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Long-term monitoring revealed fish assemblage zonation in the Three Gorges Reservoir*

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Abstract Reservoirs are important artificial ecosystems that modify the hydrological and ecological characteristics of a river. Knowledge of the basic characteristics of fish assemblages in reservoirs is a first step toward the development of effective conservation policies. We used the information collected over a 10-year period (2006–2015) to assess the structure of the fish assemblages in the Three Gorge Reservoir (TGR) in a river-dam gradient. Three fish zones were detected in TGR. Species richness was the highest in the upper zone and lowest in the lower zone. The riverine zones were dominated by rheophilic species *Coreius guichenoti* and *Pelteobagrus vachelli*. The transitional zones were dominated by *Coreius heterodon* and *Rhinogobio cylindricus*. The lacustrine zones were dominated by eurytopic species *Hypophthalmichthys molitrix*, *Aristichthys nobilis*, *Hemiculter bleekeri* and *Cyprinus carpio*. For the functional characteristics, fish assemblages in riverine and transitional zones were dominated by insectivorous species, equilibrium strategists and rheophilic species (e.g., *Coreius heterodon* and *Coreius guichenoti*). In lacustrine zones, the fish assemblage was dominated by habitat generalists common to lakes and reservoirs (e.g., *Hemiculter bleekeri*, *Hypophthalmichthys molitrix*, *Aristichthys nobilis*). Moreover, 18 exotic species (e.g., *Protosalanx hyalocranius*, *Ictalurus punctatus*, *Megalobrama amblycephala*, Tilapia) were collected in TGR, most of which only existed in the lacustrine zone. The results highlight the importance of freely flowing riverine reaches for conserving native fish in the upper Changjiang River and adaptive management strategies for fisheries in TGR.

Keyword: longitudinal gradient; impoundment; functional groups; exotic species; dam effects

1 INTRODUCTION

Sites (or areas) classification based on the species assemblages is one of the main scientific practices in running water conservation ecology (Lasne et al., 2007). Many theoretical classifications of running waters, notably fish-based classifications, have been proposed in the last one hundred years (Miranda and Raborn, 2000). One of them is the Huet's fish zonation for western European streams. Huet (1959) pointed out that four distinct regions could be distinguished by the dominant species longitudinally from upstream to downstream areas of natural river systems: trout zone, grayling zone, barbel zone, and bream zone.

The zonation paradigm has been used for many decades to reveal the temporal and spatial pattern of fish assemblages, and the refined versions, which included information on ecological fish guilds, still play an important role in studies of riverine fish assemblages (Aarts and Nienhuis, 2003; McGarvey, 2011). For example, Kruk et al. (2017) detected three zones (impoverished grayling zone, barbel zone, and bream zone) within the lowland Warta River, Poland. To date, such fish zonation types have been used as the baseline state to assess river ecological and water-quality and furtherly to make robust water management and conservation practice (Vardakas et al., 2015).

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Dam reservoirs are important artificial ecosystems that modify the hydrological and ecological characteristics of a river (Tundisi, 1993). Due to changes in basin geomorphology and hydrology and, consequently, in physical, chemical, and biological variables, reservoirs exhibit gradients in conditions and resources along the transition from lotic to lentic habitat. These gradients may be divided into three zones: riverine, transitional, and lacustrine (Thornton, 1990). The riverine zone (RZ) is a typical lotic environment where the surface water and deepwater sediments are well-mixed. The transitional zone (TZ) is an ecotone between the river upstream and the lacustrine zone of the reservoir downstream. The lacustrine zone (LZ) is the stably stratified lake-like area. In such gradients, a number of studies have indicated that fish assemblages in these zones were different in structure and function (Oliveira et al., 2004; Terra et al., 2010; Sá-Oliveira et al., 2015). Understanding the structure of the fish assemblages along a river-dam gradient is necessary to manage fish biodiversity.

As the world's largest hydropower project, The Three Gorges Dam (TGD) on the Changjiang River is operated for hydropower production, flood mitigation, and navigation improvement. Its total installed capacity is 18.2 million kW, and the mean annual power output is 84.7 billion kW h. After the completion of the project, the Three Gorges Reservoir (TGR) extends 663 km from Chongqing (west) to Yichang of Hubei province (east) along the main stream of the upper Changjiang River and its tributaries and inundates a total water surface area of approximately 1080 km^2. The average depth of the reservoir is about 70 m, and maximum depth in front of the dam is about 170 m. According to the operation scheme, the reservoir is impounded to the maximum level of 175 m in the dry season (October–April) for energy generation and subsequently emptied to the base level of 145 m in the rainy season (May–September) for flood control. Before its full operation in 2009, there were three stages of water impoundment to different heights. The water level was first raised to 135 m in 2003, followed by increases to 156 m and 172 m in 2006 and 2008, respectively. The climate of the reservoir region is a subtropical monsoon, with a mean annual temperature of 15–19°C, mean annual precipitation of 1 250 mm, and relative humidity of 77% (Li et al., 2017, 2018). Previous studies in this reservoir have shown the immediate effects of impoundment on fish assemblages or single species (Duan et al., 2002; Wu et al., 2007; Gao et al., 2010, 2016). However, fish assemblage structure and spatial pattern in TGR based on long-term data remain poorly documented.

