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Evaluation of genetic diversity and population structure of five yellow catfish *Pelteobagrus fulvidraco* populations by microsatellite markers

by

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Abstract

Yellow catfish, *Pelteobagrus fulvidraco*, is an important commercial freshwater species in China. Knowledge about the genetic diversity of the yellow catfish is important to support the management and conservation programs, which would subsequently support the sustainable production of this species. To investigate the genetic diversity and the structure of yellow catfish in the middle and lower reaches of the Yangtze River, 125 individuals from five lakes were genotyped using 13 microsatellite markers. Moderate genetic diversity was determined in all populations, with the observed heterozygosity (H_O) ranging from 0.42 to 0.49 and the expected heterozygosity (H_E) ranging from 0.51 to 0.61. Low to moderate genetic differentiation among the populations was revealed from pairwise F_{ST} values ($p < 0.05$), as well as from analysis of molecular variance (AMOVA). The UPGMA dendrogram and Bayesian clustering analysis indicated a correlation between genetic differences and geographic distance – four populations from the lower reaches clustered together, whereas the Poyang Lake (PY) population formed a separate cluster. The present study would be helpful in the wild stock management and artificial propagation programs for yellow catfish in the middle and lower reaches of the Yangtze River.

Key words: *Pelteobagrus fulvidraco*, genetic diversity, population structure, microsatellite

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Introduction

The occurrence of yellow catfish *Pelteobagrus fulvidraco*, a small fish belonging to the order Siluriformes, is restricted to freshwater habitats, mostly in Asia. Because of its excellent meat quality, yellow catfish has become an important freshwater aquaculture species in China. Due to its high market value, artificial propagation and culture of this species has increased rapidly in recent years (Zhong et al. 2013). Parents of yellow catfish in artificial propagation were mostly caught in the wild. Recently, the wild stocks of yellow catfish have suffered a certain degree of damage because of overfishing and pollution. To preserve the wild sources and to ensure the quality of offspring, information on the genetic diversity and the structure of species populations is crucial.

Microsatellites are a useful tool for genetic analyses because of their abundance across genomes and the high level of polymorphism (Tautz & Renz 1984). In recent years, microsatellites have been widely used in aquaculture to analyze the genetic variation, to construct linkage maps, to map the quantitative traits loci and to perform genetic identification (DeWoody & Avise 2000). Previous studies isolated several polymorphic microsatellite makers of yellow catfish, which were then applied to investigate genetic structure of populations from the upper and middle reaches of the Yangtze River and other river basins in China (Ma et al. 2006; Liu et al. 2008; Li et al. 2009; Wu et al. 2010). However, the spawning grounds of yellow catfish are located mainly in lakes. Many lakes distributed in the middle and lower reaches of the Yangtze River form a group of shallow lakes, unique in the world. So far, there has been no report on the genetic diversity and population structure of yellow catfish from the middle and lower reaches of the Yangtze River.

In this study, we selected thirteen available microsatellite markers from the existing literature (Liu et al. 2008; Li et al. 2009; Wu et al. 2010) and genotyped five yellow catfish populations sampled from lakes in the middle and lower reaches of the Yangtze River. The objectives of the present study were as follows: (1) to fully understand the genetic diversity and population structure of yellow catfish in five lakes; (2) to gather genetic data to help artificial propagation programs, effective conservation and management of yellow catfish.

Materials and methods

Sample collection

Yellow catfish specimens were collected from five lakes in the middle and lower reaches of the Yangtze River, China, including Poyang Lake (PY) in the middle reaches, Caohu Lake (CH), Gehu Lake (GH), Hongze Lake (HZ) and Taihu Lake (TH) in the lower reaches (Fig. 1). Twenty five individuals were randomly sampled from each population. A caudal fin clip from each specimen was taken and stored in 95% ethanol for DNA extraction.

