INTRODUCTION

Geographical patterns, climate, and environmental changes have important influences on the genetic composition, population distribution, and species diversity of aquatic organisms (Hewitt, 2000; Petit et al., 2003). Avise et al. (1987) presented the concept of intraspecific phylogeography, whose basic principle was to study the relationship between gene genealogy and geography of organisms. The genealogical analysis and temporal–spatial distribution of haplotypes could be used to estimate the historical process of species differentiation between closely related species or at the intraspecific level (Avise, 1998; Zuykova, Bochkarev, & Sheveleva, 2016).
The phylogeography of organisms can be effectively revealed using multiple molecular markers. By using the mitochondrial COI and NDI genes, Ober, Matthews, Ferrieri, and Kuhn (2011) found that most mountain ranges resulted in the population differentiation of *Scaphinotus petersi* distributed on Sky Islands in southeastern Arizona during the postglacial maximum times. Based on the 16S rDNA, COI gene, and 18S rDNA molecular markers, Wang et al. (2016) concluded that the phylogenetics of the cladoceran *Daphnia pulex* located in ten habitats of the middle and lower reaches of the Yangtze River was related to its geographical location. In the nuclear genome, microsatellite markers have widely been applied to phylogeography because of their high polymorphism, stability, codominance, and Mendelian inheritance (Lane, Symonds, & Ritchie, 2016; Mobley, Small, Jue, & Jones, 2010).

Zooplankters are an important part of aquatic food chains and have important ecological roles in aquatic ecosystems. *Daphnia* is a common crustacean zooplankton, having the characteristics of wide distribution, rapid reproduction, and sensitivity to environmental changes (Su, 2013). So, *Daphnia* is often regarded as a model organism for the study of bio-toxicology, genetics, and ecology (Hebert, 1978; Lampert, 2011). Moreover, *Daphnia* has a weak swimming ability because of a small body size (Rand, 1996). *D. similoides sinensis* is distributed in eutrophic ponds and lakes in Southern Asia, from Pakistan to Indonesia, and China (Benzie, 2005). *D. similoides sinensis* perform cyclic parthenogenesis under good conditions, whereas they convert to sexual reproduction and produce resting eggs when environmental conditions worsen, such as low temperature, large predation pressure, or high population density (Figure 1). This species was previously recorded as *D. similis* or *D. carinata* in China (Gu, Xu, Lin, Henri, & Han, 2013; Jiang & Du, 1979; Xu et al., 2014). *D. similoides sinensis* was observed in some lakes located in the middle and lower reaches of the Yangtze River, China (Chen, Chen, Li, & Zhao, 2009; Ma et al., 2016), which coexisted with *Daphnia pulex* and *Daphnia galeata* (Deng et al., 2008).

The Huai River historically drained directly into the Yellow Sea, but it is now connected to the lower reaches of the Yangtze River after many floods. Along the middle and lower reaches of the Yangtze River and Huai River of China, many tributaries of the river and lakes are distributed (Figure 2). There were nineteen floods in the middle and lower reaches of the Yangtze River from 1921 to 2000 (Shi, Jiang, Su, Chen, & Qin, 2004). Many dam and sluice projects in the region have been built since 1950s in order to store water or prevent the flooding, and some lakes have changed from a natural type into a reservoir type (Wang & Dou, 1998). In Lake Chaohu, the lake was isolated from the Yangtze River due to the construction of Chaohu dam and Yuxi dam in the 1950s. Similarly, the connection of Lake Junshan with Lake Poyang and the Yangtze River was cut off after the construction of the lake embankment in 1958 (Wang & Dou, 1998). In Wuhan city, Lake Nanhu had become a closed lake as a result of the development of the city. The building of dams and sluices can form a barrier for the migration and communication of aquatic organisms (Naiman, Melillo, Lock, Ford, & Reice, 1987; Yi, Yang, & Zhang, 2010), resulting in changes in species diversity or genetic diversity. About 28 species of fish have disappeared since 1950 in Lake Zhangdu due to the construction of artificial barriers between the rivers and lakes (Wang, Hu, & Wang, 2005). In the Three Gorges reservoir area of the Yangtze River, seven *Leiocassis longirostris* populations diverged into two groups after the construction of the Three Gorges Dam (Li, 2007). Moreover, natural linkage between the Huai River system and the Yangtze River system was also isolated after the construction of Sanhe sluice in 1953. How these changes in hydrology influence the genetic diversity and

**FIGURE 1** The photograph of *Daphnia similoides sinensis* female (a: parthenogenetic female, b: sexual female)
phylogeography of aquatic organisms (e.g., *Daphnia*) located in the middle and lower reaches of the Yangtze and Huai Rivers is not yet clear.