In this study, we aimed to investigate the spatial pattern in fish assemblage related to reservoir zonation (division into LZ, TZ, and RZ). We hypothesized that nonrandom fish distribution along the river-dam gradient manifesting in differences between the three zones in assemblage variables.

2 MATERIAL AND METHOD

2.1 Study area and sampling

According to the differences in hydrological characteristics, three typical zones (riverine zone, transitional zone, and lacustrine zone) in TGR are distinguishable along its longitudinal axis. The upstream riverine zone is a lotic environment with the average water velocity of 0.6–1.5 m/s. Moreover, the water is characterized by lower conductivity and lower concentrations of NO_3-N, particulate matter, and Chl *a* relative to the downstream sites. The lacustrine zone is characterized by higher Chl *a* that was probably due to the higher phytoplankton productivity and biomass that occurs in conjunction with the low flow velocity of 0.1–0.2 m/s. The channel length is 524 km. All characteristics of the transitional zone are intermediate relative to riverine and lacustrine ones with the channel length of 140 km. For the present study, fish sampling was conducted at four localities: 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). The Hejiang reach is defined as a riverine zone, which is still under conditions of natural flow, upstream of the backwater of the TGR. The Mudong reach is about 560 km upstream from the TGD, being a typical transitional zone. Wanzhou and Zigui are both in the lacustrine zone. The Wanzhou reach, which is located 286 km upstream from the TGD, has been inundated after the first impoundment in 2003. The Zigui reach located just one kilometer away from the TGD. More sampling sites were retained in the lacustrine zone because of its relative extensive surface.

Fish samplings were conducted two times each year in spring (May–June) and autumn (September–October) from 2006 to 2015 (except Zigui from 2008 to 2015). Each sampling continued for about three weeks, with each surveyed site having approximately

