchi*	*	*	*	
Macropodus opercularis (Linnaeus)	Belontiidae	*Mope*			*	
Channa argus (Cantor)	Channidae	*Carg*	*	*	*	*

bleekeri. For Zigui reach, there are *Xenocypris argentea*, *Parabramis pekinensis*, *Siniperca chuatsi* and *Aristichthys nobilis*.

2.3　Spatial pattern of functional characteristics

A different pattern resulted from CA ordination of the functional data set was also observed. In addition to a clear division of the riverine and reservoir zones, CA axis 1 described assemblage habitat preference, trophic composition and reproductive functional groups (Fig. 4). Local assemblages with rheophilic, equilibrium, insectivorous species had the most negative values, whereas sites dominated by periphytivorous, herbivorous, planktivorous, stagnophilic species had the most positive values. Differences between river reaches scores were not significant for CA axis 2 (Fig. 4).

An ISA resulted in 10 functional groups that were significant indicators for all the samplings (Tab. 3).



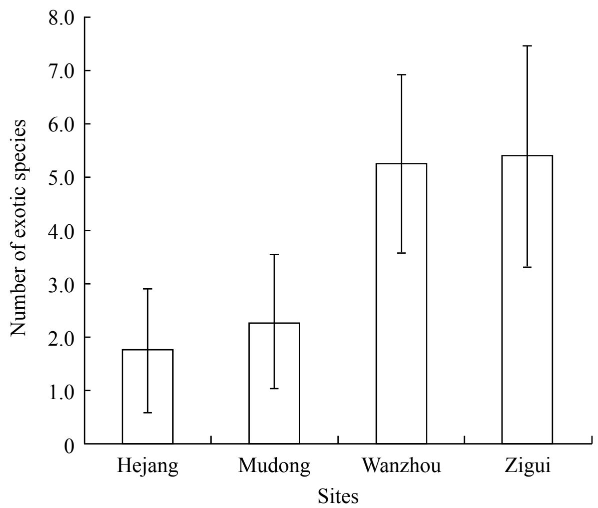


Fig. 2 The interannual number of fish species encountered in each sampling reaches along the longitudinal gradient

The highest indicator functional groups included rheophilic, equilibrium, insectivorous species for riverine regions and herbivorous, planktivorous, stagnophilic species for reservoir regions. These results confirm the CA results that there is some distinct differentiation in fish functional groups along the river-reservoir gradient.

3 Discussion

3.1 Alteration of spatial pattern longitudinally

It is generally accepted that species diversity in natural river ecosystems increases progressively toward the downstream according to the River Continuum Concept[26]. Contrastingly, the spatial pattern of fish assemblages along the river-reservoir gradient usually showed an opposite trend. In this study, the native species richness decreased while the exotic species increased from river to reservoir, covering a 600 km reach of the upper Yangtze River. Similar fish patterns also have been reported in other reservoirs

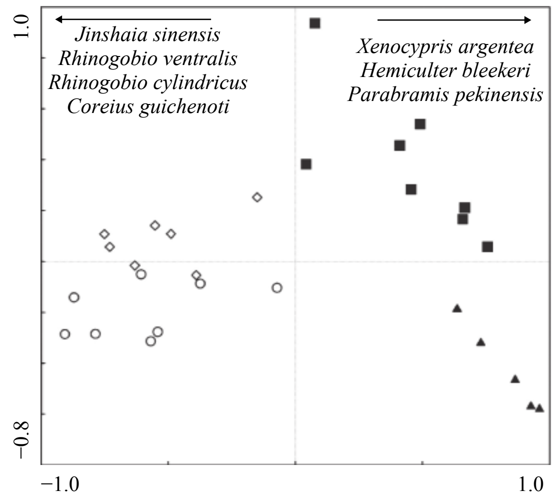


Fig. 3 Correspondence analysis of fish community data across the 28 samplings from 2005—2012 upstream of the Three Gorges Dam

First and second axes had eigenvalues of 0.390 and 0.118 and explained 34.5% and 10.4% of the variation in community structure, respectively. Arrows indicate fish species more correlated with CA1. Legend: Hejiang (○), Mudong (◇), Wanzhou(■), Zigui(▲)

and in other countries[27—29]. As in Itaipu Reservoir, higher fish diversity in the upstream reaches of reservoirs and the reduced richness of the lacustrine zone were founded[1, 30]. The reduced richness of the lacustrine zone may be a result of local and historical processes, like habitat homogenization and wide changes in water level and, consequently, water quality, with a small number of native species being adapted to the new lentic environment[3].

