



Population Genetics Reveals Invasion Origin of *Coilia brachygnathus* in the Three Gorges Reservoir of the Yangtze River, China

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Non-indigenous fish invasions have posed a serious threat to global fish diversity and aquatic ecosystem security. Studying the invasion sources, pathways, and genetic mechanisms by means of population genetics is helpful in the management and control of non-indigenous fishes. In this study, we used mitochondrial Cyt *b* gene, D-Loop region and microsatellite markers to analyze the genetic diversity and population structure of 12 *Coilia brachygnathus* populations from the native and invaded regions of the Yangtze River Basin in order to explore the invasion sources, pathways, and genetic mechanisms of *C. brachygnathus* in the Three Gorges Reservoir. The results showed that the main invasion sources of *C. brachygnathus* in the Three Gorges Reservoir were the Poyanghu Lake, Dongtinghu Lake, Changhu Lake, and other populations in the middle reaches of the Yangtze River. The invasion pathway may have involved moving upstream through the operation of ship locks. The genetic diversity of *C. brachygnathus* in the invasive populations was significantly smaller than in the native populations, indicating a founder effect. The low genetic diversity did not affect the successful invasion, confirming that genetic diversity and successful invasion do not always have a simple causal relationship. These results can provide basic data for the prevention and control of *C. brachygnathus* in the Three Gorges Reservoir and study case for understanding the mechanism of invasion genetics.

Keywords: *Coilia brachygnathus*, Three Gorges Reservoir, invasion sources, invasion pathways, invasion genetic mechanisms

INTRODUCTION

Biological invasion is a main concern to conservationists and resource managers owing to its potential threat to ecosystems and biodiversity (Mack et al., 2000; Dudgeon et al., 2006). Invaders may drastically change the functioning of the ecosystem where they are introduced, resulting in the decline or extinction of native species through competition, predation, and habitat alteration (Levine, 2008; Haubrock et al., 2021). Identifying the putative source populations and the invasion

pathways is a key first step in developing appropriate management measures to mitigate the impacts of species invasions (Bariche et al., 2017; Morim et al., 2019). Population genetic research is a powerful tool for reconstructing the invasion history (Estoup and Guillemaud, 2010).

The Yangtze River is the largest river in China, the upper reaches of the river are turbulent, and the middle and lower reaches of the river are open and the flow of water is slow. Yichang City is the dividing point between the upper reaches and the middle and lower reaches of the Yangtze River (Fish research laboratory of Institute of Hydrobiology of Hubei province, 1976). *Coilia brachygnathus* (Clupeiformes, Engraulidae, *Coilia*) is an anchovy species that prefer to live in still water environment (Whitehead et al., 1988). It was first described from the Dongtinghu Lake of the Yangtze River Basin (Kreyenberg and Pappenheim, 1908). Therefore, in the past, due to the influence of the river water velocity, it has been mainly distributed in the middle and lower reaches of the Yangtze River, especially the lakes in this section, such as Poyanghu Lake, Dongtinghu Lake, and Changhu Lake, and there was no record of the distribution of *C. brachygnathus* in the upper reaches of the Yangtze River (Fish research laboratory of Institute of Hydrobiology of Hubei province, 1976; Ding, 1994). However, *C. brachygnathus* accounted for 0.15% of the total fish assemblage biomass in the Three Gorges Reservoir of the upper Yangtze River according to investigate from 2015 to 2017 (Liao et al., 2018). Surprisingly, it has become an absolutely dominant species in the Three Gorges Reservoir according to our investigations from 2019 to 2021 (accounted for 18.90% of the total fish assemblage biomass in the Three Gorges Reservoir, unpublished data).

How did *C. brachygnathus* invade the Three Gorges reservoir? In 1981, the Gezhouba Dam was completed in the Yichang section of the upper reaches of the Yangtze River (Wei et al., 1997). Then in 2003, the Three Gorges Dam was completed 38 km upstream of the Gezhouba Dam (Xu and Milliman, 2009). The completion of these two dams, especially the construction of the Three Gorges Dam, the largest hydropower station in the world, has made the Gezhouba Reservoir and the Three Gorges Reservoir changed from turbulent water habitats to static water environments, this created feasible conditions for the survival of fish that prefer to live in still water environment, such as *C. brachygnathus* (Huang and Wu, 2018; Gao et al., 2019). (In the present study, we regard the Gezhouba Reservoir as part of the Three Gorges Reservoir; so, only the Three Gorges Reservoir will be mentioned hereafter). As for the way of *C. brachygnathus* invaded the Three Gorges Reservoir? We guess that it is most likely to spread to the Three Gorges Reservoir through the ship locks. For shipping, the Three Gorges Dam has built double-line five-grade ship locks (Stone, 2008). Similarly, Gezhouba Dam has also built three ship locks (Lin et al., 2013). While these locks provide convenience for shipping, they also create conditions for the proliferation of certain fish (Lin et al., 2013). Ships and fish are transported from below the dam to above the dam like climbing the stairs.

Moreover, how *C. brachygnathus* developed into the dominant species in the Three Gorges Reservoir so quickly, it may be related to factors such as sufficient food and strong ability to resist

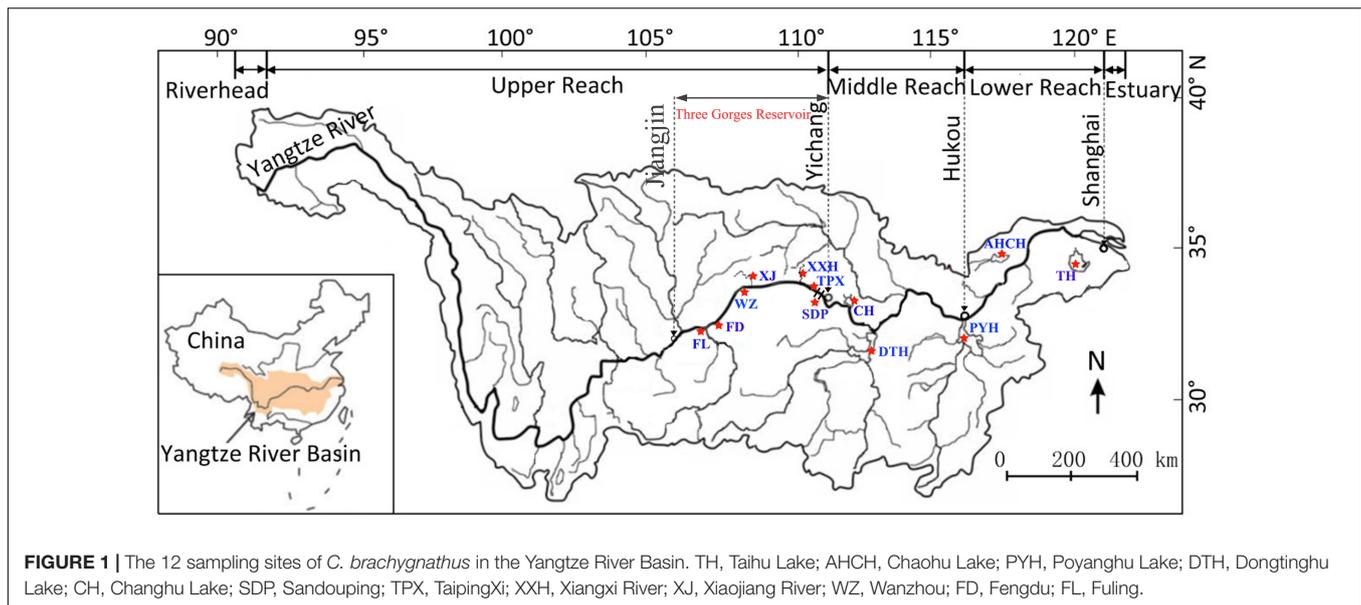
predation, as well as its high fecundity. It is a carnivorous fish that mainly feeds on zooplankton, small fish and river prawns (Fish research laboratory of Institute of Hydrobiology of Hubei province, 1976; Zhang et al., 2013). Due to overfishing of the middle and large sized fishes, many studies have showed that the small-sized fishes accounted for a great proportion in fish catches of the Three Gorges Reservoir in the past 10 years (Gao et al., 2010, 2019; Wei et al., 2021). As the water flow slowed down, the eutrophication degree of the Three Gorges Reservoir has increased, so the zooplankton has increased too (Li et al., 2019). *Coilia brachygnathus* has serrations on the edges of the upper and lower jaws and abdomen that help it to defense against predation (Meyers et al., 2008). The absolute fecundity of *C. brachygnathus* varies between 6,905 and 28,745 eggs with a mean value of 14,049, showing a strong reproductive ability (Liu, 2008).