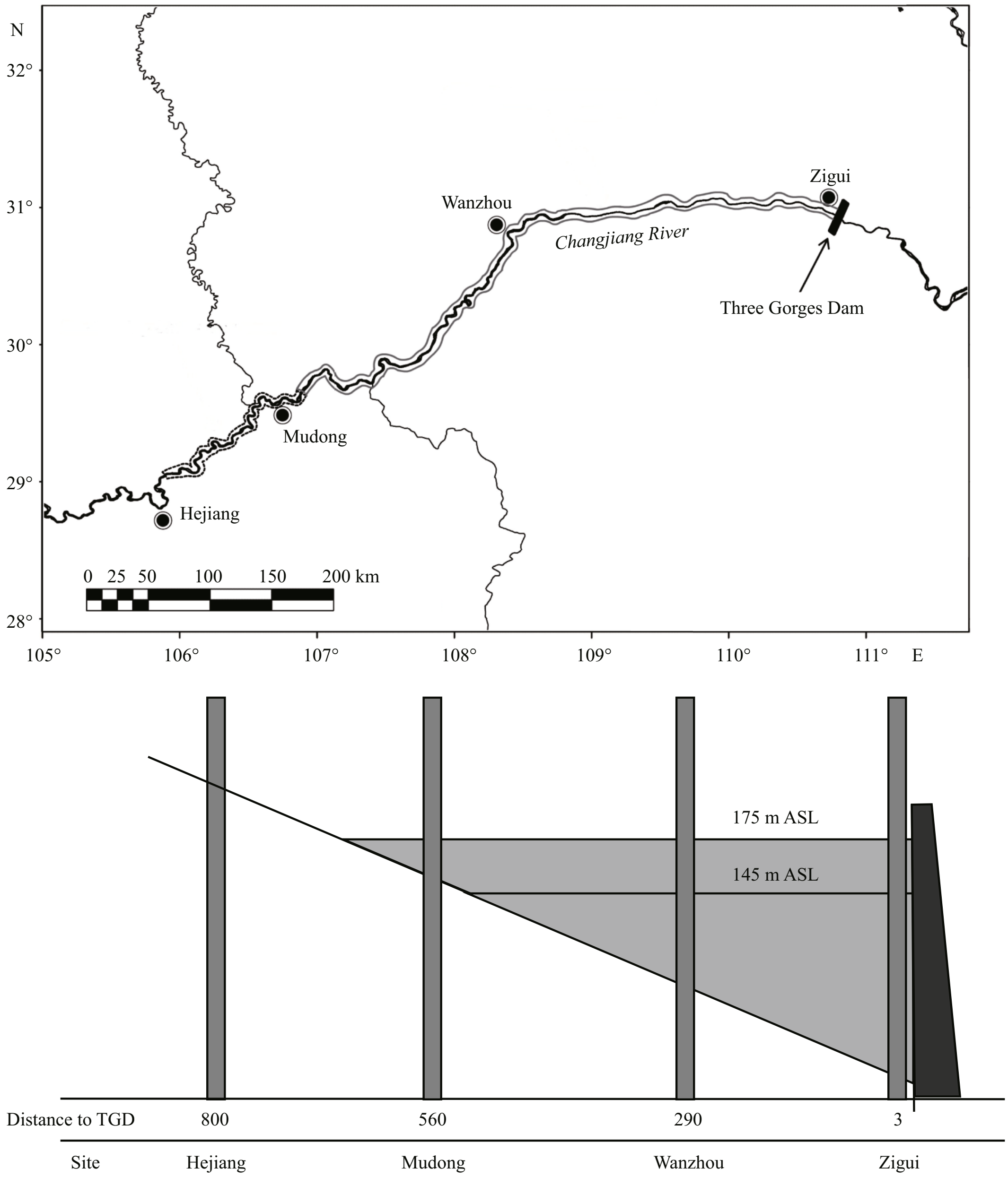

Fig.1 Study area and locations of the sampling sites upstream the Three Gorges Dam (TGD)

Fish samplings were conducted two times each year in spring (May–June) and autumn (September–October) from 2006 to 2015. ASL, above sea level; 175 m ASL is the normal pool level above sea level; 145 m ASL is the limited water level in flood season.

20–30 km long. Local experienced fishermen were employed to set the nets in the whole reach for improving the catches. The sampling area was constant in each site. To catch fish in mid-channel, drifting gill nets (100 m in length; mesh sizes ranged from 50 to 120 mm) were used to capture fish from positions near the bottom and low in the water column, and seines and trawl nets (mesh size = 1 or 2 cm) were used to capture fish from middle-upper levels of the water column. Stationary gill nets (35 m in length, mesh sizes ranged from 50 to 100 mm), hoop nets (mesh sizes of 1 cm), and long-lines (200–1 900 hooks per line) were used to capture fish in the near-shore areas. Among these, stationary gill nets and long-lines were used to capture fish from all layers of the water column, and hoop nets captured fish near the bottom. Fishing of each boat usually lasts about 12 h each day, following the fishermen's experience. Each fishing boat had one catch per day and most of the boats were investigated every day during the sampling period. Fish were identified, counted, measured (to the nearest mm) and weighed (to the nearest g). In a total of 3 440 boat-days of fish catches were sampled (Table 1).

Table 1 Details of fishing sampling involved of the upper Changjiang River

Sampling sites	Abbreviation	Zone	Sampling year	Number of boat-days
Hejiang	HJ	Riverine zone	2006–2015	785
Mudong	MD	Transitional zone	2006–2015	841
Wanzhou	WZ	Lacustrine zone	2006–2015	996
Zigui	ZG	Lacustrine zone	2008–2015	818

2.2 Data analysis

Relative abundance was calculated using the individual numbers of each species divided by the total number of individuals in sampling events. Similarly, relative biomass was calculated using the ratio of each species biomass to total biomass of the fish landings in each sampling reach. Additionally, we assessed the functional structure of increasing and declining trends using functional trait classifications including trophic guilds (Ding, 1994), life history strategies (Li, 2012; Liu, 2013), and habitat use guilds (Ding, 1994). Trophic guilds were defined by combining the information available on predominant diet and stomach examination of each species. For example, herbivorous species preyed mainly on vegetal fragments (seeds and leaves). The trophic guilds were classified as herbivorous, insectivorous, omnivorous, periphytivorous, piscivorous and planktivorous species. Fish life history strategies were classified using methods described by Li (2012) following the Winemiller and Rose (1992) life history model, which classified fishes into periodic, opportunistic, or equilibrium strategists. Habitat guild classifications were defined as those fish species requiring free-flowing lotic habitats for the whole life (i.e. rheophilic species), fish species whose all stages of life history can occur in both lotic and lentic waters (i.e. eurytopic species), or fish species whose all stages of life history are confined to lentic waters (i.e. stagnophilic species).