3.2 Difference in fish assemblage of the three water zones

Reservoirs are human-engineered habitats, and the modification of riverine environment may be working as a species filter that ultimately dictates composition of the fish assemblage[31]. Only those species with adaptations that fit the available habitats will successfully colonize in different zones.

As a riverine zone, Hejiang reach remained natural flow regime and water temperature. The rheophilous indigenous species that prefer rubble substrates, fast and moderate current velocity habitats, and that have low silt tolerance was dominant species in Hejiang reach, such as *Coreius guichenoti*, *Coreius heterodon*, *Rhinogobio ventralis*, *Rhinogobio cylindricus*. These species are a guild fishes that spawn nonadhesive, semibuoyant eggs. Spawning is believed to occur in response to floods, which increase stream flows and keep the semibuoyant eggs afloat until hatching occurs[32]. In Mudong reach where river and reservoir conditions overlap, coexistence of species

Tab. 2　Significant fish species based indicator species analysis (ISA) in the upper Yangtze River

Scientific name	Abbreviation	Sites	Value (IV)	*P* value
Lepturichthys fimbriata (Günther)	Lfim	HJ	97.4	0.0002
Leptobotia rubrilabris (Dabry)	Lrub	HJ	93.3	0.0002
Jinshaia sinensis (Sauvage *et* Dabry)	Jsin	HJ	91.4	0.0002
Glyptothorax sinensis (Regan)	Gsin	HJ	87.9	0.0002
Pseudobagrus emarginatus (Regan)	Pema	HJ	85	0.0002
Botia superciliaris Günther	Bsup	HJ	84.1	0.0004
Xenophysogobio boulengeri Tchang	Xbou	HJ	83.5	0.0002
Paracobitis potanini (Günther)	Ppot	HJ	75	0.002
Sinogastromyzon szechuanensis Fang	Ssze	HJ	74.5	0.0006
Leptobotia elongata (Bleeker)	Lelo	HJ	70.2	0.0002
Rhinogobio typus Bleeker	Rtyp	HJ	66.4	0.0002
Gobiobotia (*Gobiobotia*) *filifer* (Garman)	Gfil	HJ	66.3	0.0032
Spinibarbus sinensis (Bleeker)	Ssie	HJ	63	0.0002
Pseudobagrus pratti (Günther)	Ppra	HJ	62.5	0.0032
Liobagrus marginatoides (Wu)	Lmar	HJ	62.5	0.0028
Rhinogobio ventralis (Sauvage *et* Dabry)	Rven	HJ	61.1	0.0008
Coreius guichenoti (Sauvage *et* Dabry)	Cgui	HJ	47.6	0.0004
Pelteobagrus vachelli (Richardson)	Pvac	HJ	41.5	0.0006
Rhinogobio cylindricus Günther	Rcyl	MD	63	0.0002
Pseudogobio vaillanti (Sauvage)	Pvai	MD	57.1	0.0072
Siniperca kneri Garman	Skne	MD	56.9	0.0066
Coreius heterodon (Bleeker)	Chet	MD	50.4	0.0002
Acrossocheilus monticolus (Günther)	Amon	WZ	99.3	0.0002
Zacco platypus (Temminck *et* Schlegel)	Zpla	WZ	76.5	0.0006
Paramisgurnus dabryanus Sauvage	Pdab	WZ	70.8	0.0014
Culter mongolicus (Basilewsky)	Cmon	WZ	64.9	0.0002
Hemiculter bleekeri Warpachowski	Hwar	WZ	53.6	0.0022
Saurogobio dabryi Bleeker	Sdab	WZ	47.5	0.0002
Culter alburnus Basilewsky	Calb	WZ	42.2	0.0038
Xenocypris argentea Günther	Xarg	ZG	95.3	0.0002
Parabramis pekinensis (Basilewsky)	Ppek	ZG	88.4	0.0004
Opsariichthys bidens Günther	Obid	ZG	87.3	0.0002
Siniperca chuatsi (Basilewsky)	Schu	ZG	69.5	0.0008
Aristichthys nobilis (Richardson)	Anob	ZG	63	0.0002
Culter dabryi Bleeker	Cdab	ZG	52.8	0.0088
Carassius auratus (Linnaeus)	Caur	ZG	48.8	0.0012
Ctenopharyngodon idellus (Cuvier *et* Valenciennes)	Cide	ZG	40.9	0.0074
Cyprinus (*Cyprinus*) *carpio* Linnaeus	Ccar	ZG	36	0.0042

