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Population genetic differentiation of *Daphnia sinensis* in a lasting high-phosphorus Chinese lake, Lake Chaohu

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Ecological shifts (e.g., eutrophication) can affect the genetic differentiation of zooplankton populations in lakes. However, the role of environmental change in a lasting high-phosphorus lake driving the genetic differentiation of zooplankton population structure over time is poorly understood. In this paper, the changes of the genetic diversity and differentiation of *Daphnia sinensis* population were studied by using the mitochondrial COI gene and microsatellite markers on modern groups (from January to June 2016) and historic groups (obtained from resting eggs in the sediments) in Lake Chaohu. Based on the microsatellite markers, six modern groups were clustered into two clusters (the WG cluster and SG cluster) during the seasonal dynamics, whereas the genetic differentiation of the five historic groups showed a wave-like pattern and had evolved into four clusters. Moreover, the haplotype network showed that six modern groups had one origin center whereas five historic groups had two origin centers based on the mitochondrial COI gene marker. Fu's F_s neutral test and Tajima's test indicated that the five historic groups deviated from neutral evolution and showed a bottleneck effect in the history process. Water temperature and total dissolved phosphorus were obviously associated with the seasonal genetic differentiation of *D. sinensis*, whereas nitrogen content of the sediments was significantly related to the long-term microevolution of *D. sinensis* in the high-phosphorus environment. Therefore, the changing pattern of *D. sinensis* population genetic structure was one of the environmental selections probably combined with co-evolutionary, where rapid-increasing nitrogen level had a large impact on *D. sinensis* population genetic structure in lasting high phosphorus environment in Lake Chaohu.

KEYWORDS

Daphnia sinensis, eutrophication, genetic differentiation, resting eggs, sediment

Introduction

Understanding evolutionary responses in aquatic organisms to long-term environment change is a challenge in contemporary biology (Frisch et al., 2014). The main reason for the challenges is the lack of objective conditions and techniques for continuous and lasting sampling for a single population. Revealing long-term variation of population genetic structure and clarifying the mechanism on population genetic isolation at a specific time scale are difficult due to the seasonal succession of zooplankton in lakes. Fortunately, some investigations have been reported to reconstruct *Daphnia* population genetic structure based on genetic data of resting eggs from the sediments (Hairston et al., 1999; Decaestecker et al., 2007; Brede et al., 2009; Orsini et al., 2013a; Möst et al., 2015; Monchamp et al., 2017). In lake ecosystems, the resting eggs of *Daphnia* are buried in the sediments in chronological order and can remain alive for decades, centuries, or even longer (Brede et al., 2009; Frisch et al., 2014; Monchamp et al., 2017). Similarly, succession processes of lake environments (e.g., nutrient levels) can be also replicated by analyzing the information preserved in the sediments (Yao and Shen, 2003; Li et al., 2005). Direct observation of population genetic variations of the organisms over time, complemented by long-term environmental data, will allow us to validate our current mechanisms understanding on evolutionary responses of natural populations to environmental changes (Brede et al., 2009; Orsini et al., 2013a; Frisch et al., 2014).

Environmental changes (e.g., eutrophication) enhance the evolution of zooplankton populations (Straile and Geller, 1998; Løvik and Kjellberg, 2003; Stige et al., 2009; Hsieh et al., 2011; Frisch et al., 2017). Excessive phosphorus loading promote significantly the increase of phytoplankton biomass in lakes, and then alter the nutrition of zooplankton, such as the basic aquatic herbivores, *Daphnia* (Sterner and Elser, 2002). *Daphnia* are the phosphorus-rich consumers, which are therefore highly sensitive to changes in phosphorus loading (Elser et al., 1988). Jeyasingh and Weider (2007) found that the genetic variations of *Daphnia* populations were related to phosphorus availability. In Lake Constance, the biomass and community structure of crustacean zooplankton were affected by eutrophication (Straile and Geller, 1998). Frisch et al. (2014) observed that the population differentiation of *Daphnia pulicaria* was associated with phosphorus accumulation in Lake Minnesota (North America), and ancient population (preserved in the sediments for more than 700 years) had a higher growth rate under low-phosphorus condition and a lower growth rate under high-phosphorus condition whereas modern population exhibited the opposite trend. Similarly, in two European lakes, the changes of total phosphorus were clearly associated with a shift in *Daphnia* species composition and population structure of evolutionary lineages (Brede et al., 2009). Therefore, in order to adapt habitat environments, the genetic variations of *Daphnia* could be induced and preserved through resting eggs in lake sediments.

Daphnia species often inhabit freshwater lakes, ponds, and reservoirs, which are affected by environmental factors such as temperature, nutrient availability, competition and predation (Roff et al., 1981; Wellborn et al., 1996; Cottenie et al., 2001). *Daphnia* species perform cyclic parthenogenesis under good conditions but are concerted into sexual reproduction and produce resting eggs enclosed in the ephippium when the environment conditions become worse, such as lower temperature, larger predation pressure or higher population density. The resting eggs of *Daphnia* are preserved in lake sediments, thus forming an egg bank. When these resting eggs are suspended in water because of wind wave or other reasons, they could hatch under suitable conditions and form new populations (Hairston and Cáceres, 1996). At present, the phylogeography of *Daphnia* species is mainly focused on large-scale spatial pattern of modern populations (De Gelas and De Meester, 2005; So et al., 2015; Ma et al., 2016, 2020; Kotov et al., 2021). However, fewer studies are focused on the long-term genetic differentiation of *Daphnia* species based on the information of resting eggs located in different sediment layers (Brede et al., 2009; Möst et al., 2015; Monchamp et al., 2017).