To elucidate the spatial pattern of fish distribution between river segments, Shannon-Wiener diversity index (H') of each sampling site was calculated. Simple linear regression was used to determine the relationship between the number of exotic species and the number of native species. One-way analysis of Similarity (ANOSIM) was used to conclude the significance of spatial variation in the structure of fish assemblage. Similarity percentage analysis (SIMPER) was calculated to identify species that contributed most to the dissimilarity among sampling sites at inter-zone levels. ANOSIM and SIMPER tests were performed with PRIMER v. 5.0 for Windows (Clarke and Warwick, 1994). Sampling location differences and annual differences of species richness and abundance were tested statistically with the Kruskal-Wallis test and post-hoc tests implemented in SPSS software (IBM SPSS Statistics 20; SPSS Inc., Chicago, IL, USA). All statistics were considered significant at the level of $P<0.05$. All graphs were plotted using Origin 8.0 software (OriginLab, Northampton, MA).

3 RESULT

3.1 Species richness, diversity, and abundance in the TGR

A total of 568 526 fish specimens weighing 18 611.9 kg were collected during the present study, belonging to 133 native fish species from 18 families. Overall, Cyprinidae had the greatest number of species (77), followed by Cobitidae (16), Bagridae (10), and Homalopteridae (5). Fish richness, measured as the number of native species per site, ranged from 44 to 87. Species richness decreased along a river-dam gradient, with 71, 68 and 52 species in the riverine, transitional and lacustrine zone, respectively (Fig.2a).

Variation in the diversity index (H') ranged from 1.60 to 3.04 depending on sampling location. The riverine and transitional zones (H' for Hejiang and Mudong was 2.67) presented higher average diversity index than the lacustrine zones (H' for Wanzhou and Zigui was 1.94) (Fig.2b). Moreover, a greater proportion of endemic fish species in RZ and TZ catches were both higher significantly than that in LZ (Kruskal-Wallis test, $P<0.05$) (Fig.2c, d).

3.2 Spatial distribution of exotic fish species

Eighteen exotic species from 10 families were recorded in the samples after the TGR impoundment: *Protosalanx hyalocranius*, *Salangichthys tangkahkeii*, *Hemisalanx brachyrostralis*, *Neosalanx taihuensis*, *Acipenser schrenckii*, *Polyodon spathala*, *hybrid sturgeon Huso dauricus* × *Acipenser schrenckii*, *Tinca tinca*, *Megalobrama amblycephala*, *Cirrhinus molitorella*, *Ietalurus punetaus*, *Micropterus salmoides*, *tilapia*, *Lucioperca lucioperca*, *Clarias leather*, *Colossoma brachypomus*, *Ameiurus melas*, *Gambusia affinis*. Among these exotic species, only *P. hyalocranius*, *I. punetaus*, *M. amblycephala*, tilapia, are very common and widespread in TGR.