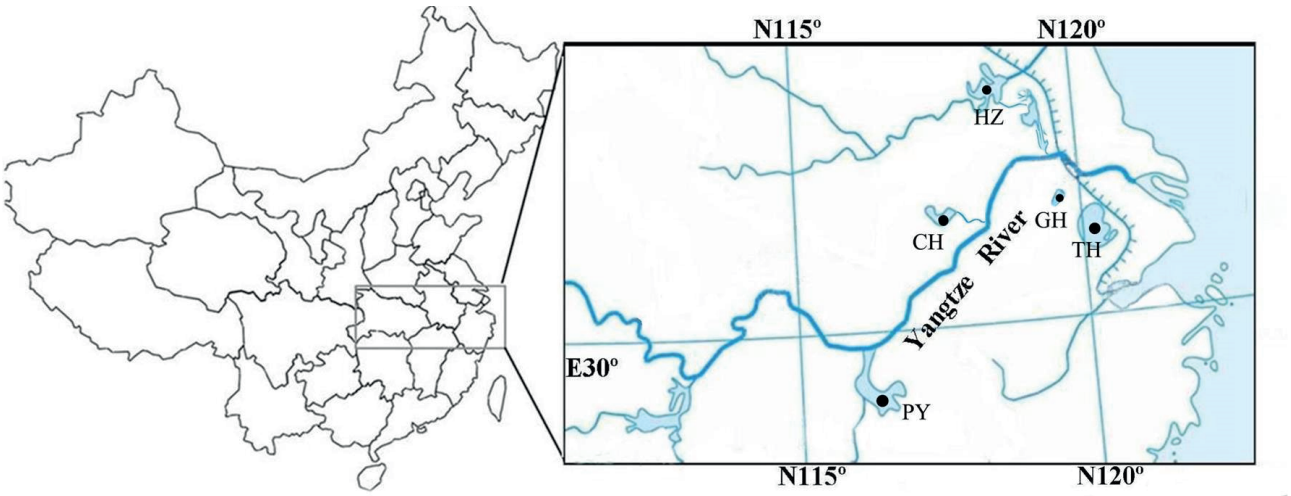

Figure 1

Map of sampling locations (indicated by •) of yellow catfish from five lakes in the middle and lower reaches of the Yangtze River, China. The five sampling lakes were Taihu Lake (TH), Gehu Lake (GH), Hongzehu Lake (HZ), Chaohu Lake (CH), and Poyang Lake (PY)

Genomic DNA extraction, amplification, and genotyping

Total genomic DNA was extracted from the tail fin using the Ezup Column Animal Genomic DNA Kit (Sangon, Shanghai) following the manufacturer's protocol. Quantity and quality of the extracted DNA were estimated on 1% agarose gels stained with ethidium bromide (EB). Thirteen specific microsatellite loci of yellow catfish (Table 1) were amplified by PCR on a Mastercycler gradient apparatus (Eppendorf).

PCR was conducted in a reaction mixture of 20 µl containing 1 µl genomic DNA (50 ng μl^{-1}), 2µl of 10 × PCR buffer [40 mmol KCl, 8 mmol Tris-HCl (pH 8.8), 120 nmolKCl, 1.2 mmol $MgCl_2$], 400 nmol each of reverse and forward primers, 0.5 U Taq DNA polymerase. The PCR amplification conditions used herein were as follows: initially denatured at 94°C for 5 min followed by 30 cycles (denaturation at 94°C for 30 sec, annealing at 51–60°C for 30 sec, and extension at 72°C for 1 min), with a final extension for 10 min at 72°C. Electrophoresis was conducted in 1.4% agarose gel to confirm successful DNA amplification.

The PCR products were run on 8% polyacrylamide gels in 0.5 × TBE buffer for 2–3 hours. After electrophoresis, the gels were silver stained and photographs were taken using a Nikon Coolpix 4500 digital camera. The 25 bp DNA Ladder (Invitrogen, USA) was used to determine the allele size. Each sample was screened 2–3 times for each primer in order to reduce allele misscoring.