Lake Chaohu (Anhui province, China) is a large subtropical eutrophic lake located in the middle reaches of the Yangtze River, with a total surface area of 755 km². Phosphate rocks are abundant in the north shore of the lake, and the exploitation of phosphate rock has led to the long-term phosphorus-rich state in the water since the 1960s (Xie, 2009). It has been reported that the lake water has suffered from eutrophication since the 1970s (Yao and Shen, 2003; Zhang and Kong, 2015). The average total phosphorus and total nitrogen concentrations reached the peak (0.417 and 4.62 mg/L, respectively) in 1995 (Xie, 2009). Although total phosphorus (TP) and total nitrogen (TN) concentrations dropped from 1995 to 2007 because of the control of waste water and sewage draining, the water quality of the lake still maintained a high nutrient level after 2008 (Zhang and Kong, 2015). In 1980–1981, only a few individuals of *Daphnia* sp. were occasionally observed in Lake Chaohu (Ye, unpublished data). In 2002–2003, 23 species of crustacean zooplankton belonging to 20 genera were recorded in Lake Chaohu, and three *Daphnia* species (*D. sinensis*, *D. pulex*, and *D. galeata*) dominated in spring, and then disappeared in mid-summer (Deng et al., 2008). In recent years, *Daphnia* had also dominated in spring and early summer (Li et al., 2015). These long-term changes of *Daphnia* density were consistent with the ephippia or resting eggs of *Daphnia* observed in the lake sediments over time (Zhang et al., 2020). Limited information was available on the study of zooplankton community structure in the lake, especially on the genetic diversity and phylogenetics of *Daphnia* species in a lasting high-phosphorus environment.

In this study, population genetic structure and differentiation of *D. sinensis* were studied using mitochondrial *COI* gene and microsatellite markers in Lake Chaohu. We used five historical groups that were hatched from resting eggs preserved in 15-cm sediment layers (long-term) and six modern groups that were collected during January and June of 2016 (short-term). The

effects of environmental factors (particularly nutrients and water temperature) on the genetic structure and phylogenetics of *D. sinensis* population in Lake Chaohu at short-term and long-term scales were discussed. We hypothesized environmental shifts to coincide with the shifts in genetic structure of *D. sinensis* population in Lake Chaohu, potentially indicating that rapid-increasing nitrogen level could lead to an evolutionary response of *D. sinensis* in lasting high-phosphorus environment. Additionally, we also proposed that under a lasting high-phosphorus environment, population genetic differentiation should be consistent with the law of neutral mutations and genetic drift.

Materials and methods

Collection and culture of *Daphnia sinensis*

In 2016, *D. sinensis* were collected monthly from 12 sampling sites using a 13# plankton net (112 μ m) for short-term samples (Figure 1). Additionally, 20 L of mixed water samples were filtered to determine the density of *D. sinensis* using a 25# plankton net (64 μ m) at a 0.5 m or 1 m interval. According to previous literatures (Deng et al., 2008; Li et al., 2015), no *D. sinensis* individuals were found from July to December in Lake Chaohu. In this study, the individuals collected in each month were defined as a group, with a total of six modern

groups. The species was identified under a microscope (Olympus CX31, Japan) according to Jiang and Du (1979) and Benzie (2005). Two hundred and eighty-six individuals were employed to estimate the genetic structure and differentiation of *D. sinensis* population during January and June (Table 1). Each individual employed in the experiment was cultured monoclally at $(25 \pm 1)^\circ\text{C}$ with 12 h light:12 h dark photoperiod (Zhang et al., 2015). Tap water that had been filtered and aerated for 48 h was utilized as the culture medium. *Tetrademus obliquus* was used as the food.

For long-term samples, four sediment cores of 24–30 cm in length were collected from the center of Lake Chaohu (6#) using a columnar gravity (Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences) with PVC tubes of 84 mm in diameter in August 2014 (Zhang et al., 2020). The sedimentary core was sectioned through a 1-cm cutting ring and stored in a sealed bag, then taken back to the laboratory and preserved at 4°C .

All 1 cm-thick sections from three sediment cores were used to examine the resting eggs enclosed in the ephippium of *D. sinensis*. Each 1 cm-thick section was rinsed with aerated tap water and then filtered through a 300 mesh sieve (48 μ m). The remaining part was put into a 50 mL beaker. All remains were observed under a microscope (Olympus CX31, Japan), and the ephippia containing resting eggs of *D. sinensis* were gathered with a glue head dropper and transferred to a 1 mL EB tube at 4°C for preservation. Few of these ephippia containing resting eggs were found in the sedimentary layers of below 15 cm (Zhang et al., 2020). Therefore, the ephippia containing resting eggs in the 0–15 cm sedimentary layers were selected in this study. These resting eggs were, respectively, placed in a 50 mL beaker and hatched in an intelligent incubator (Ningbo Saifu, Ningbo, China) at $25 \pm 1^\circ\text{C}$ with illumination period of L:D = 12 h:12 h. Each hatched individual was cultured monoclally in a 150 mL beaker containing 100 mL culture medium (aerated tap water over 48 h). *Tetrademus obliquus* was used as the food. In order to confirm the activity and genetic integrity of resting eggs, hatched individuals rather than resting eggs were used to evaluate the genetic structure and microevolution of *D. sinensis*. All hatched individuals of *D. sinensis* at 3 cm interval along the 15 cm sediment layers according to the changes of nutrient contents were regarded as a group (Zhang et al., 2020). In total, five historic groups (namely respectively, Pop1, 1–3 cm; Pop2, 4–6 cm; Pop3, 7–9 cm; Pop4, 10–12 cm; and Pop5, 13–15 cm) were obtained.