Beginning in 2020, a “10-year ban on fishing” has been implemented in the Yangtze River (Liu et al., 2021). With the disappearance of fishing pressure, the population of *C. brachygnathus* in the Three Gorges Reservoir may further increase, and this will pose a serious threat to aquatic organisms and ecosystems in the Three Gorges Reservoir. It is necessary to identify the invasion sources and pathways of *C. brachygnathus* in the Three Gorges Reservoir for formulating management measures. Therefore, we used mitochondrial Cyt *b* gene, D-Loop region and microsatellite markers to analyze the population structure and genetic diversity of 12 *C. brachygnathus* populations from the donor and recipient regions in the Yangtze River Basin in order to gain insights into the invasion origin and process of the non-indigenous fish *C. brachygnathus* in the Three Gorges Reservoir. The results will provide a theoretical basis for formulating management measures to mitigate the impacts of *C. brachygnathus* invasion and understanding the mechanism of invasion genetics.

MATERIALS AND METHODS

Sample Collection and DNA Extraction

Samples of *C. brachygnathus* were collected from 12 different sampling sites in the Yangtze River Basin from August 2019 to August 2020 (Each sample site was more than 30 individual). From downstream to upstream, these were Taihu Lake (TH), Chaohu Lake (AHCH), Poyanghu Lake (PYH), Dongtinghu Lake (DTH), Changhu Lake (CH), Sandouping (SDP), Taipingxi (TPX), Xiangxi River (XXH), Xiaojiang River (XJ), Wanzhou (WZ), Fengdu (FD), and Fuling (FL). TH and AHCH are affiliated lakes in the lower reaches of the Yangtze River; PYH, DTH, and CH are affiliated lakes in the middle reaches of the Yangtze River, the original distribution of *C. brachygnathus* in the Yangtze River Basin. SDP is located between the Gezhouba Dam and the Three Gorges Dam; TPX, XXH, XJ, WZ, FD, and FL belong to the Three Gorges Reservoir, of which XXH and XJ are tributaries of the Three Gorges Reservoir, the invasion region of *C. brachygnathus* in the Yangtze River Basin (Figure 1). Through our investigations, it was found that *C. brachygnathus* was scarce in the river section above Fuling in the Three Gorges Reservoir, where is still flowing water



habitat. Therefore, these 12 sampling sites basically covered the distribution range of *C. brachygnathus* in the Yangtze River Basin. Species identification mainly refers to Fauna Sinica Osteichthyes Cypriniformes II (Chen, 1998).

After the fish samples were collected, tissues from the dorsal muscles were cut and stored in 95% alcohol at -20°C in a centrifuge tube. Approximately 50 mg of muscles were used to extract genomic DNA using the animal tissue genomic DNA extraction kit of Chengdu Forge Biotechnology Co., Ltd.

mtDNA Amplification and Sequencing

The amplification primers for the mitochondrial DNA *Cyt b* fragment were L14724 5'-GAC TTG AAA AAC CAC CGT TG-3' (forward) and H15915 5'-CTC CGA TCT CCG GAT TAC AAG AC-3' (reverse) (Xiao et al., 2001). The amplification primers for the mitochondrial DNA D-Loop fragment were DF1 5'-CTA ACT CCC AAA GCT AGA ATT CT-3' (forward) and DR2 5'-ATC TTA GCA TCT TCA GTG-3' (reverse) (Tang et al., 2007). The total volume for the Polymerase Chain Reaction (PCR) was 30 μL : 15 μL of 2 \times Taq PCR MasterMix (containing Taq DNA polymerase, dNTPs, MgCl_2 , reaction buffer, Beijing Adler Biotechnology Co., Ltd.), template DNA 3 μL , forward and reverse primers 1 μL each, ddH₂O 10 μL . The PCR amplification procedure was as follows: pre-denaturation at 94°C for 4 min, followed by 35 cycles of denaturation at 94°C for 45 s, annealing at 55°C for 45 s, extension at 72°C for 1 min, and finally extension at 72°C for 10 min. After the PCR products were subjected to agarose gel electrophoresis, the samples with accurate and clear target bands were sent to Tianyi Huiyuan Biotechnology Co., Ltd. for purification, recovery, and sequence determination. The mitochondrial DNA *Cyt b* fragment was measured in both directions, and the D-Loop fragment was only sequenced in the reverse direction due to the presence of repeated fragments in the forward direction.

Simple Sequence Repeats Amplification and Genotyping

There are no published microsatellite [also known as simple sequence repeats (SSR)] primers for *C. brachygnathus*, but many microsatellite primers have been published for *Coilia nasus*. Because *C. brachygnathus* and *C. nasus* are closely related species, a total of 50 pairs of microsatellite primers of *C. nasus* were selected from references for primer screening with eight DNA templates of *C. brachygnathus* (Du et al., 2019; Yu et al., 2019). Finally, eight pairs of primers with higher polymorphism were screened out by the capillary electrophoresis method. The specific sequences, repeat motif, and optimum annealing temperature of each primer are listed in **Supplementary Table 1**. Then, the 5' ends of the eight pairs of forward primers were labeled with fluorescent groups (FAM). The primer screening and fluorescent labeling of the primers were entrusted to Tianyi Huiyuan Biotechnology Co., Ltd. The total volume for the PCR was 10 μL : 5 μL of 2 \times Taq PCR MasterMix (containing Taq DNA polymerase, dNTPs, MgCl_2 , reaction buffer, Beijing Adler Biotechnology Co., Ltd.), template DNA 1 μL , forward and reverse primers 0.5 μL each, ddH₂O 3 μL . The PCR amplification procedure was as follows: pre-denaturation at 94°C for 3 min, followed by 30 cycles of denaturation at 94°C for 30 s, annealing at suitable temperature for 40 s, extension at 72°C for 1 min, and finally extension at 72°C for 10 min. The amplified products were sent to Tianyi Huiyuan Biotechnology Co., Ltd. for microsatellite genotyping.

mtDNA Sequence Analysis

MEGA7 was used to align and rectify the nucleotide sequences by referring to the sequencing map (Kumar et al., 2016). DnaSP v5.10 was used to calculate the numbers of variable sites and haplotypes, haplotype diversity (H_d), nucleotide diversity (P_i), and gene flow (N_m) between groups (Librado and Rozas, 2009). *T*-test was used to test whether the genetic diversity

parameters or gene flow of different groups are significantly different. Arlequin version 3.0 was used to perform analysis of molecular variance (AMOVA) and to compute pairwise genetic differentiation index F_{ST} values (Excoffier et al., 2005). MEGA7 was used to construct genetic distance trees by the neighbor-joining method (Kumar et al., 2016). Network 4.6 was used to construct haplotype network using the median-joining algorithm (Bandelt et al., 1999).

Simple Sequence Repeats Data Analysis

Genotypes were checked for large allele dropout, null alleles, and scoring errors due to stuttering by Micro-checker v2.2.1 (Van Oosterhout et al., 2004). Tests for deviations from Hardy-Weinberg Equilibrium (HWE) and Linkage Disequilibrium (LD) across all pairs of loci were checked by GENEPOP v4.7.0 (Rousset, 2008) using exact tests with a Markov chain algorithm (P -values were estimated from 10,000 dememorizations, 100 batches, and 5,000 iterations per batch) (Guo and Thompson, 1992). Significance levels were adjusted for multiple comparisons using the sequential Bonferroni correction (Rice, 1989).

Number of alleles (A), observed heterozygosity (H_o), expected heterozygosity (H_e), and polymorphic information content (PIC) per locus were calculated by Cervus v3.0 (Kalinowski et al., 2007). Standardized allelic richness (Ar) was calculated using Fstat v2.9.3.2 (Goudet, 2001). T -test was used to test whether the genetic diversity parameters or gene flow of different groups are significantly different. Arlequin v3.0 was used to perform AMOVA and to compute pairwise genetic differentiation index F_{ST} and gene flow index N_m (Excoffier et al., 2005). In addition, genetic differentiation among populations was depicted by two-dimensional plots from a principal components analysis (PCA) of the allele frequencies matrix in GENALEX 6.4 (Peakall and Smouse, 2006).