Data analysis

The expected heterozygosity corrected for sampling bias, the observed heterozygosity (H_O), the expected heterozygosity (H_E), the polymorphic information content (PIC), the inbreeding coefficient (F_{IS}) and the estimated null allele frequencies were calculated for each locus across each population using POPGEN32 (Rousset & Raymond 1995). The GENEPOP 3.4 software (Raymond & Rousset 1995) was used to perform the exact test for the Hardy-Weinberg equilibrium (HWE) using the Markov Chain method with 1000 iterations and considering heterozygote deficiency as the alternative hypothesis. Exact tests for deviations from HWE were performed using the GENEPOP software and applying the default parameters (dememorization number 1000; batches 100; and repetitions per batch 1000). In addition, to

Table 1

Information of the thirteen microsatellite loci analyzed in five populations of yellow catfish

Locus	Motif	Primer sequence (5′–3′)	Temp. (°C)	Expected size (bp)	Number of alleles	Reference
AG12	$(GA)_6A(AG)_{26}$	F: TTCTGAGGGGATGGTG R: GCGGTGCTCTGTGGTTGTC	60	228–335	5	Wu et al. 2010
AG48	$(AG)_{13}GGT(GA)_5GC(GA)_9$	F:GCTGATACATTCTTTATTAGGGCACC R: GTCGCACTTCCCCTCTGTCA	57	185–451	6	
AG128	$(AG)_{23}$	F: AAACCGACGGGACAAAAGAT R: CTCTGCCTCACTAACT	51	91–145	9	
CT30	$(CT)_9T(TC)_2TT(TC)_{21}$	F: ACACCAAAACATTGTGCTAC R: ATTCAGGAGATCCCGACACT	55	237–298	4	
CT42	$(TC)_6$	F: GCAGAGGGTTGCTTTTGCCTTTTA R: CAACAATCACATTCTATGAGGAGT	55	125–150	3	
CT81	$(CT)_6G(TC)_4TG(TC)_8$	F: GTCTCCATCACTGCCACAT R: TCAGCAATTATGTGAAAAGTGTCT	55	126–176	5	
HLJYC13	$(CA)_{23}$	F:GACCCAGTTCCCACATTG R:GGCTACCACATCCCTCAT	58	179–207	4	Li et al. 2009
HLJYC17	$(TG)_{25}$	F:ATGGTATAAACATGGTGCTA R:ATGATGCTGATAGGGTGA	58	170–188	3	
HLJYC31	$(CA)_{26}$	F:CAGGATGGAGGTGTAAAG R:ATAAAGCTGTGATGTGCC	55	285–317	4	
HLJYC45	$(TG)_{29}$	F:TGGGTCTCTCTGGGTTCA R:GCGGCTTCACTCACTTCC	56	278–312	3	
HLJYC60	$(CA)_{28}(TTTG)_7$	F:GATCAACGTCCAACAGAG R:GGAAAGAAAGATGGCTAG	56	250–282	4	
HLJYC66	$(TG)_{27}$	F:ACACTGACATACACTGGCATAA R:CTGGCAACGTGTTTCTGGCATAA	56	243–295	4	
HSY105	$(CTAT)_{14}$	F:ACTCACGTTGTCAGTTTATCAC R:ACACAAGAAATCCCCTCG	53	150–172	4	Liu et al. 2008

Motif – sequences inside parenthesis indicate the motif sequence of the microsatellite DNA and subscripted numbers indicate the number of repeats; Temp. – annealing temperature for PCR

determine whether deviations from HWE were toward heterozygote excess or deficit, HWE tests were carried out for each locus in each population along with a global test for all populations. Corrections for multiple significance tests were performed using Fisher's method. Analysis of molecular variance (AMOVA) was performed with Arlequin version 3.01 (Excoffier et al. 2005) to test for significant differences in genetic diversity between the populations.

The MEGA 6.0 software package (Tamura et al. 2013) was used to construct an UPGMA tree of relationships between the populations. Bayesian clustering analysis implemented with Structure 2.3.4 (Pritchard et al. 2000) was performed to estimate the most likely number of genetic clusters (K) of populations and assign individuals to those clusters without prior information on the origin of samples. The admixture model was employed, with 20 000 burn-in periods and 1 000 000 Markov-chain Monte Carlo (MCMC) iterations based on the discriminating loci. To identify the most likely posterior probability K value, the simulation program was run with increasing numbers of clusters (K) from two to five, and a plateau was used to indicate the most likely K (Falush et al. 2007). For each successive value of K, the inferred clusters were analyzed and visualized as colored box plots using the Distruct program (Rosenberg 2004).