All 1 cm-thick sections of one sediment core were dried in the laboratory to measure dating and nutrient contents (Zhang et al., 2020). The dry samples were ground and filtered using a 100-mesh sieve (150 μ m). ^{137}Cs and ^{210}Pb were measured by a high purity germanium gamma spectrometer (AMETEK-AMT ORTEC) at State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences. According to the attenuation law of radioactive isotope, the radioactive dates were calculated using the constant rate of supply (CRS) ^{210}Pb dating model (Chen et al., 2014).

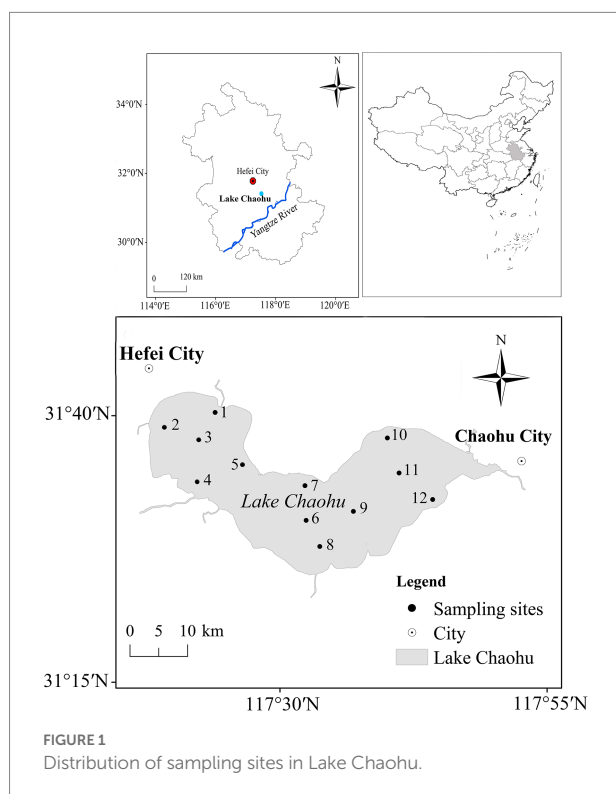


TABLE 1 Genetic diversity indexes of 11 *D. sinensis* groups in Lake Chaohu.

Subpopulation	Na	Ne	h	I	P	Fis	Hd	π	D	No. individuals
January	1.667	1.223	0.141	0.226	66.67%	0.172	0.808	0.003	0.003	48
February	1.561	1.216	0.135	0.213	56.41%	0.199	0.829	0.004	0.004	48
March	1.684	1.215	0.138	0.223	68.38%	0.284	0.909	0.004	0.004	36
April	1.650	1.214	0.135	0.217	64.96%	0.214	0.923	0.008	0.008	47
May	1.615	1.209	0.130	0.208	61.54%	0.300	0.879	0.006	0.006	59
June	1.650	1.206	0.130	0.212	64.96%	0.262	0.936	0.005	0.006	48
Pop1	1.458	1.192	0.119	0.188	45.80%	0.124	0.973	0.009	0.009	12
Pop2	1.550	1.199	0.124	0.197	54.96%	0.083	0.896	0.007	0.007	36
Pop3	1.435	1.180	0.110	0.172	43.51%	0.228	0.667	0.002	0.005	18
Pop4	1.374	1.175	0.107	0.167	37.40%	0.141	0.945	0.006	0.002	9
Pop5	1.290	1.172	0.101	0.152	29.01%	0.062	0.833	0.006	0.006	5

Na stands for the observed number of alleles, Ne-the effective number of alleles, h-Nei's gene diversity, I-Shannon's diversity index, P-percentage of polymorphic loci, Fis-inbreeding coefficient, Hd-haplotype diversity, π -Nucleotide diversity, D-the genetic distance within groups. Moreover, Hd, π , and D are based on the COI marker whereas Na, Ne, h, I, P, and Fis are based on the SSR marker.

Determination of physical and chemical parameters

For short-term samples, water samples were collected using a 2.5 L modified Patalas' sampler at 0.5 or 1 m interval from each sampling site. Water temperature (WT) and dissolved oxygen were measured *in situ* using a portable dissolved oxygen/temperature analyzer (HANNA, Italy). pH was measured with a portable pH/ORP analyzer (HACA, United States), and transparency was measured using a Secchi disk. One liter of water sample mixture was used to determine the nutrient concentrations. In the laboratory, the mixed lake water was filtered with Whatman GF/C filter prior to measuring dissolved total phosphorus (DTP) concentrations. TP and DTP concentrations were measured by colorimetry after the water samples were digested with $K_2S_2O_8$ to orthophosphate (Ebina et al., 1983). By contrast, TN were analyzed by the UV spectrophotometric method (Huang, 1999) after the water samples were digested with $K_2S_2O_8 + NaOH$.

Fifty milligram of each 1 cm-thick dried sample was used to measure the TN and TP contents in the sediment using $K_2S_2O_8$ digestion method (Qian et al., 1990).