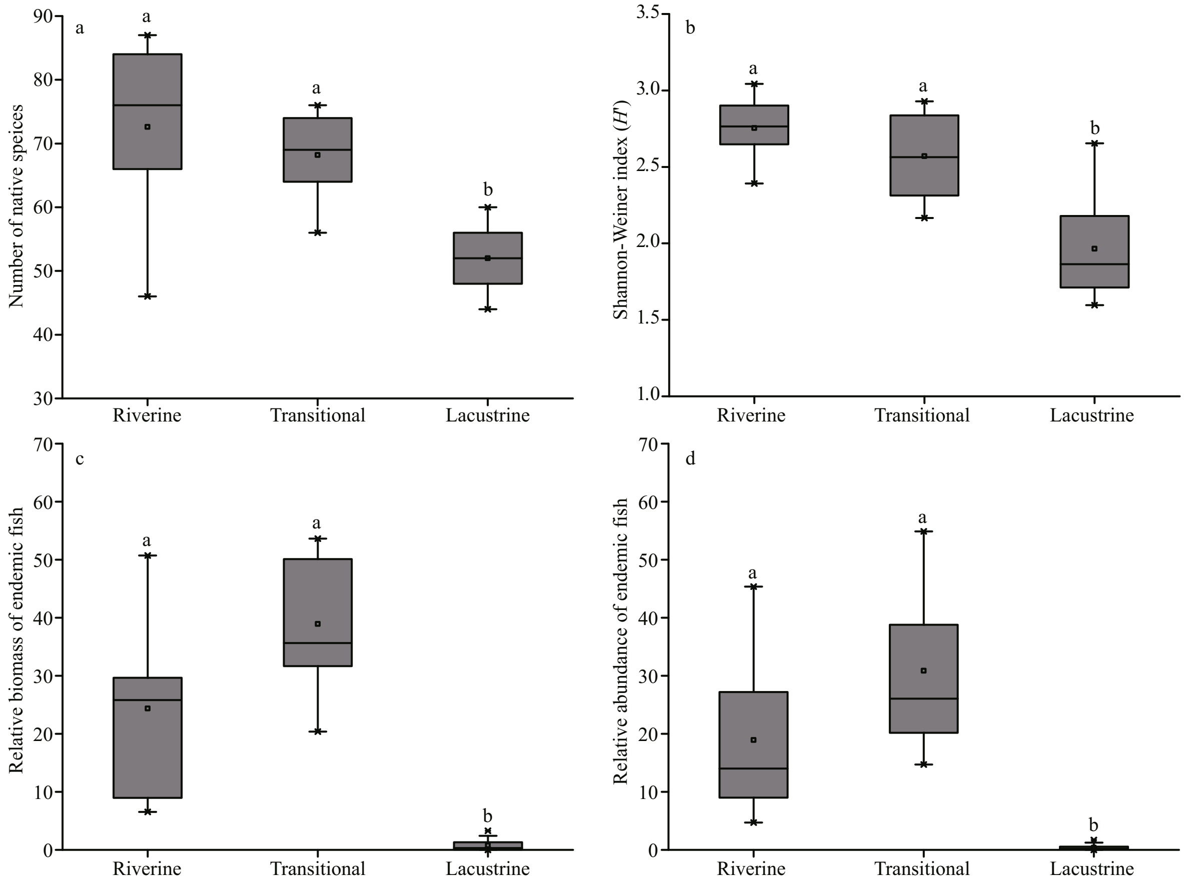

Fig.2 Boxplots of the diversity indices of fish assemblages (a and b) and changes in the relative biomass and the individual percentage of the endemic fish species (c and d) in the three zones

Boxes represent the interquartile range, central bars represent the median, and solid lines represent the data range. Corresponding letters denote means that do not statistically differ from one another.

Furthermore, significantly more exotic species individuals per year were sampled in LZ (Kruskal-Wallis test, $P<0.05$) (Fig.3). Combined with the spatial distribution of native species, our results indicated that the presence of exotic species was correlated with decreasing richness of native fishes by the linear regression ($R^2=0.968$).

3.3 Assemblages structure and fish zonation

Fish assemblages were found very different among the three zones. The average dissimilarity between RZ and LZ was 62.7%. Seventeen species contributed nearly 60% of the observed dissimilarity in the fish assemblages. Among them, six species, *Coreius guichenoti*, *Coreius heterodon*, *Pelteobagrus vachelli*, *Rhinogobio ventralis*, *Silurus meridionalis*, *Rhinogobio cylindricus*, were abundant in RZ while five species, *Aristichthys nobilis*, *Hemiculter bleekeri*, *Cyprinus carpio*, *Hypophthalmichthys molitrix*, *Pseudobrama simoni*, were abundant in LZ (Table 2).

The average dissimilarity between TZ and LZ was 64.5%. SIMPER analysis showed that 14 species contributed to nearly 62% of the dissimilarity. Among the 14 species, *Coreius heterodon* and *Coreius guichenoti* were still the dominant species with the

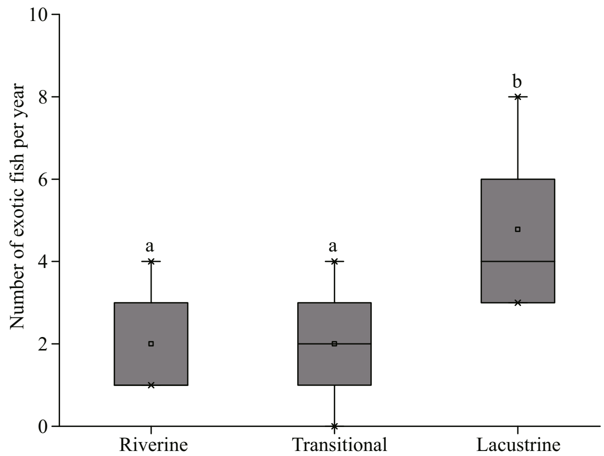

Fig.3 Spatial variability in the number of exotic species in the three zones upstream of TGD

Explanations are the same as in Fig.2.