Results

Genetic Variability

For the 125 individuals from the five populations, a total of 58 alleles were identified across 13 microsatellite loci ranging from 90 to 450 bp. The average number of alleles per locus was 4.4, ranging from 3 (loci CT42, HLJYC31 and HSY105) to 9 (loci AG128). The observed heterozygosity (H_O) and the expected heterozygosity (H_E) of all microsatellite loci were 0.46 and 0.60, respectively. The polymorphic information content (PIC) ranged from 0.08 to 0.81, with an average of 0.53 per locus (Table 2).

Diversity measures for each population showed that the mean number of alleles per locus was very similar in each population. The GH and HZ populations were the most diverse populations having the highest allelic richness, 3.13 and 3.08 respectively, while the PY population – the lowest one (2.61). The observed heterozygosity (H_O) and the expected heterozygosity (H_E) for each population ranged from 0.42 (PY) to 0.49 (CH) and 0.51 (PY) to 0.61 (CH and GH). For all populations, the observed heterozygosity values were marginally lower than the expected values. The polymorphic information content (PIC) ranged from 0.46 to 0.55. Most populations were found to be highly informative (PIC > 0.50), except the PY population. Data on each locus for each population are given in Table 2.

Of the 65 population-locus cases, 42 (64.6%) were in HWE ($p > 0.05$), while another 23 (35.4%) showed significant deviation ($p < 0.05$). Significant deviations from HWE at the locus level were found at HLJYC17 in five populations. At the locus AG12 and HSY105, departure for HWE was observed in four populations. Of the 13 markers assessed for HWE by the multi-population test, significant and highly significant departures were observed in two loci. However, global HWE tests revealed no deviations ($p > 0.05$) in all populations (Table 3). This was also reflected by the positive inbreeding coefficient (F_{IS}) value. The F_{IS} value in each population was moderate and ranged from 0.182 (PY) to 0.257 (GH).

Genetic differentiation and population structure

The pairwise F_{ST} presented in Table 4 showed a significant difference between PY and the other four populations, indicating a moderate genetic differentiation ($0.05 < F_{ST} < 0.15$), whereas there was a low genetic difference between the other four populations. The genetic distances (D_A), displaying large variation between pairs of the populations, revealed close relationships between the HZ and TH populations (0.0541) and the GH and HZ populations (0.0551). The D_A value for the PY-HZ pair (0.1409) was comparatively greater, which further supported the highest degree of divergence between these populations (Table 4). AMOVA showed significantly low to moderate population differentiation, with 4.67% of the molecular variance among the populations from five lakes ($p < 0.001$), while most variation was found within the populations (95.33%). There were significant differences between the middle and low groups, accounting for 0.44% of the total variation (Table 5).

A UPGMA dendrogram of the five populations based on genetic distance estimates is shown in Fig. 2. The PY population from the lake located in the middle reaches of the Yangtze River separated as an independent branch and the other four populations from the lakes in the lower reaches of the Yangtze River clustered together as a separate branch. Bayesian clustering suggested the presence of two groups (K = 2) as the most likely, although most individuals showed mixed ancestry. There was a relatively little admixture exhibited by the PY population. The Bayesian clusters were similar to those revealed by UPGMA typology (Fig. 3).

Table 2

Polymorphic information at 13 microsatellite loci of five populations of yellow catfish