DNA extraction and PCR amplification

After starving for 24 h, adult *D. sinensis* individuals were rinsed with double-distilled water and crushed with a sterile 10 μ L tip before extraction. Total DNA of *D. sinensis* was extracted using the TNAMP Micro DNA Kit (Tiangen Biotech Co., Ltd., Beijing, China).

Fourteen SSR primers were used in this study, including 11 pairs primers developed in the laboratory (NCBI accession number: KY440958, KY440961, KY440963, KY440966, KY440964, KY440968, KY440960, KY440965, KY440959, KY440962, and KY440967; Wu et al., 2019b) and three pairs primers downloaded

from NCBI (accession number: AF233360, AF233362, and AY057865). Mitochondrial COI gene was amplified with the COI F (5'-AYCAATCATAAGGACYATTGGRAC-3') and the COI R (5'-KGTGATWCCNACHGCTCAKAC-3'). The PCR reaction system (25 μ L) of COI gene and the PCR reaction system (25 μ L) of the SSR were referred to Wu et al. (2019a).

Electrophoresis and sequencing

The PCR amplification products of mitochondrial COI genes were analyzed by gel electrophoresis, purified by Biological Engineering Company (Shanghai, China), and sequenced with forward and reverse primers (GenScript, Nanjing, China). Sequence alignment was conducted using SeqMan software in DNASTar (version 7.1, DNASTar, Madison, United States). According to the peak in SeqMan, the bidirectional sequencing of nucleotide sequence was proofread by DNASTar to delete the unreliable bases at both ends. PCR products were detected by agarose gel electrophoresis and capillary electrophoresis, and then was analyzed by ABI 3730 sequencer (Shanghai Generay Biotech Co., Ltd).

Data analysis

Genetic distances among groups were calculated using the Kimura two-parameter (K-2P) model in MEGA version 4.0 (Tamura et al., 2007). Pairwise F_{ST} values among groups were analyzed by DNAsp version 5.0 software (Librado and Rozas, 2009). The haplotype network was drawn using Network 2.3.1, and the differences of nucleic acid sequence among different *D. sinensis* groups were systematically analyzed (Excoffier and Lischer, 2010). Fu's F_s test, Tajima's neutral test, and mismatch distribution were conducted by using Arlequin 3.5 software (Tajima, 1989; Fu, 1997;

Excoffier and Lischer, 2010) to detect the historical change of the genetic structure of *D. sinensis* population in Lake Chaohu.

GeneMarker 2.25 software was used to assess the quality of microsatellite markers by peak diagram. The observed number of alleles, effective number of alleles, Nei's genetic diversity, Shannon's diversity index, and percentage of polymorphic loci were calculated based on the transformed peak diagram data using Popgene version 1.31 software (Yeh et al., 1999). Based on the microsatellite markers, the pairwise F_{st} values were performed by Arlequin 3.5 software to analyze the differences in the genetic diversity of *D. sinensis* among modern and historic groups, respectively. The population genetic structure of *D. sinensis* was reconstructed using the 14 polymorphic microsatellite loci in STRUCTURE HARVESTER v0.6094 (<http://taylor0.biology.Ucla.edu/structureHarvester/>). Posterior likelihood values were calculated from $K=1$ to $K=12$ (Evanno et al., 2005). The assumed K value of 1–12 was repeated 10 times to confirm the best K value (Supplementary Figure 1). The genetic structure of *D. sinensis* was analyzed by Structure 2.3.3 software (Pritchard et al., 2000).

The non-metric multidimensional scaling (NMDS) ordination method was used to analyze the discrepancies of genetic diversity indexes based on both mitochondrial COI gene and microsatellite markers among 11 *D. sinensis* groups according to Euclidean distances in Past 3.0 software (<http://folk.uio.no/ohammer/past/>). Principal component analysis (PCA) with CANOCO 5.0 was used to analyze the relationships between environmental factors (e.g., WT, TN, DTP and TP) and genetic diversity indexes (including N_a , N_e , h , I , P , F_{is} , H_d , π , and D) of *D. sinensis* in both water and the sediments. The data was transformed into $\log_{10}(x+1)$ before running the program. SPSS 19.0 software was used to analyze the differences on the genetic diversity between modern and historical groups of *D. sinensis* by independent sample t -tests.

Results

Environment parameters and population dynamics of *Daphnia sinensis* in Lake Chaohu

During the sampling period, water temperature showed an increasing trend, with the minimum value (3.1°C) in January and the maximum value (27.6°C) in June. The lake water was alkaline, with a pH range of 7.83 in April to 9.15 in January. The average water depth was 3.17 ± 0.47 m, with the maximum depth (3.96 m) in June and the lowest depth (2.74 m) in February. The concentrations of Chl *a* ranged from 12.37 µg/L (March) to 70.41 µg/L (June). The average TP and DTP concentration were 0.35 ± 0.29 mg/L and 0.15 ± 0.12 mg/L. The maximum values of both TP and DTP concentrations were 0.82 mg/L and 0.31 mg/L in May. The average TN concentration was 2.28 ± 0.31 mg/L, and it gradually decreased from January (2.22 mg/L) to March (1.77 mg/L) and then raised to its maximum in June (2.68 mg/L; Supplementary Table 1). The values of TN and TP contents in the sediments were from previously published data (Zhang et al., 2020).