from both lotic and lentic systems was observed by the indicator species analysis. *Rhinogobio cylindricus*, a migratory species typical of lotic systems, and *Siniperca kneri*, a species displayed a preference for a still water and with low swimming capacity, were recorded. The same phenomenon also occurred in other reservoirs[3]. As pointed out by Oliveira, *et al.* (2003), ecotones play an important role in fish diversity and community structure in reservoirs, insofar as they usually have specific features such as physical shelters, well developed riparian vegetation and spawning areas[33]. In the lacustrine zones of reservoirs, Wanzhou and Zigui reach inhabited by fewer fish species, and supported mainly the piscivore *Culter mongolicus* and *Siniperca chuatsi* which migrates to the littoral to feed, and the planktivore *Hypophthalmichthys molitrix*, *Aristichthys nobilis*, which inhabits deep pelagic areas. Both of these species have adaptations

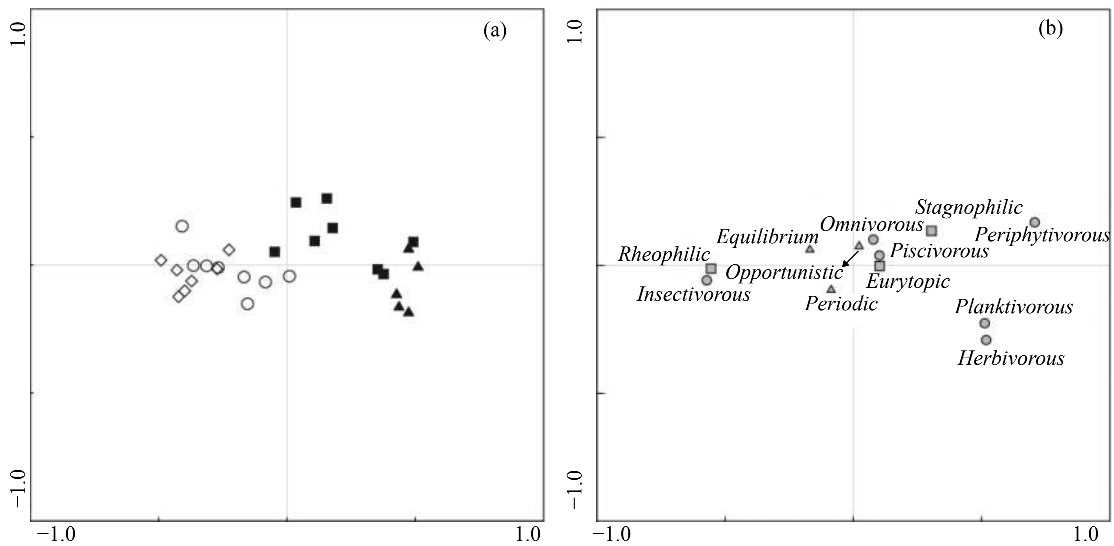


Fig. 4 Correspondence analysis of the 28 samplings and fish functional group based on the fish functional group data from 2005—2012
First and second axes had eigenvalues of 0.101 and 0.012 and explained 71.3% and 18.4% of the variation in community structure, respectively. Legend: Hejiang (○), Mudong (◇), Wanzhou(■), Zigui(▲)

Tab. 3 Significant functional groups of fish assemblages based indicator species analysis (ISA) in the upper Yangtze River