Locus	CH					GH					HZ					PY					TH					Overall				
	Ae	H_O	H_E	PIC	F_{IS}	Ae	H_O	H_E	PIC	F_{IS}	Ae	H_O	H_E	PIC	F_{IS}	Ae	H_O	H_E	PIC	F_{IS}	Ae	H_O	H_E	PIC	F_{IS}	Ae	H_O	H_E	PIC	F_{IS}
AG12	2.81	0.52	0.66	0.58	0.193	4.24	0.68	0.78	0.72	0.110	3.24	0.72	0.71	0.64	-0.041	4.50	0.68	0.79	0.74	0.126	3.98	0.68	0.76	0.71	0.092	4.07	0.66	0.76	0.68	0.096
AG48	4.39	0.60	0.79	0.74	0.223	4.05	0.68	0.77	0.71	0.097	4.18	0.92	0.78	0.72	-0.209	3.38	0.64	0.72	0.65	0.091	3.64	0.48	0.74	0.68	0.339	4.61	0.66	0.79	0.70	0.106
AG128	5.43	0.84	0.83	0.79	-0.029	7.10	0.84	0.88	0.84	0.022	6.10	0.56	0.85	0.82	0.330	5.00	0.84	0.82	0.77	-0.050	5.81	0.84	0.84	0.81	-0.015	6.48	0.78	0.85	0.81	0.053
CT30	3.69	0.44	0.74	0.67	0.396	2.51	0.32	0.61	0.52	0.468	3.56	0.64	0.73	0.67	0.110	2.80	0.34	0.66	0.59	0.503	2.89	0.60	0.67	0.60	0.082	3.59	0.46	0.72	0.61	0.307
CT42	1.22	0.20	0.19	0.18	-0.082	1.08	0.08	0.08	0.08	-0.031	1.04	0.04	0.04	0.04	-0.020	1.00	0.00	0.00	0.00	NA	1.08	0.08	0.08	0.08	-0.031	1.08	0..08	0.08	0.08	-0.055
CT81	1.47	0.28	0.32	0.31	0.123	1.51	0.36	0.34	0.31	-0.061	1.18	0.16	0.15	0.08	-0.070	1.33	0.28	0.26	0.24	-0.118	1.28	0.24	0.23	0.21	-0.087	1.35	0.26	0.26	0.23	-0.032
HLJYC13	3.62	0.72	0.74	0.67	0.006	3.23	0.56	0.70	0.63	0.189	3.37	0.60	0.72	0.65	0.147	1.79	0.44	0.45	0.37	0.004	3.62	0.56	0.74	0.67	0.227	3.57	0.58	0.72	0.60	0.123
HLJYC17	2.57	0.40	0.62	0.53	0.345	3.06	0.44	0.69	0.61	0.346	3.54	0.76	0.73	0.67	-0.059	2.68	0.48	0.64	0.55	0.235	3.10	0.56	0.70	0.63	0.185	3.59	0.53	0.72	0.60	0.204
HLJYC31	2.59	0.36	0.63	0.54	0.414	2.83	0.44	0.66	0.57	0.320	2.93	0.36	0.67	0.59	0.454	2.96	0.28	0.68	0.59	0.577	2.83	0.40	0.66	0.57	0.382	2.96	0.37	0.66	0.57	0.430
HLJYC45	2.94	0.76	0.67	0.56	-0.152	2.88	0.68	0.67	0.59	-0.042	3.34	0.52	0.72	0.64	0.258	3.16	0.64	0.70	0.63	0.064	3.73	0.60	0.75	0.68	0.180	3.39	0.64	0.71	0.62	0.067
HLJYC60	3.82	0.60	0.75	0.69	0.187	3.04	0.44	0.68	0.62	0.345	3.45	0.56	0.72	0.65	0.212	3.10	0.64	0.69	0.63	0.056	3.01	0.56	0.68	0.60	0.162	3.43	0.56	0.71	0.64	0.192
HLJYC66	2.75	0.44	0.65	0.58	0.308	3.71	0.24	0.75	0.68	0.671	2.92	0.28	0.67	0.61	0.575	1.22	0.16	0.19	0.18	0.138	3.05	0.44	0.69	0.61	0.345	3.03	0.31	0.67	0.53	0.459
HSY105	1.44	0.20	0.31	0.28	0.347	1.45	0.20	0.32	0.28	0.354	1.18	0.12	0.15	0.14	0.202	1.04	0.04	0.04	0.04	-0.020	1.28	0.12	0.22	0.21	0.449	1.27	0.14	0.21	0.19	0.335
Average	2.98	0.49	0.61	0.55	0.180	3.13	0.46	0.61	0.55	0.233	3.08	0.48	0.59	0.53	0.168	2.61	0.42	0.51	0.46	0.162	3.03	0.47	0.60	0.54	0.190	3.26	0.46	0.60	0.53	0.187

Ae – Effective allelic number; H_O – observed heterozygosity; H_E – expected heterozygosity; PIC – polymorphic information content; F_{IS} – inbreeding coefficient