The density of *D. sinensis* in the water showed an increasing trend and then decreasing trend (Figure 2C). The densities of *D. sinensis* increased from 0.57 ± 0.53 ind./L in January to 2.63 ± 3.29 ind./L in February, and reached the peak (25.51 ± 21.62 ind./L) in March. Then, it remained at higher levels (16.5–20.0 ind./L) from April to June, and disappeared in July, which was consistent with the classification of two clusters based on the microsatellites markers (Figure 2A).

Genetic diversity and genetic differentiation of the *Daphnia sinensis* population in Lake Chaohu

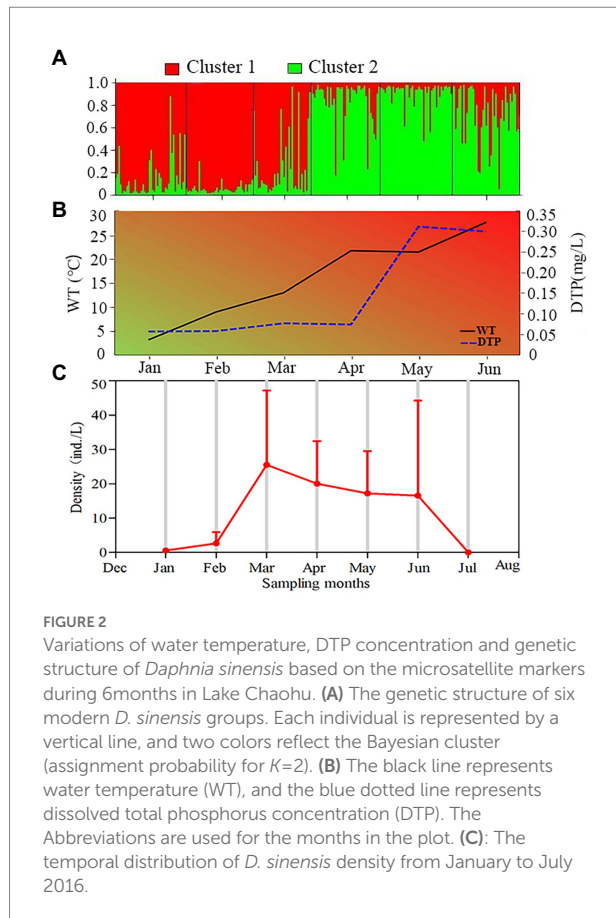
Based on the microsatellite markers, the six modern *D. sinensis* groups were clustered into two groups (Figure 2A). The specimens collected in January, February and March were clustered into the winter and spring group (WG, Cluster 1), whereas the specimens collected in April, May and June were clustered into the spring and summer group (SG, Cluster 2; Figure 2A).

The five historic *D. sinensis* groups were grouped into four clusters (Figure 3). These historic *D. sinensis* groups were mainly composed of two dominant clusters (Clusters 1 and 2). Cluster 3 appeared intermittently in different sedimentary depths, indicating that time isolation occurred in this group. Cluster 4 was observed in each sedimentary depth, but it only dominated in the Pop 2 group.

Based on the microsatellite markers, both N_a and N_e in lake water were higher than those in the sediment, and there were significant differences (N_a : $F = 2.387$, $p < 0.01$; N_e : $F = 4.787$, $p < 0.01$). The Nei's genetic diversity and Shannon's diversity index of six modern *D. sinensis* groups ranged from 0.129 to 0.141 and from 0.208 to 0.226, respectively, whereas those of the five historic *D. sinensis* groups ranged from 0.101 to 0.124 and from 0.152 to 0.197, respectively. The genetic diversity indexes (except F_{is}) of the Pop1 and Pop2 groups located in the surface sedimentary layers were higher than those of the Pop3, Pop4, and Pop5 groups located in the lower sedimentary layers. The peaks of all these indexes appeared in Pop2, except for F_{is} (Table 1).

Based on the mitochondrial COI gene sequence, the haplotype diversity (H_d) of the six modern *D. sinensis* was between 0.808 and 0.936, whereas that of the five historic *D. sinensis* was between 0.667 and 0.973. The nucleotide diversity (π) of these 11 *D. sinensis* was between 0.002 and 0.009 (Table 1).

Based on all genetic diversity indexes in Table 1, the temporal trends in genetic differentiation among *D. sinensis* groups of Lake Chaohu were showed in Figure 4. The stress values for all NMDS configurations were lower than 0.08 based on Euclidean distances. For NMDS analysis, *D. sinensis* groups exhibited significant temporal shifts based on genetic diversity indexes (Global $r = 0.595$, $p = 0.006$; Figure 4). There was the highest similarity of genetic diversity indexes in modern *D. sinensis* groups between May and other months, whereas the genetic diversity indexes of Pop3 and Pop5 groups were significantly different from that of the other