The number of genetically differentiated clusters (K) was inferred using Bayesian assignment analysis by STRUCTURE v2.3.4 (Pritchard et al., 2000). Each assumed K (1–12) were performed 10 replications under an admixture model and correlated allele frequencies within populations (400,000 iterations with 100,000 burn-in periods) (Falush et al., 2003). The optimal K was selected according to the mean log probability $\ln P$ (K) and the ΔK value for each K (Evanno et al., 2005) using Structure Harvester (Earl and vonHoldt, 2012).¹

RESULTS

mtDNA Marker

Genetic Diversity

For the Cyt *b* gene, a 1 141 bp sequence was obtained for 424 individuals after alignment. No insertions or deletions were observed. Within the 1 141 bp region, 59 sites were variable, including 30 singleton variable sites and 29 parsimony informative sites. We identified 60 haplotypes (GenBank accession numbers: OK172180–OK172239) from the 424 individuals, and the numbers of haplotypes ranged from 2 to 23

for each sampled population. For the 12 populations, haplotype diversity ranged from 0.157 to 0.958, with a mean value of 0.643. Nucleotide diversity ranged from 0.051 to 0.347%, with a mean value of 0.278%. On the whole, whether concerning the number of haplotypes, haplotype diversity, or nucleotide diversity, the non-invaded habitat (TH, AHCH, PYH, DTH, CH) was significantly ($P < 0.05$) greater than the invaded habitat (SDP, TPX, XXH, XJ, WZ, FD, FL) (Table 1).

For the D-Loop region, an 882 bp sequence was obtained for 408 individuals after alignment. Within the 882 bp region, 63 sites were variable, including 27 singleton variable sites and 36 parsimony informative sites. We identified 78 haplotypes (GenBank accession numbers: OK172240–OK172317) from the 408 individuals, and the numbers of haplotypes ranged from 2 to 20 for each sampled population. For the 12 populations, haplotype diversity ranged from 0.114 to 0.946, with a mean value of 0.704. Nucleotide diversity ranged from 0.026 to 0.674%, with a mean value of 0.518%. On the whole, whether concerning the number of haplotypes, haplotype diversity, or nucleotide diversity, the non-invaded habitat (TH, AHCH, PYH, DTH, CH) was significantly ($P < 0.05$) greater than the invaded habitat (SDP, TPX, XXH, XJ, WZ, FD, FL) (Table 1).

Population Structure

For the Cyt *b* gene, the pairwise F_{ST} values suggested no significant genetic differentiation between TH and AHCH populations, but these were significantly different from all other populations. The three populations that represent the lakes attached to the middle reaches of the Yangtze River (PYH, DTH and CH) had no significant genetic differentiation, but there was significant genetic differentiation between them and some populations in the Three Gorges Reservoir. The seven populations in the Three Gorges Reservoir (SDP, TPX, XXH, XJ, WZ, FD, and FL) had no significant genetic differentiation. For the D-Loop region, the pairwise F_{ST} values suggested no significant genetic differentiation among the populations that represented the lakes attached to the middle reaches of the Yangtze River (PYH, DTH, and CH), and this was the same for the seven populations in the Three Gorges Reservoir (SDP, TPX, XXH, XJ, WZ, FD, and FL), while there was significant genetic differentiation between any other two populations (Table 2). Based on the results of the genetic analyses of the two mtDNA genes and geographic distance, we divided the 12 populations into three groups for AMOVA. The three groups were the lower Yangtze River (TH, AHCH), the middle Yangtze River (PYH, DTH, CH), and the Three Gorges Reservoir (SDP, TPX, XXH, XJ, WZ, FD, FL). The results suggested that most of the genetic variation occurred among groups and within populations, with only slight genetic variation (Cyt *b*: 0.51%; D-Loop: 0.61%) occurring among populations within groups, thus suggesting that the group division was reasonable (Table 3).

The results showed that the genetic distance tree could be divided into two branches, one being TH and AHCH and the other comprising PYH, DTH, CH, SDP, TPX, XXH, XJ, WZ, FD, and FL. This suggested that the Three Gorges Reservoir population is closer to the midstream population and farther from the downstream population (Figure 2). Consistent with

¹<http://taylor0.biology.ucla.edu/structureHarvester/>

TABLE 1 | Genetic diversity of *C. brachygnathus* from 12 sample sites in the Yangtze River Basin.

Molecular marker	Parameter	TH	AHCH	PYH	DTH	CH	SDP	TPX	XXH	XJ	WZ	FD	FL	Total
Cyt <i>b</i>	Sample size	36	35	37	36	36	39	35	35	29	36	36	34	424
	Variable Site	26	28	18	18	19	4	4	4	3	4	4	4	59
	N	20	23	15	12	13	2	2	2	2	2	2	2	60
	<i>H_d</i>	0.930	0.958	0.818	0.689	0.829	0.335	0.420	0.393	0.192	0.157	0.286	0.258	0.643
D-Loop	<i>P_i</i>	0.00247	0.00234	0.00242	0.00214	0.00347	0.00117	0.00147	0.00138	0.00051	0.00055	0.00100	0.00091	0.00278
	Sample size	31	34	35	35	36	34	34	36	33	34	30	36	408
	Variable Site	38	30	26	24	26	2	3	3	2	2	2	2	63
	N	20	19	19	20	19	2	3	3	2	2	2	2	78
SSR	<i>H_d</i>	0.940	0.888	0.929	0.946	0.914	0.258	0.415	0.427	0.170	0.114	0.287	0.286	0.704
	<i>P_i</i>	0.00630	0.00372	0.00599	0.00501	0.00674	0.00059	0.00091	0.00094	0.00039	0.00026	0.00065	0.00065	0.00518
	Sample size	32	32	32	32	32	32	32	32	32	32	32	32	384
	A	7.375	8.125	5.750	5.750	5.125	3.500	3.500	3.625	3.375	3.250	3.250	3.125	10.875
Ar	7.036	7.839	5.501	5.508	5.005	3.445	3.358	3.498	3.249	3.210	3.125	3.043	6.641	
Ho	0.531	0.597	0.637	0.619	0.627	0.461	0.482	0.561	0.445	0.485	0.512	0.530	0.541	
He	0.636	0.696	0.615	0.605	0.596	0.437	0.442	0.472	0.419	0.461	0.465	0.477	0.638	

N, Number of haplotypes; *H_b*, Haplotype diversity; *P_i*, Nucleotide diversity; A, number of alleles; Ar, allelic richness; Ho, observed heterozygosity; He, expected heterozygosity.

this, the haplotype network indicated that there were two clades of all the haplotypes for both the Cyt *b* gene and D-Loop region. One clade was almost exclusively occupied by individuals from the TH and AHCH populations, with only a few individuals from the PYH, DTH, and CH populations, the other clade was occupied by individuals from the PYH, DTH, CH, SDP, TPX, XXH, XJ, WZ, FD, and FL populations, indicating that the invaded populations only shared haplotypes with midstream populations (Figure 3). The gene flow between the Three Gorges Reservoir and the middle Yangtze River was significantly ($P < 0.05$) greater than those between the Three Gorges Reservoir and the lower Yangtze River (Table 4).

Simple Sequence Repeats Marker Genetic Diversity

A total of 384 samples from 12 localities and 8 polymorphic SSR loci were used in the present study. No evidence for scoring errors due to stuttering, large allele dropout, or null alleles was detected by Micro-Checker. Ten of 96 population × locus combinations were significantly different from the HWE after Bonferroni correction, whereas no significant deviation from the HWE was detected in any locus across all populations. No loci pairs showed evidence of LD after Bonferroni correction. When data from all populations were pooled, the number of alleles at each locus ranged from 6 to 25, so all the eight loci were polymorphic (Supplementary Table 2).

The observed allele, allelic richness, observed heterozygosity, and expected heterozygosity of each locus for the 12 *C. brachygnathus* populations were listed in Supplementary Table 2. The average number of alleles per population ranged from 3.125 to 8.125, and the average allelic richness per population ranged from 3.043 to 7.839. The average observed heterozygosity per population ranged from 0.445 to 0.637, whereas the average expected heterozygosity per population ranged from 0.419 to 0.696. On the whole, whether considering the number of alleles, allelic richness, observed heterozygosity, or expected heterozygosity, the non-invaded habitat (TH, AHCH, PYH, DTH, CH) was significantly ($P < 0.05$) greater than the invaded habitat (SDP, TPX, XXH, XJ, WZ, FD, FL) (Table 1).