Table 2 The dissimilarity of fish assemblage among the three zones in TGR based on the analysis of similarity (ANOSIM)

Species	Average abundance		Contribution (%)
	Riverine	Transitional	
RZ versus TZ (global test, R=0.711, P<0.05), average dissimilarity=45.4			
Silurus meridionalis	8.53	1.15	5.94
Rhinogobio cylindricus	3.72	22.04	5.91
Coreius heterodon	8.89	35.71	5.89
Aristichthys nobilis	6.7	1.17	5.05
Spinibarbus sinensis	3.33	0.13	4.93
Rhinogobio ventralis	6.17	2.59	4.58
Pelteobagrus vachelli	15.63	4.61	4.10
Botia superciliaris	2.2	0.43	3.73
Cyprinus carpio	6.23	3.31	3.30
Coreius guichenoti	13.87	10.52	3.23
Ctenopharyngodon idellus	3.19	0.91	3.13
Hypophthalmichthys molitrix	2.08	0.23	2.93
Rhinogobio typus	1.66	3.24	2.79
Leiocassis longirostris	2.36	1.28	2.49
Leptobotia elongata	1.98	0.56	2.41
RZ versus LZ (global test, R=0.911, P<0.05), average dissimilarity=62.7			
Coreius guichenoti	13.87	0.14	6.18
Hemiculter bleekeri	0.22	10.62	5.28
Coreius heterodon	8.89	1.82	4.25
Pelteobagrus vachelli	15.63	2.23	4.13
Rhinogobio ventralis	6.17	0.01	4.00
Silurus meridionalis	8.53	1.53	3.89
Rhinogobio cylindricus	3.72	0	3.80
Pseudobrama simoni	0.15	5.47	3.79
Hypophthalmichthys molitrix	2.08	8.32	3.58
Aristichthys nobilis	6.7	17.36	3.52
Spinibarbus sinensis	3.33	0.39	3.07
Carassius auratus	1.27	5.43	2.86
Botia superciliaris	2.2	0.01	2.81
Leptobotia elongata	1.98	0.01	2.66
Cyprinus carpio	6.23	10.16	2.60
Parabramis pekinensis	0.01	2.94	2.55
Silurus asotus	1.51	2.96	2.45
TZ versus LZ (global test, R= 0.939, P<0.05), average dissimilarity=64.5			
Rhinogobio cylindricus	22.04	0	8.44
Coreius heterodon	35.71	1.82	8.42
Coreius guichenoti	10.52	0.14	6.43
Aristichthys nobilis	1.17	17.36	5.74
Hemiculter bleekeri	1.1	10.62	4.71
Hypophthalmichthys molitrix	0.23	8.32	4.50
Pseudobrama simoni	0.16	5.47	4.10
Cyprinus carpio	3.31	10.16	3.10
Carassius auratus	0.91	5.43	3.09
Silurus asotus	0.37	2.96	2.74
Saurogobio dabryi	1.53	4.35	2.71
Parabramis pekinensis	0.11	2.94	2.70
Squalidus argentatus	0.58	3.02	2.53
Ctenopharyngodon idellus	0.91	3.17	2.53