Table 3

p-value of Hardy-Weinberg test on five populations of yellow catfish

Locus	Test in each population					Multi-population test
	CH	GH	HZ	PY	TH	
AG12	0.000[b]	0.808	0.009[b]	0.015[a]	0.028[a]	0.015[a]
AG48	1.000	0.386	0.386	0.060	0.072	0.465
AG128	0.543	0.645	0.345	0.345	0.004[b]	0.345
CT30	0.000[b]	0.033[a]	0.018[a]	0.100	0.095	0.000[b]
CT42	0.970	0.999	1.000	1.000	0.999	0.978
CT81	0.877	0.805	0.987	0.906	1.000	0.999
HLJYC13	0.840	0.114	0.213	0.989	0.044[a]	0.115
HLJYC17	0.015[a]	0.042[a]	0.003[b]	0.000[b]	0.032[a]	0.067
HLJYC31	0.118	0.003[b]	0.089	0.061	0.095	0.114
HLJYC45	0.089	0.028[a]	0.011[a]	1.000	0.005[b]	0.034[a]
HLJYC60	0.027[a]	0.065	0.083	0.299	0.156	0.318
HLJYC66	0.252	0.089	0.384	0.275	0.198	0.987
HSY105	0.001[b]	0.123	0.015[a]	0.015[a]	0.022[a]	0.009[b]
multi-locus test	0.387	0.957	0.215	1.000	1.000	1.000

[a] $p < 0.05$, [b] $p < 0.01$

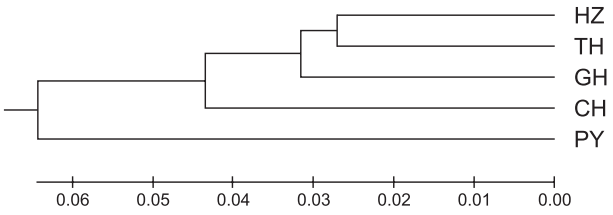

Figure 2

UPGMA tree based on genetic distances between five yellow catfish populations

Table 4

Pairwise F_{ST} values (above diagonal) and genetic distances (below diagonal) between populations

Population	CH	GH	HZ	PY	TH
CH	***	0.0302[b]	0.0275[b]	0.0810[b]	0.0471[b]
GH	0.0806	***	0.0170[a]	0.0642[b]	0.0258[b]
HZ	0.0722	0.0551	***	0.0852[b]	0.0169[a]
PY	0.1377	0.1107	0.1409	***	0.0746[b]
TH	0.1077	0.0712	0.0541	0.1253	***

[a] $p < 0.05$, [b] $p < 0.01$

Discussion

Most of the microsatellite loci analyzed in this study were highly informative (PIC > 0.5, Botstein et al. 1980). The overall number of effective alleles per locus and the expected heterozygosity were consistent with the comprehensive research of DeWoody & Avise 2000 on microsatellite variation in freshwater fish (A_E = 7.5 and H_E = 0.46). Similar to previous reports, all diversity analyses consistently indicated a moderate genetic diversity of yellow catfish (Wu et al. 2010; Liu et al. 2008; Li et al. 2009; Ma et al. 2006). However, the effective number of alleles was small in all these studies, which was most likely due to the reduced effective population size and the severe historical bottleneck (Zhong et al. 2013). Overfishing and water pollution might be responsible for the small effective size of yellow catfish in China. High fishing pressure can lead to a reduction in the effective population size and yield, and ultimately the loss of genetic diversity and population viability. Previous studies based on the analysis of mitochondrial DNA sequences have confirmed the rapid expansion following the historical bottleneck of yellow catfish (Zhong et al. 2013).