Population Structure

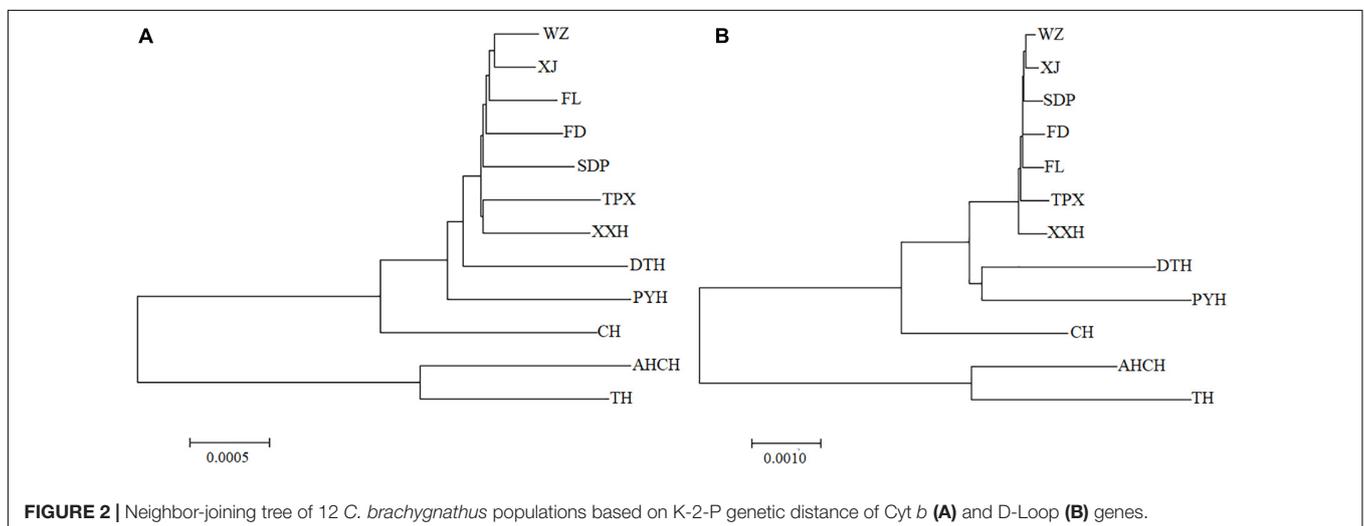
The pairwise *F_{ST}* values suggested no significant genetic differentiation among the three populations that comprised the lakes attached to the middle reaches of the Yangtze River (PYH, DTH, and CH), and the same was true for the six out of the seven invasive populations in the Three Gorges Reservoir (TPX, XXH, XJ, WZ, FD, and FL), but there was significant genetic differentiation between any other two populations (Table 5). We also divided the 12 populations into three groups for AMOVA; the results indicated that the sources of genetic variation were mainly among groups (25.71%) and within populations (73.12%); only a slight amount of genetic variation (1.17%) occurred among populations within groups (Table 3). When conducting STRUCTURE analysis, LnP(*K*) showed a peak when *K* = 5, inferring there were five genetic clusters in the *C. brachygnathus* samples (Figure 4). In the figure, the five colors represent five clusters. The results showed that TH and AHCH populations in

TABLE 2 | Pairwise F_{ST} values based on Cyt *b* analysis of 424 samples (below diagonal) and D-Loop analysis of 408 samples (above diagonal) of *C. brachygnathus* from 12 different sites in the Yangtze River Basin, China.

	TH	AHCH	PYH	DTH	CH	SDP	TPX	XXH	XJ	WZ	FD	FL
TH		0.04589*	0.54150*	0.57060*	0.46001*	0.70321*	0.69498*	0.69956*	0.70586*	0.71277*	0.68967*	0.70705*
AHCH	0.02870		0.61251*	0.64341*	0.52734*	0.79399*	0.78389*	0.78627*	0.79878*	0.80544*	0.78419*	0.79554*
PYH	0.58526*	0.60556*		0.00166	0.02402	0.21729*	0.18176*	0.18112*	0.24012*	0.25916*	0.19860*	0.21396*
DTH	0.61391*	0.63347*	-0.00112		0.02629	0.23924*	0.19849*	0.19759*	0.26537*	0.28657*	0.21932*	0.23488*
CH	0.48595*	0.50538*	0.00399	0.01187		0.16712*	0.13796*	0.13779*	0.18663*	0.20328*	0.15103*	0.16449*
SDP	0.68262*	0.70161*	0.06294	0.03267	0.08594*		-0.00448	0.00386	-0.01544	0.01223	-0.03088	-0.02794
TPX	0.66792*	0.68683*	0.04758	0.02650	0.06971	-0.00989		-0.02675	0.04239	0.08541	-0.01685	-0.01371
XXH	0.67044*	0.68953*	0.04915	0.02482	0.07186*	-0.02003	-0.02729		0.05425	0.09839	-0.01009	-0.00686
XJ	0.70162*	0.72289*	0.10767*	0.07163	0.11734*	0.04024	0.10862	0.08296		-0.02312	-0.00647	-0.00418
WZ	0.71349*	0.73348*	0.13446	0.09801*	0.14197*	0.03169	0.10287	0.07603	-0.01797		0.02745	0.02805
FD	0.68734*	0.70686*	0.07622	0.04314	0.09593	-0.02245	0.01195	-0.00402	0.01332	0.00357		-0.03152
FL	0.68933*	0.70919*	0.08465	0.05067	0.10181	-0.01653	0.02673	0.00802	0.00123	-0.00899	-0.02794	

* $P < 0.05$ after Bonferroni correction.**TABLE 3** | Analysis of molecular variance (AMOVA) for 12 *C. brachygnathus* populations based on mtDNA and SSR analyses.

Molecular marker	Source of variation	df	Sum of squares	Variance components	Percentage variation	Fixation indices	P
Cyt <i>b</i>	Among groups	2	265.995	1.08072	52.82	0.52819	0
	Among populations within groups	9	11.882	0.01037	0.51	0.01074	0.07527
	Within populations	412	393.453	0.95498	46.67	0.53326	0
	Total	423	671.330	2.04607			
D-Loop	Among groups	2	440.146	1.87751	60.05	0.60046	0
	Among populations within groups	9	16.870	0.01894	0.61	0.01516	0.00782
	Within populations	396	487.215	1.23034	39.35	0.60652	0
	Total	407	944.230	3.12679			
SSR	Among groups	2	326.304	0.72696	25.71	0.25710	0
	Among populations within groups	9	37.704	0.03316	1.17	0.01578	0
	Within populations	756	1562.969	2.06742	73.12	0.26883	0
	Total	767	1926.977	2.82754			

**FIGURE 2** | Neighbor-joining tree of 12 *C. brachygnathus* populations based on K-2-P genetic distance of Cyt *b* (A) and D-Loop (B) genes.

the lower Yangtze River had similar genetic cluster components; PYH, DTH, and CH populations in the middle Yangtze River had similar genetic cluster components; SDP, TPX, XXH, XJ, WZ, FD, and FL populations in the Three Gorges Reservoir had similar

genetic cluster components, and the Three Gorges Reservoir populations shared some genetic cluster components with middle Yangtze River populations. The PCA analysis showed that the lower Yangtze River populations were completely separated from