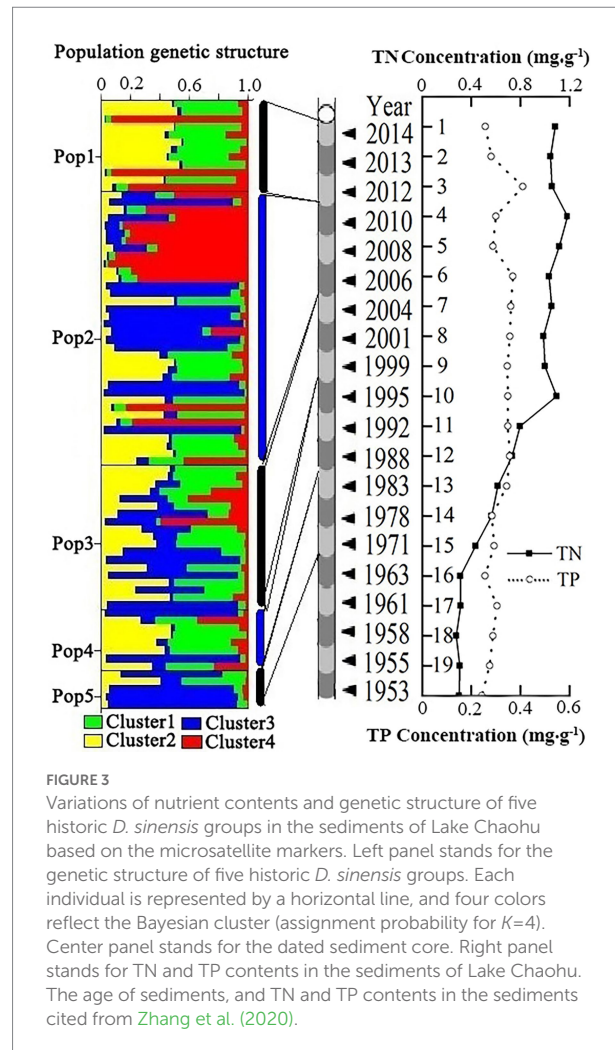
three groups. Moreover, the distance of modern *D. sinensis* group in February was closer with both Pop2 and Pop1 groups in the sediments, indicating that they had higher similarity (Figure 4).

Based on the microsatellite markers, the pairwise F_{ST} values among the six modern *D. sinensis* groups ranged from 0.048 to 0.113 (Supplementary Table 2). The minimum F_{ST} value was found between March and April groups (0.048), whereas the maximum (0.113) occurred between February and May groups. The pairwise F_{ST} values of *D. sinensis* population increased gradually with the season, indicating that the seasonal genetic differentiation of *D. sinensis* increased with the increase of water temperature (Figure 2B).

Pairwise F_{ST} values among the five historic *D. sinensis* groups ranged from 0.015 to 0.096 (Supplementary Table 3). Moreover, the pairwise F_{ST} value between Pop3 and Pop4 groups was the smallest (0.015), whereas the maximum (0.096) occurred between Pop1 and Pop5 groups.

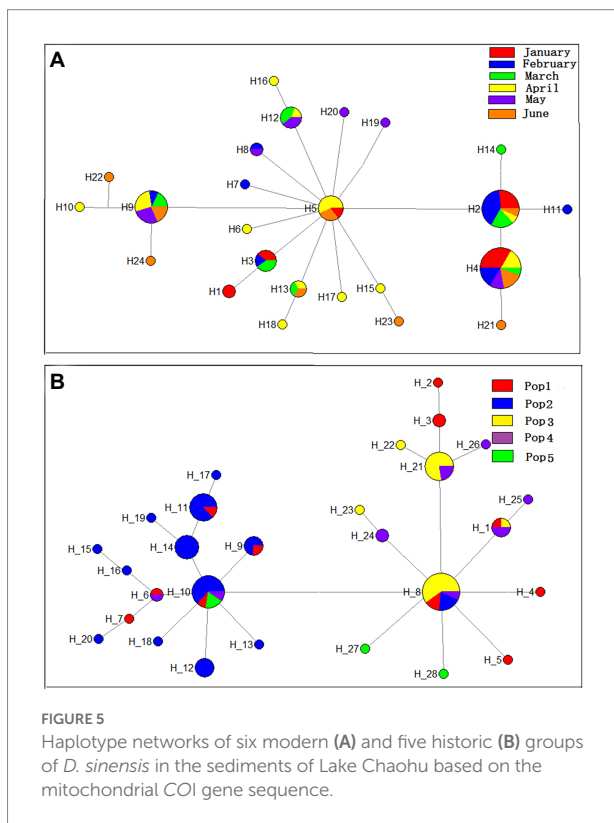
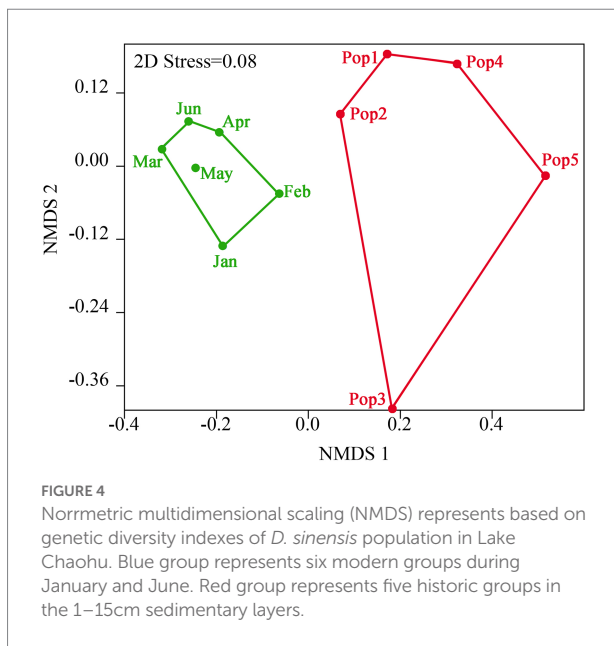
Evolution of *Daphnia sinensis* haplotypes in Lake Chaohu

Twenty-four haplotypes, including 15 specific and nine shared haplotypes, were obtained from the six modern *D. sinensis* groups. The haplotype network showed one origin (H5) (Figure 5A).