In this study, both mitochondrial (COI gene) and nuclear (14 microsatellite primers) markers were jointly used to study the genetic diversity of *D. similoides sinensis*. This study aims to compare the differences in phylogenetics and population genetics of *D. similoides sinensis* located in the middle and lower reaches of the Yangtze River and to explore the influence of the geographical pattern on the phylogenetics of *D. similoides sinensis*. Specifically, we have made a hypothesis that the construction of dam and sluices in the middle and lower reaches of the Yangtze River promoted the genetic differentiation of *D. similoides sinensis*.

2 MATERIALS AND METHODS

2.1 Animal culture and DNA extraction

*Daphnia similoides sinensis* was collected from water bodies located in the middle and lower reaches of the Yangtze River, belonging to water systems of the Yangtze River and Huai River (Table 1). In the laboratory, animals were identified (Benzie, 2005; Jiang & Du, 1979) and then monoclonally cultured in an intelligent light incubator (Ningbo Saifu, China) with the illumination of 12 hr light: 12 hr dark at (25 ± 1)°C. *Scenedesmus obliquus* was used as their food.

Before extracting complete DNA of monoclonal *D. similoides sinensis*, each adult individual was drawn by a straw and rinsed with double-distilled water, and then crushed with a sterile 10 μl pipette tip. Genomic DNA of *D. similoides sinensis* was extracted by the TIANamp Micro DNA Kit (Tiangen, Beijing).

2.2 PCR amplification

Fourteen pairs of primers were used for the microsatellite markers (Table 2). The COI gene was amplified with the LCO1490 (5′-GGTCAAACAAATCATAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAATCA-3′) (Xu et al., 2014).

The PCR system (25 μl) of the COI gene contained 1.0 μl of genomic DNA (100 ng/μl), 2.5 μl of 10 × LA‐Taq Buffer II, 4.0 μl of dNTPs (2.5 mM) (Shanghai Shenggong, China), 0.5 μl of MgCl₂ (25 mM), 1.0 μl of each primer (10 mM) (Shanghai Shenggong, China), 0.25 μl of DNA polymerase TaKaRa‐LA‐Taq (5 U/μl) (Clontech, USA), and 14.75 μl of double-distilled H₂O. The PCR system (25 μl) of the SSRs contained 1.0 μl of genomic DNA (100 ng/μl), 1.0 μl of each primer (10 mM) (Shanghai Shenggong, China), 12.5 μl of 2 × Taq Master Mix (BioTeke Corporation, China), and 9.5 μl of double-distilled H₂O.

The conditions of the COI gene amplification included an initial denaturing step of 1 min at 95°C, 35 cycles of 40 s at 95°C, 40 s at 45°C, and 1 min at 72°C, as well as a final extension of 72°C for 10 min. The conditions of the SSR amplification included an initial denaturing step of 3 min at 95°C, 35 cycles of 45 s at 95°C, 45 s at 54°C, and 45 s at 72°C, as well as a final extension of 72°C for 10 min.

2.3 Electrophoresis, sequencing, and data analyses

The PCR amplification products of the COI gene were checked by gel electrophoresis and then purified by the AxyPrep DNA Gel Recovery Kit (AxyPrep, USA) and sequenced with the forward and reverse primers (GenScript, Nanjing). The sequence alignment was carried out using the SeqMan software in DNAStar. DNAspV5 was used to analyze the site variations, haplotype diversity, and nucleotide diversity of *D. similoides sinensis* among the COI sequences, as well as *Fₜₐ* among populations. *Fu’s Fs* test, *Tajima’s* neutrality test, and mismatch distribution were used to detect the evolutionary history of *D. similoides sinensis* populations (Fu, 1997; Tajima, 1989) using DnaSP Version 5. The dendrogram (NJ/MP) of seven *D. similoides sinensis* populations based on the *Fₜₐ* values was constructed with MEGA 4.1. The genetic distances of seven *D. similoides sinensis* populations were calculated using MEGA 4.1. The genetic distances...
among sequences were calculated by the Kimura’s two-parameter model with 1,000 bootstraps. Phylogenetic tree of *Daphnia* individuals based on Maximum likelihood (ML) estimates was constructed with MEGA 4.1 and bootstrap resampled 1,000 times.