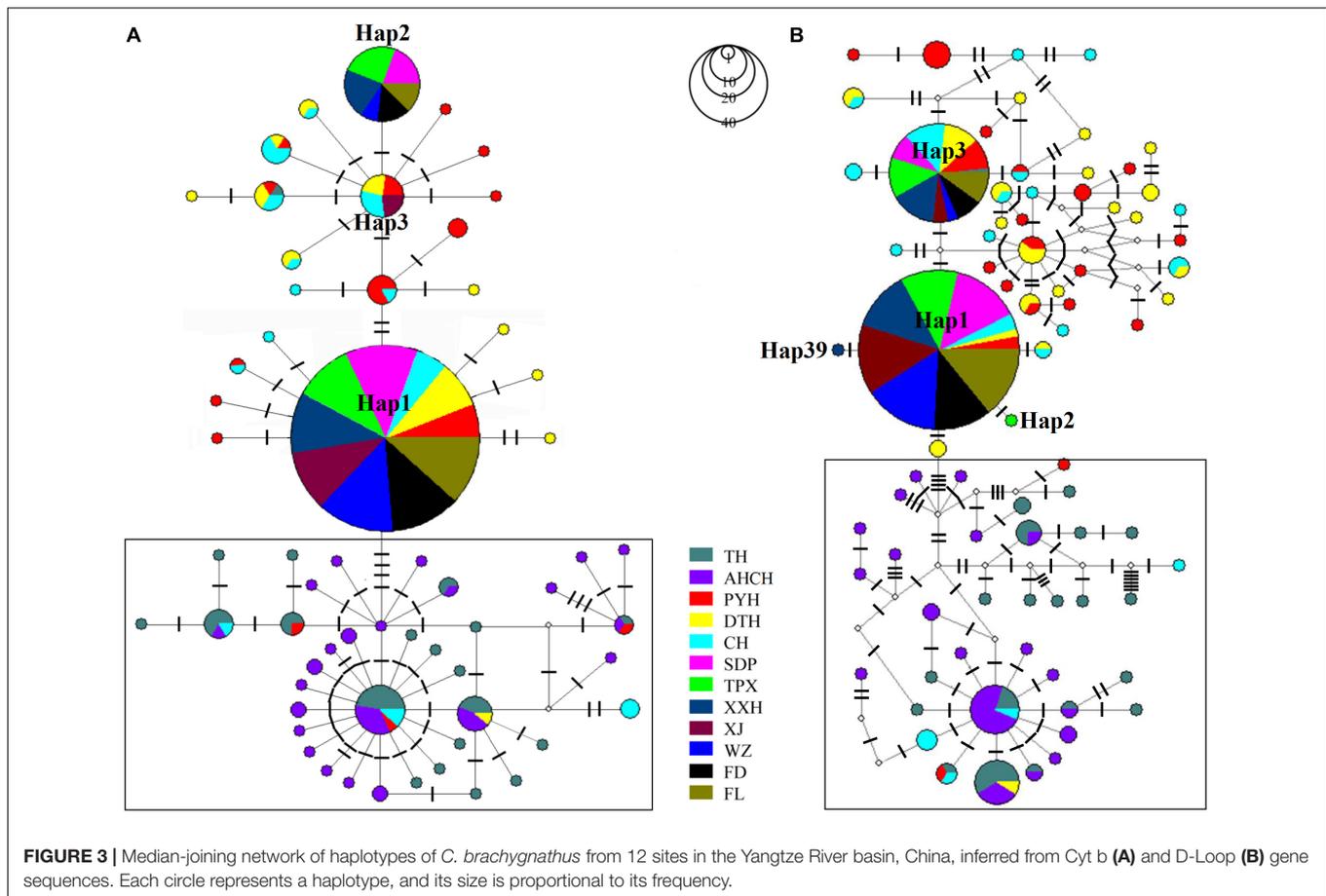


TABLE 4 | Gene flow between different groups based on mtDNA and SSR analyses.

Molecular marker	Cyt b	D-Loop	SSR
Three Gorges Reservoir—middle Yangtze River	3.20	1.00	1.55
Middle Yangtze River—lower Yangtze River	0.19	0.19	0.70
Three Gorges Reservoir—lower Yangtze River	0.11	0.08	0.38

the middle Yangtze River populations and the Three Gorges Reservoir populations; the middle Yangtze River populations and the Three Gorges Reservoir populations could also be clearly distinguished, but there were some overlapping areas (Figure 5). The gene flow between the Three Gorges Reservoir and the middle Yangtze River was significantly ($P < 0.05$) greater than those between the Three Gorges Reservoir and the lower Yangtze River (Table 4).

DISCUSSION

Population Genetic Structure and Invasion Sources

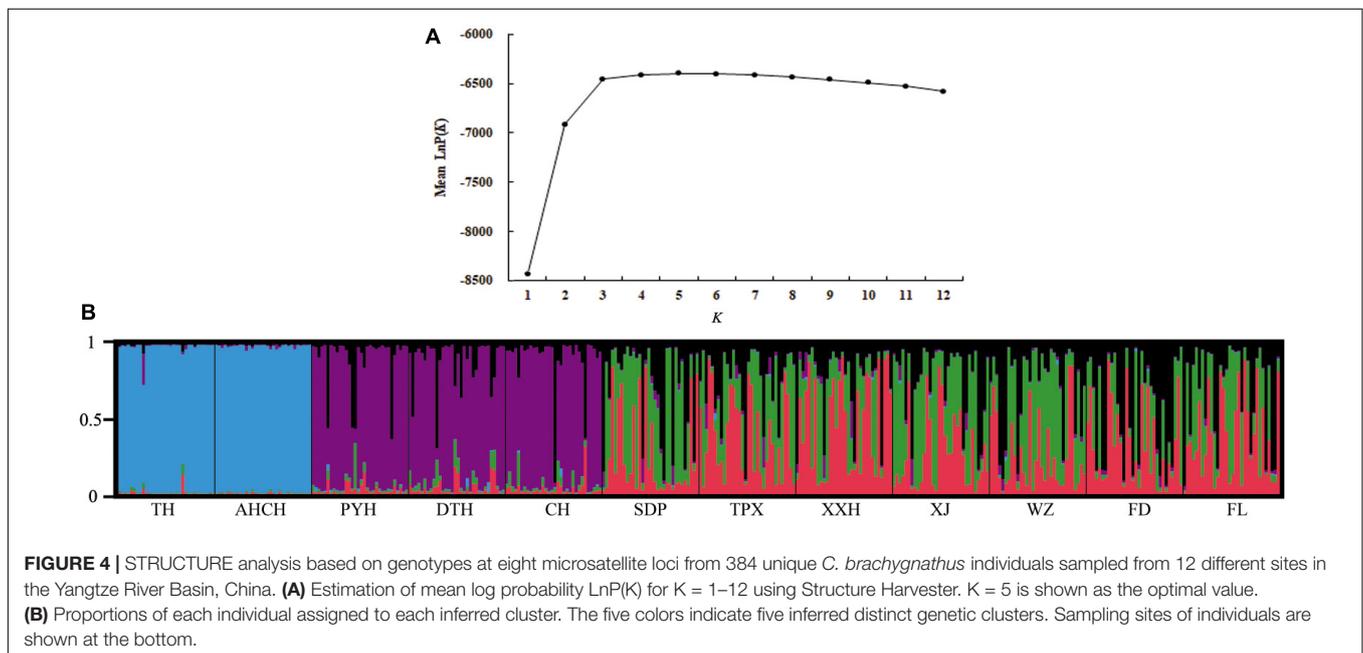
Identifying the invasion source and pathway of *C. brachygnathus* in the Three Gorges Reservoir was the top priority in this study, because the acquisition of this information is important for

the prevention and control of *C. brachygnathus* in the Three Gorges Reservoir (Ficetola et al., 2008). Through this study, we speculated that the main invasion source of *C. brachygnathus* in the Three Gorges Reservoir was the middle Yangtze River instead of the lower Yangtze River. There were several results supporting this speculation. Firstly, the genetic differentiation, genetic distance between the Three Gorges Reservoir and the middle Yangtze River were smaller than between the Three Gorges Reservoir and the lower Yangtze River, and the gene flow result was opposite. Secondly, network of haplotypes indicated that there were shared haplotypes between the Three Gorges Reservoir populations and the middle Yangtze River populations, but no shared haplotypes between the Three Gorges Reservoir populations and the lower Yangtze River populations; the STRUCTURE analysis showed that the Three Gorges Reservoir populations only have some of the same genetic cluster components as the middle Yangtze River populations; PCA showed that the Three Gorges Reservoir populations only have some overlapping areas with the middle Yangtze River populations. Yang (2019) also found that the genetic distance of *C. brachygnathus* between the Three Gorges Reservoir populations and Dongtinghu Lake population was small. The reason for the middle Yangtze River population being the main invasion source, instead of the lower Yangtze River population, of *C. brachygnathus* in the Three Gorges Reservoir may be related to

TABLE 5 | Pairwise F_{ST} values based on SSR analysis of 384 samples of *C. brachygnathus* from 12 different sites in the Yangtze River Basin, China.