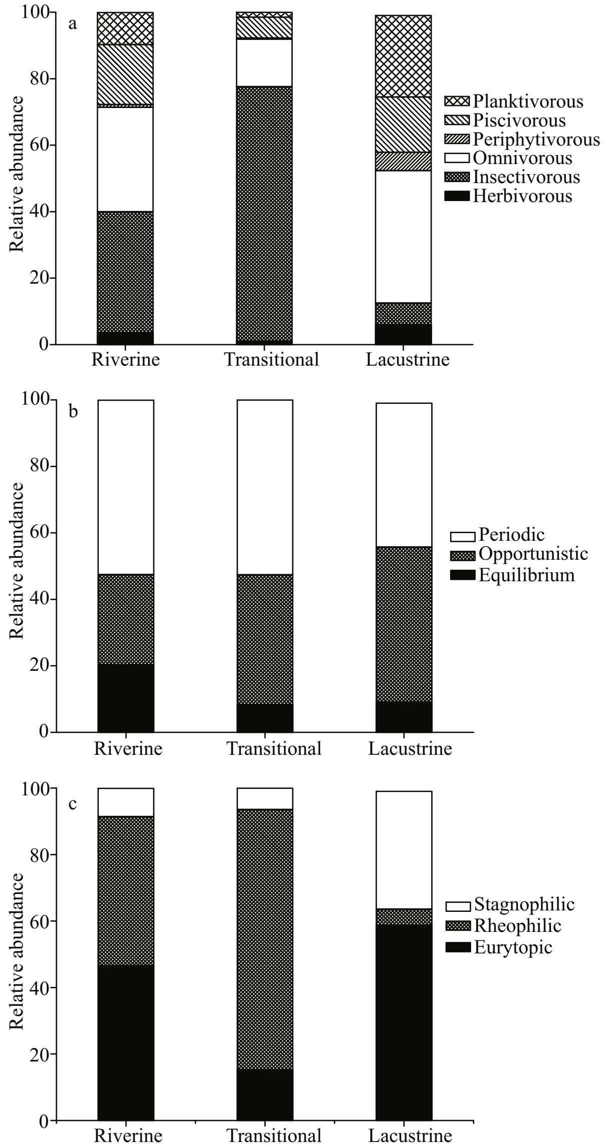

Fig.4 Stacked bar plot of the trophic, reproductive and habitat guilds in the three zones upstream of TGD

Relative abundance (%) was calculated using the individual numbers of each species divided by the total number of individuals in sampling events. Trophic guilds were classified as herbivorous, insectivorous, omnivorous, periphytivorous, piscivorous and planktivorous species; life history strategies were classified as periodic, opportunistic, or equilibrium strategists; habitat guilds were defined as rheophilic species, eurytopic species, and stagnophilic species.

mean relative abundances greater than 45% in TZ. However, the mean relative abundances of *Coreius guichenoti*, *Coreius guichenoti*, *Rhinogobio cylindricus* declined to less than 1% in LZ (Table 2).

3.4 Functional characteristics of fish zones

Functional groups of the fish assemblages were found very different among the three zones (Fig.4).

Higher percentages of insectivorous species were found in riverine and transitional zones. The lacustrine zone had distinct fish assemblages dominated by omnivorous and planktivorous species and a few insectivorous species after the TGR impoundment. For life history strategies, fish assemblages in the lacustrine zone had a proportionally higher representation of the opportunistic strategists than that in the riverine and transitional zone, which had a proportionally higher representation of the periodic strategists. For habitat guilds, the riverine and transitional zone was dominated by rheophilic species. On the contrary, these species were largely absent in the lacustrine zone, where had assemblages dominated by eurytopic and stagnophilic species.

4 DISCUSSION

4.1 TGR impacts on the upper Changjiang River fish assemblage

Long-term changes have occurred to the upper Changjiang River fish assemblage since the creation of TGR. The most obvious changes were: (1) species richness declined from the fluvial to the lacustrine zones; (2) a reduction in the abundance of piscivorous, insectivorous species, equilibrium strategists, and rheophilic species in lacustrine zones; (3) the establishment of populations of non-native fish species in TGR. In general, fish zonation reflected declines of rheophilic and endemic species and an increased proportion of wide-adapted species in TGR.

Many studies have reported substantial changes in upstream fish assemblages resulting from impoundment (Quinn and Kwak, 2003; Quist et al., 2005). For example, Taylor et al. (2001) reported that the fish assemblage in an Illinois stream upstream from a reservoir shifted from a cyprinid-dominated to a centrarchid-dominated assemblage following impoundment. Winston et al. (1991) reported similar results wherein the construction of a small impoundment on an Oklahoma stream resulted in the extirpation of native cyprinids from upstream reaches. For the upper Changjiang River, the findings of the present study revealed distinct differences in species composition in space and time.

Prior to the impoundments of TGR, both lotic and lentic species were abundant in catches sampled from reaches upstream of TGD (Ding, 1986). However, water regime and habitat environmental conditions changed in the post-impoundment period because of TGD impoundment, which results in fish zonation in TGR. As a riverine zone, the Hejiang reach remained natural flow regime. The comparatively highly structured habitat of the Hejiang reach, comprised of stones and rocks of different sizes supported high biodiversity (Liu et al., 2012). Fish assemblages in Hejiang reach were dominated by species preferring rubble substrates and fast to moderate current velocity habitats, such as *C. guichenoti*, *C. heterodon*, *R. ventralis*, *R. cylindricus*. Many species probably were forced to move upstream and congregated into the riverine zone upstream because of the TGR impoundment, which was another cause of high diversity in Hejiang reach. In general, the transition zone functions as an ecotone, usually associated with higher overall species diversity. For Mudong reach, where river and reservoir conditions overlap, the coexistence of species from both lotic and lentic systems was observed by our investigation. *Rhinogobio cylindricus*, a migratory species typical of lotic systems, and *A. nobilis*, a habitat generalists species were recorded. These may increase local species richness and diversity, and the same phenomenon occurred in other reservoirs (Terra et al., 2010).