The *D. similoides sinensis* samples from seven populations located in the middle and lower reaches of the Yangtze River were amplified using the 14 microsatellite fluorescent labeled primers (Table 2). The PCR products were checked by both agarose gel electrophoresis and capillary electrophoresis using an ABI 3730 sequencer. The number of observed and effective alleles, expected heterozygosity, shannon information index and polymorphic ratio were calculated using the Popgene version 1.31 software (Yeh,
Yang, & Boyle, 1999), as well as the genetic distances among populations. Based on the microsatellite markers, Fst among populations were performed by Arlequin 3.5 software to analyze the differences in the genetic diversity among seven *D. similoides sinensis* populations. The population genetic structure of *D. similoides sinensis* was reconstructed using the 14 polymorphic microsatellite loci in Structure 2.3.1. Posterior likelihood values were calculated from K = 1 to K = 10 using the LOCPRIOR model (Hubisz, Falush, Stephens, & Pritchard, 2009). For each K, 10 simulations with a burn-in of 10,000 Markov Chain Monte Carlo (MCMC) iterations were run, and then 100,000 iterations after burn-in were performed. The most likely value for K was estimated from the greatest rate of change in the likelihood function (ΔK) of successive K values (Evanno, Regnaut, & Goudet, 2005; Frisch et al., 2017). Mantel’s tests were used to measure the geographical distances and genetic distances (Fst) among seven geographical populations of *D. similoides sinensis* with tools for population genetic analyses (TFPGA) version 1.3 (Miller, 1997).

## 3 | RESULTS

### 3.1 | Analysis on the genetic diversity and haplotype structures of seven *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River based on the COI gene marker

Among seven *D. similoides sinensis* populations, 172 mitochondrial gene sequences were obtained, and the number of identified base sites was 478. The nucleotide diversity (π) and haplotype diversities (Hd) were, respectively, 0.0053 and 0.784. A total of 24 haplotypes were detected, including 8 shared haplotypes and 16 specific haplotypes. The haplotype networks indicated that seven *D. similoides sinensis* populations had one ancestral haplotype (H-2) and two main clades (Figure 2), which showed the specificity of geographical distributions. The specific haplotypes were mainly distributed in HBDH and JSTH populations, which are located in the upper reaches of the Huai River tributary and lower reaches of the Yangtze River, respectively. In addition, both JSH population (H-2, H-3, and H-19) and WHNH population (H-2, H-4, and H-24) were mainly composed of three haplotypes, which had significant differences from the other five populations.

### 3.2 | Genetic diversity and genetic structure of seven *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River based on the 14 SSR markers

Among seven *D. similoides sinensis* populations, the ranges of observed alleles, effective alleles, and shannon information index were 1.094–1.648, 1.063–1.185, and 0.053–0.195, respectively. The ranges of observed heterozygosity and expected heterozygosity were 0.383–0.611 and 0.471–0.692, respectively. The haplotype diversity (Hd) and nucleotide diversity (π) ranged from 0.553 to 0.936 and from 0.0014 to 0.0092, respectively (Table 3).

Based on the microsatellite markers, the molecular variances were 4.305 within populations and 0.561 among populations, suggesting that the genetic variation in *D. similoides sinensis* located in the middle and lower reaches of the Yangtze River occurred mostly within populations. The Nei’s genetic distances among seven *D. similoides sinensis* populations ranged from 0.002 to 0.008 (Table 4). The maximum genetic distance appeared between the HBDH and JSH populations, whereas the minimum was between the WHNH and JSTH populations.

Seven *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River were grouped into three clusters (Figure 3). Among them, cluster 1 dominated in the WHNH population, CH population, and JSTH population, and cluster 3 dominated in the JSH population, which is distributed in the Yangtze River basin. However, cluster 2 dominated in the HBSH population and HBDH population which distributed in the Hua River basin, as well as in the HDL population which located in the lower reaches of the Yangtze river.