Twenty-eight haplotypes, including 19 specific and nine shared haplotypes, were obtained from the five historic *D. sinensis* groups in Lake Chaohu. The haplotype network showed two origins (Figure 5B). As one of the origin centers, the haplotype H-10 appeared in the most groups. The haplotypes H-14, H-12, and H-6 were mainly distributed in the Pop1 and Pop2 groups. As the other origin center, the haplotype H-8 was mainly distributed in the Pop1, Pop3, Pop4, and Pop5 groups. Therefore, the genetic differentiation of *D. sinensis* population could be divided into two stages in the last 50 years. The Pop3, Pop4, and Pop5 groups were regarded as one branch, in which the evolutionary direction of the haplotypes was simpler. The Pop1 and Pop2 groups were regarded as the other branch, in which the evolutionary direction of the haplotypes was dispersed, and the two sub-centers of H-14 and H-6 were also observed.

Based on the mitochondrial *COI* gene sequences of the five historic *D. sinensis* groups, Fu's F_S neutral test ($D=-16.744$, $p=0.000$) and Tajima's test ($D=-1.798$, $p<0.05$) indicated that the five historic *D. sinensis* groups deviated from neutral evolution, and bottleneck effect and population expansion had occurred in the evolution history of *D. sinensis* in Lake Chaohu.



Relationships between the genetic diversity of *Daphnia sinensis* and environmental factors in Lake Chaohu

Principal Component Analysis (PCA) showed distinct patterns in the evolution of the genetic diversity of 11 *D. sinensis*

groups in Lake Chaohu, which could be well separated with time scale in the ordination space (Figure 6). For Figure 6A, the first axis (PCA1) was mainly described by the inbreeding coefficient (*Fis*) in May and June groups. Total phosphorus (TP) and dissolve total phosphorus (DTP) had significant effects on *Fis* index in May and June groups, as well as total nitrogen and water temperature. For Figure 6B, the second axis (PCA2) is mainly related to *Fis* of Pop3 (1999–2006) group in the sediments. Total phosphorus contents of the sediments had significant effects on *Fis* index in Pop3 (1999–2006) and Pop4 (1988–1999). However, total nitrogen contents were positively correlated with other genetic diversity indexes (*I*, *h*, *Ne*) in Pop2 (2006–2011) group in the sediment but negatively correlated with *I*, *h* and *Ne* of modern *D. sinensis* groups in lake water.

Discussion

The phylogenetic evolution of *Daphnia sinensis* in Lake Chaohu

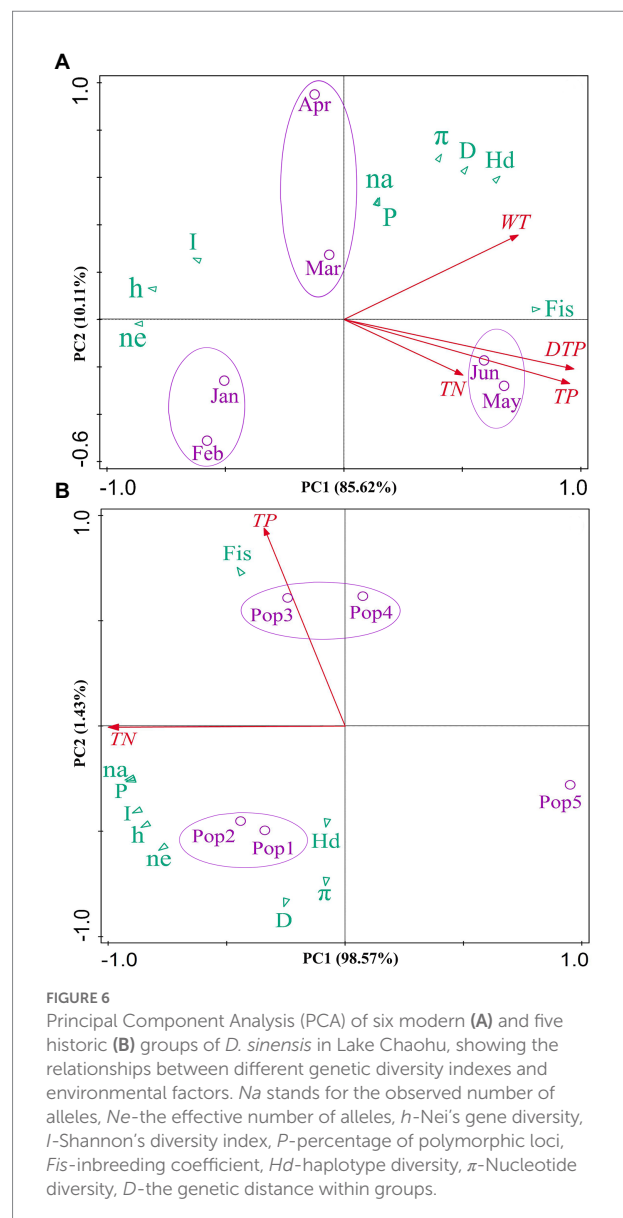
In this study, the population genetic variation of an aquatic organism (*D. sinensis*) from resting eggs deposited in the lake sediments were reconstructed. The resting egg bank typically could provide an accurate ecological and evolutionary representation of past populations (Monchamp et al., 2017). In Lake Chaohu, the density of *Daphnia* species was low in 1980–1981 (unpublished data), but it remained at higher levels in 2002–2003 (Deng et al., 2008) and in 2013 (Li et al., 2015). According to Zhang et al. (2020), the variations of the occurrence and densities of *Daphnia* resting eggs in the sediments were consistent with the densities in Lake Chaohu that were observed in the literatures (Ye, unpublished data; Deng et al., 2008; Li et al., 2015). Therefore, it was reliable and appropriate by employing resting eggs deposited in the sediments to study population genetic variation of *Daphnia* in Lake Chaohu.