On the other hand, localized extirpations and dramatic reductions in species diversity occurred in lacustrine zones (Wanzhou and Zigui) (Fig.2). Our results showed that the lacustrine zone was inhabited by fewer native species, and supported mainly the omnivorous *H. bleekeri*, which migrates toward the littoral to feed, and the planktivore *H. molitrix*, *A. nobilis*, which inhabits deep pelagic areas. All these species were belonging to the eurytopic and stagnophilic guilds. However, the fish composition in Wanzhou was similar to that in Mudong before the impoundment (Ding, 1986). *C. guichenoti* and *C. heterodon*, both of them were typical rheophilic species, having a relative biomass of more than 70% of the catches in Wanzhou reach in the 1970s. However, it is estimated that the abundance decreased to 16.8% from 1997 to 2000 and furtherly decreased to 8.5% from 2005 to 2006 (Duan et al., 2002; Wu et al., 2007). Now, these rheophilic species were encountered hardly in the catches of the lacustrine zones (Table 1). It is suggested that the new environmental conditions that occur in the LZ impose a severe environmental filter (dos Santos et al., 2017). Species adapted to lacustrine environments may colonize and become dominant, while other rheophilic species are locally eliminated (Welcomme et al., 2006; Lasne et al., 2007; Ferreira and Petrere, 2009).

In this study, another significant incidence is that 18 exotic fish species had been found. However, there were no exotic fish records in the upper Changjiang River before TGR impoundment (SCYFIT, 1975; Ding, 1986). The results of the present study indicated that the maximum number of exotic species occurred in Zigui reach. *H. brachyrostralis*, *P. spathala*, *C. molitorella*, *C. leather*, *A. melas*, *G. affinis* was captured only in lacustrine zones. Previous studies also indicated that some populations had been in the stage of the outbreak in Zigui reach (Gong et al., 2009). The reasons for the occurrence of exotic fish were likely related to (1) escaped of exotic fish from the net-cages in the reservoir could increase the invasion probability in local waters; (2) impoundments provided greater opportunities for exotic fish to spread in the newly constructed reservoir because of the vacant niches.

Though we did not determine the specific mechanism for changes in fish assemblage structure upstream of TGD in our study, habitat alteration (altered flow regimes and water quality) and the introduction and/or colonization of exotic species may be the main causes (Taylor et al., 2001; Reid, 2004). As explained by Taylor et al. (2001) for the fish communities in North American, observed shifts in TGR species may attribute to: (1) the loss of flowing habitat required for species such as *C. guichenoti*, *R. ventralis*; (2) the creation of abundant still and vegetated habitats suitable for eurytopic and stagnophilic species for spawning and nursery; and (3) the susceptibility of native cyprinid species to piscivorous exotic species.

4.2 Management and conservation strategy

In view of the results from this study and some previous research, different management and conservation strategies in different zones should be taken. Firstly, RZ and TZ were the main habitats of the endemic species inhabiting the upper Changjiang River. After a large development of cascade hydropower plants in the upper reaches according to the integrated plan for the Changjiang River basin, these areas can provide a major refuge for the native fishes, particularly for the endemic species (Park et al., 2003; Chen et al., 2006). As result, protection of the endemic species and law enforcement in RZ and TZ should be strengthened. It is recommended that fish priority protected areas to be established in TZ. Further studies should be conducted to understand the life history processes. This could help to develop effective plans for the conservation of the endemic species. Secondly, sustainable ecological fisheries in TGR should be carried out, including stocking enhancement and fishing management. Thirdly, close attention should be paid to the related effects and other issues caused by the exotic fish in the TGR. Previous studies have concluded that exotic fish may be seriously harmful to the fishery resources and aquatic ecological systems through competition with and predation on native species, thereby further threatening the structure and function of the receiving ecosystem (Moyle, 1986; Mack et al., 2000; Carpenter et al., 2007). However, research on the invasive fish in TGR has not been carried out yet. For this reason, we recommended that intensive monitoring would be carried out to reveal the invasive reasons and mechanisms of these exotic fish. And further, we could establish a sound early warning system and control measures.

5 CONCLUSION

The construction and operation of TGR had resulted in three distinct fish zones in TGR. These zonations have distinctive fish assemblage composition as well as functional groups. A high proportion of endemic fish species in RZ and TZ might be caused by the upstream migration of fishes from the reservoir after the impoundment. Fish assemblages in riverine and transitional zones were dominated by insectivorous species, equilibrium strategists, and rheophilic species. By contrast, fish assemblages in lacustrine zones were characterized by habitat generalists and more exotic species, such as *A. nobilis*, *H. molitrix*, and *C. carpio*.

6 DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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