### 3.3 | Genetic differentiation of seven *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River

Based on the microsatellite markers, there was lower Fst between the HBSH population and other six populations (Table 5), especially between the HBSH population and HBDH population (0.027). The

| TABLE 3 | Summary of genetic variation in seven *Daphnia similoides sinensis* populations |
|---------|------------------------------------------|
|         | Hd | π   | Tajima’s D | Fu and Li’s D | na | ne | h   | l   | Exp_Het | Obs_Het |
| CH      | 0.936 | 0.0054 | −0.683 | −1.149 | 1.604 | 1.185 | 1.119 | 0.194 | 60.430 | 0.663 | 0.500 |
| HBDH    | 0.871 | 0.0092 | −1.176 | −0.534 | 1.432 | 1.155 | 0.100 | 0.160 | 43.170 | 0.572 | 0.383 |
| HBSH    | 0.751 | 0.0082 | −1.243 | −2.242 | 1.453 | 1.177 | 0.112 | 0.177 | 45.320 | 0.608 | 0.485 |
| JSH     | 0.591 | 0.0014 | −0.711 | −0.951 | 1.648 | 1.170 | 0.115 | 0.195 | 64.750 | 0.692 | 0.438 |
| JSTH    | 0.801 | 0.0074 | −2.087 | −3.673 | 1.152 | 1.173 | 0.110 | 0.178 | 51.080 | 0.630 | 0.516 |
| WHNH    | 0.553 | 0.0022 | 1.002 | −0.229 | 1.432 | 1.151 | 0.095 | 0.151 | 43.170 | 0.531 | 0.338 |
| HDL     | 0.553 | 0.0022 | 1.002 | −0.229 | 1.432 | 1.151 | 0.095 | 0.151 | 43.170 | 0.531 | 0.338 |

Notes. Exp_Het: expected heterozygosity; h: Nei’s gene diversity; Hd: haplotype diversity; l: Shannon’s diversity index; na: the observed number of alleles; ne: the effective number of alleles; Obs_Het: observed heterozygosity; P: percentage of polymorphic loci; π: nucleotide diversity. *Significance at the 5% level.
The value between the JSH population and other six populations was very high (Table 5), implying that there was genetic isolation between the JSH population and other six populations. At the same time, based on the mitochondrial marker, the $F_{st}$ values between the JSH population and other six populations were also higher (Table 5). The $F_{st}$ values based on the mitochondrial marker were
3.4 | Phylogeography of seven *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River

Because of the lower sample size of the HDL population, phylogenetic trees (NJ/ME) of only six populations (CH, HBDH, HBSH, JSH, JSTH, and WHNH population) were constructed based on both mitochondrial and microsatellite markers. Based on the microsatellite markers, the dendrogram (NJ/ME) showed that six *D. similoides sinensis* populations were obviously divided into three clades (Figure 4a). In the lower reaches of the Yangtze River, the JSTH population located in a separate clade, whereas the CH population and JSH population were clustered into another clade. The WHNH, HBSH, and HBDH populations were clustered into the third clade, among which the WHNH population is distributed in the middle reaches of the Yangtze River and the HBDH and HBSH populations in the upper reaches of the Huai River tributary. Based on the mitochondrial genes marker, the dendrogram (NJ/ME) indicated that six *D. similoides sinensis* populations were clustered into two main clades (Figure 4b). The JSH, CH, and JSTH populations were clustered into a clade, whereas the WHNH, HBDH, and HBSH populations were in the other clade. According to the mitochondrial and microsatellite markers, it was obvious that there were two evolutionary directions of *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River. Moreover, the phylogenetic tree (ML) of *D. similoides sinensis* individuals showed also two major evolutionary clades (clade A and clade B) (Figure 5). Clade A mainly included the individuals of HBDH, HBSH, and WHNH populations, whereas clade B mainly contained the individuals of JSH, CH, and JSTH populations.

Based on the mitochondrial gene sequences, the distribution of base mismatches indicated that there was a single peak, implying that the *D. similoides sinensis* population located in the middle and lower reaches of the Yangtze River experienced an expansion process (Figure 6). Both Fu’s Fs neutral test (*D* = −3.673, *p* < 0.02) and Tajima’s test (*D* = −2.087, *p* < 0.05) showed that the JSTH population deviated from neutral evolution, whereas the other six populations did not deviate from neutral evolution.