Functional groups	Sites	Value (IV)	*P* value
Rheophilic	HJ	39.1	0.0002
Equilibrium	HJ	33.8	0.0002
Insectivorous	MD	40.1	0.0002
Piscivorous	WZ	30.2	0.0238
Omnivorous	WZ	28.7	0.0184
Opportunistic	WZ	27.6	0.0132
Herbivorous	ZG	49.1	0.0002
Planktivorous	ZG	41.2	0.0024
Stagnophilic	ZG	34.1	0.0056
Eurytopic	ZG	28.2	0.0372

for lentic environments, but longer lifespans. However, historical data showed that fish assemblages in both Wanzhou and Zigui reaches were dominanted by two typical lotic species, *C. guichenoti* and *C. heterodon*. The relative biomass of two *Coreius* species accounted for more than 70% of the gross catch of the Wanzhou reach in the 1970s[34]. But now, these lotic species have almost disappeared in the lacustrine zones[15]. Based on these results, it indicated that the new reservoir environment could no longer satisfy the ecological requirements of these lotic species which increases the probability of regional extinction of native species. On the other hand, the non-native species, such as *P. hyalocranius*, *I. punctatus*, *M. amblycephala*, *Tilapia* sp., were abundant in lacustrine zones and some populations had been in the stage of outbreak[35]. It showed that the regulation had longer-term negative effects on the assemblage composition in the TGR.

3.3 Management implications

Results confirmed our hypothesis that spatial pattern in the fish assemblage structure are affected by reservoir impoundment. The lacustrine and riverine zones are occupied differentially depending on the ecological needs of fish species. In view of the results from this study and some previous research, management actions should be targetedly implemented to achieve desired outcomes.

Firstly, because rheophilous indigenous species dominated assemblages in the riverine zones (e.g., Hejiang reach), maintaining the natural habitat conditions and fish assemblages in these areas will contribute to long-term persistence of native species, particularly for the endemic species inhabiting the upper Yangtze. Secondly, in lentic zones where natural habitat conditions have been highly altered by reservoir impoundment, conservation actions for native lotic fishes would be rarely practical. On the other hand, we should pay close attention to the related effects and other issues caused by the non-native species in the TGR. It is urgent to build the early warning and prevention systems of non-native species, to assess of intentional introduced activities rigorously, and intensive study the successful invasive reasons and mechanisms of non-native species.

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三峡水库蓄水后长江上游鱼类群聚沿河流-水库梯度的空间格局

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摘要: 研究对2005—2012年长江上游合江、木洞、万州和秭归江段的鱼类群聚结构进行了调查, 以分析三峡水库蓄水后长江上游鱼类群聚沿河流-水库梯度的空间格局。结果显示, 在三峡蓄水后, 在合江至秭归江段累计采集到土著鱼类368706尾, 合计132种, 隶属于17科, 其中鲤科鱼类为优势类群。沿河流-水库纵向梯度, 土著鱼类物种数下降而外来鱼类物种数增加。对应分析表明, 合江至秭归江段的鱼类群聚呈现出明显分化: 库区以上河段鱼类组成以流水性鱼类为主, 库区鱼类则以静水缓流型为主。指示物种分析进一步指出, 河流区鱼类以犁头鳅(*Lepturichthys fimbriata*)、红唇薄鳅(*Leptobotia rubrilabris*)、圆口铜鱼(*Coreius guichenoti*)、圆筒吻鮈(*Rhinogobio cylindricus*)等22种鱼类为指示物种, 其功能群特征表现为偏好流水生境、生活史为均衡主义及食性为昆虫食性; 库区鱼类以宽口光唇鱼(*Acrossocheilus monticolus*)、宽鳍鱲(*Zacco platypus*)、鳊(*Parabramis pekinensis*)、鳙(*Aristichthys nobilis*)等16种鱼类为指示物种, 其功能群特征表现为偏好静水生境、食性为草食性或浮游食性。以上研究表明, 三峡水库蓄水导致的水环境变化是影响长江上游鱼类纵向格局的主要驱动力。建议相关管理部门根据不同河段鱼类群聚特征制定不同的渔业管理措施, 如保护土著鱼类资源、控制外来入侵鱼类。

关键词: 鱼类群聚; 河流-水库梯度; 指示种; 三峡水库