	TH	AHCH	PYH	DTH	CH	SDP	TPX	XXH	XJ	WZ	FD	FL
TH												
AHCH	0.02971*											
PYH	0.28764*	0.23085*										
DTH	0.29727*	0.24228*	0.00149									
CH	0.30233*	0.24850*	-0.00046	0.0054								
SDP	0.40955*	0.37237*	0.14514*	0.13291*	0.12093*							
TPX	0.40974*	0.37738*	0.16550*	0.14394*	0.15817*	0.05318*						
XXH	0.38759*	0.35168*	0.14686*	0.13114*	0.14705*	0.04877*	0.02026					
XJ	0.41927*	0.38665*	0.15975*	0.13951*	0.14720*	0.03663*	0.01826	0.01945				
WZ	0.39245*	0.35704*	0.13772*	0.11563*	0.13364*	0.03942*	0.00212	0.01036	0.00287			
FD	0.38955*	0.35231*	0.12256*	0.09911*	0.11353*	0.03418*	0.01832	0.00703	0.00969	-0.00222		
FL	0.39014*	0.35677*	0.15903*	0.13743*	0.15255*	0.05050*	0.01261	-0.00044	0.02319	0.00816	0.0053	

* $P < 0.05$ after Bonferroni correction.



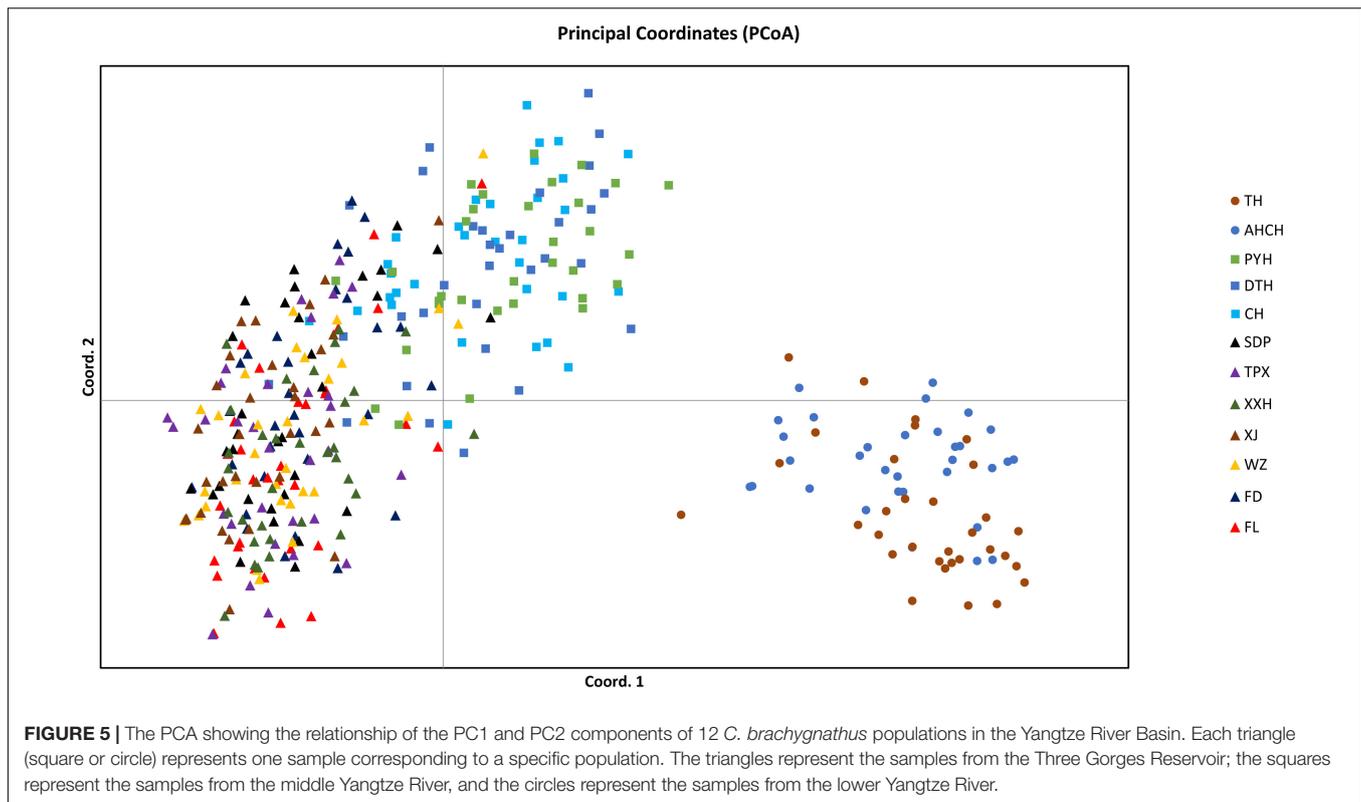
geographic distance and the dispersal ability of *C. brachygnathus* (Radinger and Wolter, 2014; Radinger et al., 2017). Due to limited diffusion capacity, *C. brachygnathus* in the middle reaches of the Yangtze River can spread to the Three Gorges Reservoir, while *C. brachygnathus* in the lower Yangtze River hardly spread to the Three Gorges Reservoir.

As for the invasion pathway, we speculated that the most probable pathway for *C. brachygnathus* to have invaded the Three Gorges Reservoir was individuals from Poyang Lake, Dongting Lake, Changhu Lake, and other middle reaches of the Yangtze River actively moving upstream to the Three Gorges Reservoir through the operation of ship locks. When the ship was transported from under the dam to above the dam by cascade ship lock, the fish were also transported up. Lin et al. (2013) combined fish catch surveys and hydroacoustic detection to explore the fish passing ability of the ship locks of the Gezhouba and Three Gorges Dam; in the fish catch surveys of the two locks, a total of

21 species were identified, and the fish catch at the Gezhouba ship lock contained *C. brachygnathus*. Consistent with this, Xiang et al. (2015) used sonar (DIDSON) to detect and record the number of fish crossing up and down the Gezhouba ship lock and found that fish were able to pass the ship lock under natural conditions. Therefore, it is reasonable that *C. brachygnathus* spread to the Three Gorges Reservoir through the ship locks.

Genetic Diversity and Invasion Success

For many invasive species, the level of genetic diversity of an invaded area is often lower than that in the area of origin, because the invaded population is often produced from a few individuals from the original area; this is known as the founder effect (Allendorf and Lundquist, 2003; Crawford and Whitney, 2010; Peischl and Excoffier, 2015). In the present study, whether considering mitochondrial genes or microsatellites, the genetic diversity of *C. brachygnathus* in the non-invaded habitats (TH,



AHCH, PYH, DTH, CH) was significantly greater than that in the invaded habitats (SDP, TPX, XXH, XJ, WZ, FD, FL), indicating that the invaded populations experienced a founder effect. However, some studies have found that the genetic diversity of invasive species in the invaded region was not lower than that in the original area or was even higher than that in the area of origin (Frankham, 2005; Stepien et al., 2005). For example, Diez-del-Molino et al. (2013) found that Mosquitofish populations from the invaded Spanish streams had similar levels of genetic diversity as in the native American samples, suggesting these invasive populations did not appear to have undergone substantial loss of genetic diversity during the invasion process. The occurrence of this anomaly might be attributed to a single large number of individual invasions or to multiple introductions (Roman and Darling, 2007; Dlugosch and Parker, 2008). A single invasion of a large number of individuals makes the invading individuals include almost all the genetic diversity of the original population, and multiple introductions comprise genetic diversity of multiple ranges. Hybridization between individuals from different sources will also increase the genetic diversity of the population (Ellstrand and Schierenbeck, 2006).

The above discussion suggests that among the successful invasion cases, there are two contrasting patterns of genetic diversity comparisons of native and invaded ranges for different invasion cases. Therefore, what is the relationship between genetic diversity and successful invasion? It is generally believed that a high level of genetic diversity is beneficial to the settlement and maintenance of alien species in the new environment (Kolbe et al., 2004; Crawford and Whitney, 2010; Kanarek and Webb,

2010). Low levels of genetic diversity may be accompanied by reduced heterozygosity and inbreeding depression, restricting the population's evolutionary potential and ability to adapt to environmental changes and increasing the risk of population extinction (Altizer et al., 2003; Pinsky and Palumbi, 2014). Reed and Frankham (2003) conducted a meta-analysis of 34 research studies involving genetic diversity and population fitness and found that the level of population genetic diversity was significantly positively correlated with population fitness. However, in the present study, the genetic diversity of the invasive *C. brachygnathus* was relatively low due to founder effect. Why then has the *C. brachygnathus* invasion been so successful? We speculate that the successful invasion of *C. brachygnathus* could be related to its life history characteristics and its niche in the fish community of the Three Gorges Reservoir. *C. brachygnathus* has sufficient food, high fecundity, and strong ability to resist predation in the Three Gorges Reservoir, as introduced in the introduction, and these factors provide the species a competitive advantage over other fish. Therefore, the relationship between fish genetic diversity and successful invasion is not a simple causal relationship. The success of fish invasion is related not only to the genetic diversity but also to the life history characteristics of the invasive species and the environmental conditions.