4 | DISCUSSION

4.1 | Genetic diversity and genetic structure of *D. similoides sinensis* located in the middle and lower reaches of the Yangtze River

Haplotype diversity (Hd) and nucleotide diversity (π) are two important parameters to study population genetic diversity of organisms (Tajima, 1983; Weir, 1990). Higher Hd and lower π values in the natural population means that the organism could expand after a period of lower population size and enhance the retention of new mutations (Crandall, Sbrocco, Deboer, Barber, & Carpenter, 2011; Grant & Bowen, 1998). In this study, based on mitochondrial COI gene sequences, higher Hd and lower π values suggested that *D. similoides sinensis* located in the middle and lower reaches of the Yangtze River experienced a bottleneck in the process of population formation. This phenomenon may be related to the rapid expansion of aquatic animal populations after the bottleneck effect and the quick accumulation of Hd, as well as periodic flooding events that occur in this region (Xu, Yu, & Ma, 2005). The Fu’s Fs neutral test and Tajima’s test suggested that the *D. similoides sinensis* JSTH population had experienced a bottleneck effect in the history. The JSTH population is located in Lake Taihu, which is part of the lower reaches of the Yangtze River. To improve water quality, two water transfer projects from the Yangtze River to Lake Taihu were conducted from 2002 to 2003 (Hu, Zhai, Zhu, & Han, 2008). However, the ecosystem in Lake Taihu became unstable after water transfers (Zhai, Hu, & Zhu, 2010). These water transfer projects might have resulted in the JSTH bottleneck and affected the population structure of *D. similoides sinensis* in Lake Taihu.

In this study, seven *D. similoides sinensis* populations located in the middle and lower reaches of the Yangtze River were grouped into three clusters based on the microsatellite markers. According to the location of these populations, three clusters appeared to be related to geography, which cluster 2 was dominant in the Huai River basin whereas cluster 1 dominated along of the Yangtze River. Moreover, the dendrogram (NJ/ME) based on the mitochondrial genes marker showed that six *D. similoides sinensis* populations were obviously clustered into two main clades, whereas there were three clades based on the microsatellite markers. One reason for the differing results between the mitochondria and nuclear
data is significant differences in the evolutionary rate and level of polymorphism between different molecular markers (Bai & Zhang, 2014). The mitochondrial DNA have the characteristics of maternal inheritance (Avise et al., 1987), whereas the nuclear genes have higher mutation rates and are more appropriate for determining the genetic differences in organisms among different geographic populations (Al-Hamidhi et al., 2015; Selkoe & Toonen, 2006). The above results suggested that *D. similoides sinensis* located in the middle and lower reaches of the Yangtze River show significant genetic differentiation.

**4.2 | Influence of geographic isolation on the phylogeography of *D. similoides sinensis* located in the middle and lower reaches of the Yangtze River**

The influences of geographic isolation on the phylogeography of aquatic organisms have extensively been researched in the world. Machordom and Doadrio (2001) found that the geographic isolation caused the interruption of gene flow of *Luciobarbus* and then affected the phylogenetic differentiation and geographical distribution of *Luciobarbus* population. Slechtova, Bohlen, Freyhof,
The observed pairwise difference (red line) and the expected mismatch distributions under the sudden expansion model (green line) based on the mitochondrial gene sequences of *Daphnia similoides sinensis* populations located in the middle and lower reaches of the Yangtze River.

In conclusion, there is significant genetic structure of the *D. similoides sinensis* populations in the middle and lower reaches of the Yangtze River. The *D. similoides sinensis* distributed in the region had formed two clades, namely the Yangtze River clade and the Huai River clade. The *D. similoides sinensis* habitats in the middle and lower reaches of the Yangtze River have been fragmented because of the construction of dams and sluices since the 1950s. Habitat discontinuity and geographic segregation could accelerate regional genetic differentiation of *D. similoides sinensis* in the middle and lower reaches of the Yangtze River.

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**CONFLICT OF INTEREST**

None declared.

**AUTHORS’ CONTRIBUTIONS**

J.-X.W., D.-G.D., and Z.-Z.Z conceived and designed the experimental plan. J.-X.W., K.Z, W.-P. Z. S.-X.P, and X.-X.X. performed the experiments. J.-X.W. and Y.-N.Z. analyzed and interpreted the sequence data. J.-X.W. and D.-G.D. drafted the manuscript. All authors have read and approved the final manuscript.

**DATA ACCESSIBILITY**

The sequencing data of *Daphnia similoides sinensis* in this study were deposited in DRYAD (https://doi.org/10.5061/dryad.66p5487).
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