Table 5

AMOVA analysis of five populations of yellow catfish

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	Fixation index	*p* values
One group						
Among populations	4	52.276	0.18565 Va	4.67	F_{ST} = 0.047	< 0.001
Within populations	245	927.680	3.78645 Vb	95.33		
Two group (middle vs low)						
Among groups	1	23.946	0.18128 Va	4.44	F_{CT} = 0.044	< 0.001
Among populations within groups	3	28.330	0.11314 Vb	2.77	F_{SC} = 0.029	
Within populations	245	927.680	3.78645 Vc	92.79	F_{ST} = 0.072	

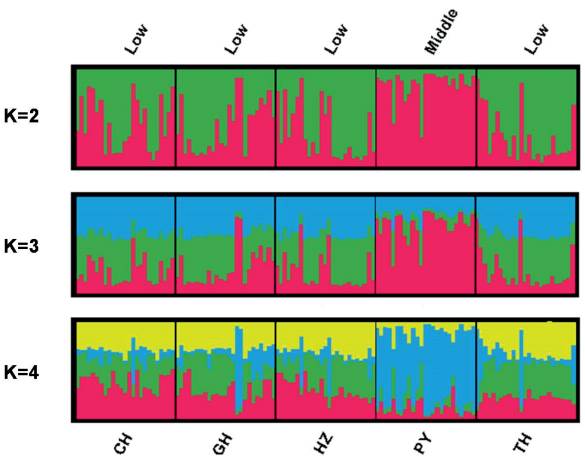

Figure 3

Bayesian clustering analysis for five populations of yellow catfish. The bar plot represents admixture coefficients. Each vertical bar denotes one individual

The comparison of the expected and observed heterozygotes indicated the heterozygote deficit in all populations. A similar phenomenon was also observed in the previous analysis of other closely related bagrid species (Powell 2012). Furthermore, positive moderate F_{IS} values confirmed the lack of heterozygotes in the five populations. The heterozygote depression could be a result of physical mixing of populations with different allele frequencies (Wahlund effect) or inbreeding under the survival pressure of overfishing as well as water pollution.

The F_{ST} values showed low to moderate genetic differentiation among the five populations. The observed results were comparable to the genetic differentiation among the populations from other river basins in previous reports (Ma et al. 2006; Li et al. 2009; Wu et al. 2010; Zhong et al. 2013). AMOVA analysis also revealed a significant genetic differentiation between the middle and lower groups, indicating a correlation between the genetic differences and the geographic distance. These results were confirmed by the UPGMA phylogenetic tree and structure simulations. It could be speculated that the divergence between the middle and lower groups was due to a long-term geographic separation and limited natural gene flow. The artificial gene flow might have also contributed to the low genetic differentiation among the lower populations.

To preserve the wild sources in China, hatchery-produced juveniles have been released annually into the lower reaches of the Yangtze River over the last two decades. However, many of these practices have been undertaken without a thorough understanding of the genetic background (Chen et al. 2012). The effective size of wild populations could be reduced through introductions of large numbers of hatchery-reared juveniles that have lower levels of genetic variation (Ryman & Laikre 1991). Large releases of sea urchins (*Strongylocentrotus intermedius* and *Pseudocentrotus depressus*) in Japan (Agatsuma et al. 2003) and shrimp (*Penaeus chinensis*) in coastal waters of China (Wang et al. 2006) for stock enhancement have lowered the level of genetic diversity of wild stocks. Therefore, a careful identification of broodstocks in artificial propagation would be necessary to avoid admixture and hybridization among these genetically different spawning stocks. In addition, the adverse impact of anthropogenic effects, such as overfishing and habitat loss, has been increasing. The continued loss of habitat could result in the future in reduced numbers and erosion of genetic variation (Chen et al. 2012). Thus, the present study might be helpful in preserving the wild stocks of yellow catfish resources in the middle and lower reaches of the Yangtze River. Low population structures of yellow catfish should be managed independently. In addition, artificial propagation should be implemented to enlarge the wild population size after effective genetic assessment. Although the patterns determined in this study were clear, our results also indicate that further geographic sampling was necessary. Future sampling should include the upper and other tributaries in the middle of the Yangtze River basins, to fully describe the complete pattern of the population structure of yellow catfish.

In conclusion, thirteen microsatellite loci revealed a moderate level of genetic diversity of the five yellow catfish populations from the middle and lower reaches of the Yangtze River. A moderate genetic differentiation was determined between the middle and lower groups, while low genetic differentiations were found within the lower populations. In situ conservation strategies should be preferred, and artificial propagation should also be adopted to enlarge the population size.

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