CONCLUSION AND PROSPECT

This study suggests that the main invasion source of *C. brachygnathus* in the Three Gorges Reservoir was PYH,

DTH, CH, and other populations in the middle reaches of the Yangtze River. The invasion pathway may have been via moving upstream through the operation of ship locks. After *C. brachygnathus* invaded the Three Gorges Reservoir, a founder effect occurred, and the genetic diversity was significantly lower than in the native populations, but the number of *C. brachygnathus* in the Three Gorges Reservoir area had risen sharply.

Studies have shown that when alien species are introduced into a new area, if there is a significant difference between the new environment and the original environment, then the alien species may undergo rapid evolutionary changes under the pressure of natural selection caused by the new environment (Whitney and Gabler, 2008; Colautti and Lau, 2015). In addition, recent studies have shown that evolutionary events can occur on a relatively short time scale (Thompson, 1998; Whitney and Gabler, 2008). Therefore, we predict that *C. brachygnathus* in the Three Gorges Reservoir may evolve rapidly, and the genetic structure of each generation may change. Indeed, this study found that *C. brachygnathus* in the Three Gorges Reservoir contained some novel haplotypes and genotypes. In order to monitor the genetic dynamics of *C. brachygnathus* in the Three Gorges Reservoir with time and provide basic data for the prevention of *C. brachygnathus* in the Three Gorges Reservoir, we plan to conduct sampling and genetic testing of *C. brachygnathus* in the Three Gorges Reservoir every year. The inter-annual changes of the genetic structure of *C. brachygnathus* in the Three Gorges Reservoir can thus be examined on a longer time scale. In addition, more sensitive markers than mitochondrial gene and microsatellite markers, such as SNP, can be used for related research in the future.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repository and accession number(s) can be found below: NCBI (accession: OK172180–OK172317).

REFERENCES

- Allendorf, F. W., and Lundquist, L. L. (2003). Introduction: population biology, evolution, and control of invasive species. *Conserv. Biol.* 17, 24–30. doi: 10.1046/j.1523-1739.2003.02365.x
- Altizer, S., Harvell, D., and Friedle, E. (2003). Rapid evolutionary dynamics and disease threats to biodiversity. *Trends Ecol. Evol.* 18, 589–596. doi: 10.1016/j.tree.2003.08.013
- Bandelt, H. J., Forster, P., and Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Mol. Biol. Evol.* 16, 37–48. doi: 10.1093/oxfordjournals.molbev.a026036
- Bariche, M., Kleitou, P., Kalogirou, S., and Bernardi, G. (2017). Genetics reveal the identity and origin of the lionfish invasion in the Mediterranean Sea. *Sci. Rep.* 7:6782. doi: 10.1038/s41598-017-07326-1
- Chen, Y. Y. (1998). *Fauna Sinica, Osteichthyes Cypriniformes II*. Beijing: Science Press.
- Colautti, R. I., and Lau, J. A. (2015). Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Mol. Ecol.* 24, 1999–2017. doi: 10.1111/mec.13162
- Crawford, K. M., and Whitney, K. D. (2010). Population genetic diversity influences colonization success. *Mol. Ecol.* 19, 1253–1263. doi: 10.1111/j.1365-294X.2010.04550.x
- Diez-del-Molino, D., Carmona-Catot, G., Araguas, R. M., Vidal, O., Sanz, N., Garcia-Berthou, E., et al. (2013). Gene flow and maintenance of genetic diversity in invasive mosquitofish (*Gambusia holbrooki*). *PLoS One* 8:e82501. doi: 10.1371/journal.pone.0082501
- Ding, R. H. (1994). *The Fishes of Sichuan, China*. Chengdu: Sichuan Publishing House of Science and Technology.
- Dlugosch, K. M., and Parker, I. M. (2008). Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Mol. Ecol.* 17, 431–449. doi: 10.1111/j.1365-294X.2007.03538.x
- Du, F. K., Tang, Y. K., Yu, J. H., Su, S. Y., Yu, F., Li, J. L., et al. (2019). Development and validation of a transcriptome-based simple sequence repeats markers in *Coilia nasus*. *Pak. J. Zool.* 51, 1335–1341. doi: 10.17582/journal.pjz/2019.51.4.1335.1341
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Leveque, C., et al. (2006). Freshwater biodiversity: importance, threats,

ETHICS STATEMENT

The animal study was reviewed and approved by the Jiangnan University.

AUTHOR CONTRIBUTIONS

DZ contributed to sampling, performed the laboratory work, and wrote the manuscript. FX and WJ designed the study and revised the manuscript. BL and HL helped to data analysis. CL helped to laboratory work. XD and DC helped to revised the manuscript. All authors read and approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.783215/full#supplementary-material>

- status and conservation challenges. *Biol. Rev.* 81, 163–182. doi: 10.1017/S1464793105006950
- Earl, D. A., and vonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conserv. Genet. Resour.* 4, 359–361. doi: 10.1007/s12686-011-9548-7
- Ellstrand, N. C., and Schierenbeck, K. A. (2006). Hybridization as a stimulus for the evolution of invasiveness in plants? *Euphytica* 148, 35–46. doi: 10.1073/pnas.97.13.7043
- Estoup, A., and Guillemaud, T. (2010). Reconstructing routes of invasion using genetic data: Why, how and so what? *Mol. Ecol.* 19, 4113–4130. doi: 10.1111/j.1365-294X.2010.04773.x
- Evanno, G., Regnaut, S., and Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Mol. Ecol.* 14, 2611–2620. doi: 10.1111/j.1365-294X.2005.02553.x
- Excoffier, L., Laval, G., and Schneider, S. (2005). Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evol. Bioinform.* 1, 47–50. doi: 10.1177/117693430500100003
- Falush, D., Stephens, M., and Pritchard, J. K. (2003). Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. *Genetics* 164, 1567–1587. doi: 10.1093/genetics/164.4.1567
- Ficetola, G. F., Bonin, A., and Miaud, C. (2008). Population genetics reveals origin and number of founders in a biological invasion. *Mol. Ecol.* 17, 773–782. doi: 10.1111/j.1365-294X.2007.03622.x
- Fish research laboratory of Institute of Hydrobiology of Hubei province. (1976). *The Yangtze River Fish*. Beijing: Science Press.
- Frankham, R. (2005). Resolving the genetic paradox in invasive species. *Heredity* 94, 385–385. doi: 10.1038/sj.hdy.6800634
- Gao, X., Fujiwara, M., Winemiller, K. O., Lin, P. C., Li, M. Z., and Liu, H. Z. (2019). Regime shift in fish assemblage structure in the Yangtze River following construction of the Three Gorges Dam. *Sci. Rep.* 9:4212. doi: 10.1038/s41598-019-38993-x
- Gao, X., Zeng, Y., Wang, J. W., and Liu, H. Z. (2010). Immediate impacts of the second impoundment on fish communities in the Three Gorges Reservoir. *Environ. Biol. Fish.* 2010, 163–173. doi: 10.1007/s10641-009-9577-1
- Goudet, J. (2001). *FSTAT, a Program to Estimate and Test Gene Diversities and Fixation Indices*. Available online at: <http://www.unil.ch/izea/software/fstat.html> (accessed August 23, 2005).
- Guo, S. W., and Thompson, E. A. (1992). Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* 48, 361–372. doi: 10.2307/2532296
- Haubrock, P. J., Pilotto, F., Innocenti, G., Cianfanelli, S., and Haase, P. (2021). Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. *Glob. Change Biol.* 27, 606–623. doi: 10.1111/gcb.15442
- Huang, Z. L., and Wu, B. F. (2018). *Three Gorges Dam*. Berlin: Springer.
- Kalinowski, S. T., Taper, M. L., and Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* 16, 1099–1106. doi: 10.1111/j.1365-294X.2007.03089.x
- Kanarek, A. R., and Webb, C. T. (2010). Allee effects, adaptive evolution, and invasion success. *Evol. Appl.* 3, 122–135. doi: 10.1111/j.1752-4571.2009.00112.x
- Kolbe, J. J., Glor, R. E., Schettino, L. R. G., Lara, A. C., Larson, A., and Losos, J. B. (2004). Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431, 177–181. doi: 10.1038/nature02807
- Kreyenberg, W., and Pappenheim, P. (1908). Ein Beitrag zur Kenntnis der Fische der Jangtze und seiner Zuflüsse. *Sitzungsber. Ges. Naturf. Freunde Berlin* 1908, 95–109.
- Kumar, S., Stecher, G., and Tamura, K. (2016). MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol. Biol. Evol.* 33, 1870–1874. doi: 10.1093/molbev/msw054
- Levine, J. M. (2008). Biological invasions. *Curr. Biol.* 18, R57–R60. doi: 10.1016/j.cub.2007.11.030
- Li, X. H., Huang, J., Filker, S., Stoock, T., Bi, Y. H., Yu, Y. H., et al. (2019). Spatio-temporal patterns of zooplankton in a main-stem dam affected tributary: a case study in the Xiangxi River of the Three Gorges Reservoir, China. *Sci. China Life Sci.* 62, 1058–1069. doi: 10.1007/s11427-018-9523-0
- Liao, C. S., Chen, S. B., De Silva, S. S., Correa, S. B., Yuan, J., Zhang, T. L., et al. (2018). Spatial changes of fish assemblages in relation to filling stages of the Three Gorges Reservoir, China. *J. Appl. Ichthyol.* 34, 1293–1303. doi: 10.1111/jai.13798
- Librado, P., and Rozas, J. (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25, 1451–1452. doi: 10.1093/bioinformatics/btp187
- Lin, P. C., Brosse, S., Gao, X., Liu, C. C., and Liu, H. Z. (2013). Species composition and temporal pattern of fish passing through the navigation locks in the middle reach of Yangtze River: implications for fish conservation. *J. Appl. Ichthyol.* 29, 1441–1444. doi: 10.1111/jai.12362
- Liu, P. Z., Liu, M. H., Lei, G. C., Zeng, Q., Li, Y. Y., and Bridgewater, P. (2021). Conservation of the Yangtze River Basin, China. *Oryx* 55, 331–332. doi: 10.1017/S0030605321000065
- Liu, Y. L. (2008). *Species Identification and Biological Characteristics of Coilia brachygnathus in the Poyang Lake*. Master's thesis. Nanchang: Nanchang University.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., and Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710.
- Meyers, M. A., Lin, A. Y. M., Lin, Y. S., Olevsky, E. A., and Georgalis, S. (2008). The cutting edge: sharp biological materials. *JOM* 60, 19–24. doi: 10.1007/s11837-008-0027-x
- Morim, T., Bigg, G. R., Madeira, P. M., Palma, J., Duvernell, D. D., Gisbert, E., et al. (2019). Invasion genetics of the mummichog (*Fundulus heteroclitus*): recent anthropogenic introduction in Iberia. *PeerJ* 7:e6155. doi: 10.7717/peerj.6155
- Peakall, R., and Smouse, P. E. (2006). GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol. Ecol. Resour.* 6, 288–295. doi: 10.1111/j.1471-8286.2005.01155.x
- Peischl, S., and Excoffier, L. (2015). Expansion load: recessive mutations and the role of standing genetic variation. *Mol. Ecol.* 24, 2084–2094. doi: 10.1111/mec.13154
- Pinsky, M. L., and Palumbi, S. R. (2014). Meta-analysis reveals lower genetic diversity in overfished populations. *Mol. Ecol.* 23, 29–39. doi: 10.1111/mec.12509
- Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics* 155, 945–959. doi: 10.1093/genetics/155.2.945
- Radinger, J., Essl, F., Hölker, F., Horký, P., Slavík, O., and Wolter, C. (2017). The future distribution of river fish: the complex interplay of climate and land use changes, species dispersal and movement barriers. *Glob. Change Biol.* 23, 4970–4986. doi: 10.1111/gcb.13760
- Radinger, J., and Wolter, C. (2014). Patterns and predictors of fish dispersal in rivers. *Fish Fish.* 15, 456–473. doi: 10.1111/faf.12028
- Reed, D. H., and Frankham, R. (2003). Correlation between fitness and genetic diversity. *Conserv. Biol.* 17, 230–237. doi: 10.1046/j.1523-1739.2003.01236.x
- Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* 43, 223–225. doi: 10.2307/2409177
- Roman, J., and Darling, J. A. (2007). Paradox lost: genetic diversity and the success of aquatic invasions. *Trends Ecol. Evol.* 22, 454–464. doi: 10.1016/j.tree.2007.07.002
- Rousset, F. (2008). GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Mol. Ecol. Resour.* 8, 103–106. doi: 10.1111/j.1471-8286.2007.01931.x
- Stepien, C. A., Brown, J. E., Neilson, M. E., and Tumeo, M. A. (2005). Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. *Risk Anal.* 25, 1043–1060. doi: 10.1111/j.1539-6924.2005.00655.x
- Stone, R. (2008). Three Gorges Dam: into the unknown. *Science* 321, 628–632. doi: 10.1126/science.321.5889.628
- Tang, W. Q., Hu, X. L., and Yang, J. Q. (2007). Species validities of *Coilia brachygnathus* and *C. nasus taihuensis* based on sequence variations of complete mtDNA control region. *Biodivers. Sci.* 15, 224–231. doi: 10.1360/biodiv.060263
- Thompson, J. N. (1998). Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13, 329–332. doi: 10.1016/S0169-5347(98)01378-0
- Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., and Shipley, P. (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Resour.* 4, 535–538. doi: 10.1111/j.1471-8286.2004.00684.x

- Wei, N., Zhang, Y., Wu, F., Shen, Z. W., Ru, H. J., and Ni, C. H. (2021). Current status and changes in fish assemblages in the Three Gorges Reservoir. *Resour. Environ. Yangtze Basin* 30, 1858–1869.
- Wei, Q. W., Ke, F. E., Zhang, J. M., Zhuang, P., Luo, J. D., Zhou, R. Q., et al. (1997). Biology, fisheries, and conservation of sturgeons and paddlefish in China. *Environ. Biol. Fish.* 48, 241–255. doi: 10.1023/A:1007395612241
- Whitehead, P. J. P., Nelson, G. J., and Wongratana, T. (1988). *FAO species catalogue. Vol. 7. Clupeoid Fishes of the World (Suborder Clupeioidi). An Annotated and Illustrated Catalogue of the Herrings, Sardines, Pilchards, Sprats, Shads, Anchovies and Wolf-Herrings. Part 2: Engraulididae*. Rome: FAO Fisheries Synopsis.
- Whitney, K. D., and Gabler, C. A. (2008). Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Divers. Distrib.* 14, 569–580. doi: 10.1111/j.1472-4642.2008.00473.x
- Xiang, J. W., Wang, C. F., Liu, D. F., Zhou, J. F., Feng, X., and Zhao, P. (2015). Temporal characteristics of fish passing through the Gezhouba ship lock. *Resour. Environ. Yangtze Basin* 24, 455–463.
- Xiao, W. H., Zhang, Y. P., and Liu, H. Z. (2001). Molecular systematics of Xenocyprinae (Teleostei: Cyprinidae): taxonomy, biogeography, and coevolution of a special group restricted in east Asia. *Mol. Phylogenet. Evol.* 18, 163–173. doi: 10.1006/mpev.2000.0879
- Xu, K. H., and Milliman, J. D. (2009). Seasonal variations of sediment discharge from the Yangtze River before and after impoundment of the Three Gorges Dam. *Geomorphology* 104, 276–283. doi: 10.1016/j.geomorph.2008.09.004
- Yang, F. (2019). *Genetic Diversity Comparison of Coilia Brachygnathus and Neosalanx Taihuensis Between Populations in the Three Gorges Reservoir and Dongting Lake*. Master Dissertation. El Paso, TX: Southwest University.
- Yu, A. Q., Shi, Y. H., and Deng, P. P. (2019). Microsatellite analysis of genetic diversity of wild population and selection of *Coilia nasus* in the Yangtze River. *Aquat. Sci. Technol. Inform.* 46, 121–125.
- Zhang, H., Wu, G. G., Xie, P., Xu, J., and Zhou, Q. (2013). Role of body size and temporal hydrology in the dietary shifts of shortjaw tapertail anchovy *Coilia brachygnathus* (Actinopterygii, Engraulidae) in a large floodplain lake. *Hydrobiologia* 703, 247–256. doi: 10.1007/s10750-012-1370-z

Conflict of Interest: BL and WJ were employed by Three Gorges Corporation.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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