Haplotype diversity (*Hd*) and nucleotide diversity (π) indexes could reveal different historical events, such as the founder effect, bottleneck effect and neutral evolution of organisms (Tajima, 1989; Grant and Bowen, 1998; Crandall et al., 2011). In natural population, higher *Hd* and lower π values indicated that the species could expand after lower population density (Crandall et al., 2011). Founder effect could lead to new population with the source population genetic diversity is low. Bottlenecks effect occurred after the population decline, population genetic information were from a few survived completely. In Lake Chaohu, the density of *Daphnia* species was low in Pop5. The replenishment of aquatic population mainly came from the hatch of dormant eggs of sediments in January and February, with the increase of temperature, *Daphnia* population began to carry out parthenogenesis and rapid growth. In this study, higher *Hd* and lower π values implied that *D. sinensis* population experienced a bottleneck

effect in the history process of Lake Chaohu. In Lake Chaohu, the density of *Daphnia* resting eggs was low in Pop5 (the lower layer of the sediment), and then increased obviously in the upper layers of the sediments. Moreover, the replenishment of *Daphnia* population mainly came from the hatching of resting eggs in the sediments of the lake in January and February. As the temperature rose, the *Daphnia* population began to expand rapidly by parthenogenesis. For the natural population, the genetic differentiation (F_{ST}) value ranged between 0.05 and 0.15, indicating a medium differentiation level, and the F_{ST} value were between 0.15 and 0.25, indicating a high differentiation level (Weight, 1978). In this study, the F_{ST} among the six modern *D. sinensis* groups ranged from 0.048 to 0.113. The minimum F_{ST} value (0.048) appeared between March and April groups, whereas the maximum (0.113) occurred between February and May groups. This seemed to be related to the increase of population density in *D. sinensis*. During the sampling period, the density of *D. sinensis* remained at lower levels in January and February, and the replenishment of population mainly depended on the hatching of resting eggs from the surface sediments. Under suitable conditions (e.g., higher water temperature), *D. sinensis* showed rapid population increase by cyclical parthenogenesis after March. Usually, some dormant eggs could be carried from the bottom layer to the surface layer by wind or benthic animals. This phenomenon might contribute to the population genetic evolution of *D. sinensis* in Lake Chaohu. However, the genetic differentiation of the five historic *D. sinensis* groups showed a wave-like pattern over time, yet their F_{ST} were all <0.1 , suggesting the adaptation of different *D. sinensis* groups to different environmental conditions occurred during population evolution in Lake Chaohu. Moreover, based on the COI gene sequences, the F_{ST} values of *D. sinensis* population ranged from 0.015 to 0.257 between Lake Chaohu and other lakes which were located in the middle and lower reaches of the Yangtze River (Wu et al., 2019b), indicating that *D. sinensis* had higher genetic differentiation in different lakes.

The primitive haplotypes were often distributed in the center of the evolutionary network and exhibited a broad expansion advantage, whereas new haplotypes were located at the end of the evolutionary network and had a narrow distribution (Palumbi, 2003). According to the mitochondrial COI gene sequences from the five historical *D. sinensis* groups, *D. sinensis* population originated from two distinct ancestral haplotypes over the history of Lake Chaohu.

Moreover, 13 haplotypes were found in the 4–6 cm sedimentary layer among which nine were specific (Pop2) (2006–2010). Based on the microsatellite markers, cluster 4 was mainly distributed in the 4–6 cm sedimentary layer (Pop2). These findings indicated that the genetic variation and microevolution of *D. sinensis* group (Pop2) were active and complicated between 2006 and 2010. It might result from a consequence of severe eutrophication in the 4–6 cm sedimentary layer (Pop2) in Lake Chaohu.



Effects of environmental changes on the genetic diversity and differentiation of *Daphnia sinensis* population in Lake Chaohu

Some mechanisms (e.g., phylogeographical structure, geographical isolation model, and climate change) have been used to explain how population structures of vertebrates evolve in an environment without any geographical boundaries (Gysels et al., 2004; Adams et al., 2006; Wilson, 2006). For some aquatic organisms in different environments, population genetic structure determined their ability to adapt to environmental pressure (Ma et al., 2016). Some investigations had shown that water temperature and nutrients could affect zooplankton community structure and life history strategy (DeMott et al., 2004; Sarma et al., 2005; Hsieh et al., 2011). Related literatures reported that the

nutrient levels (especially nitrogen) had increased rapidly since the 1970s (Yao and Shen, 2003; Zhang and Kong, 2015), and reached the peak in Lake Chaohu in 1995 (Xie, 2009), which was highly consistent with the changing pattern of nitrogen contents in the sediments. Water eutrophication enhanced the change in phytoplankton density, biomass and structure (such as dominant cyanobacteria) of the lake (Deng et al., 2007). Moreover, long-term eutrophication and increasing edible phytoplankton biomass affected the density and structure of crustacean zooplankton in Lake Chaohu (Deng et al., 2008). Correspondingly, in Lake Chaohu, *Daphnia* density was few and found occasionally in 1980–1981 (Ye et al., unpublished data), and then obviously increased (31.8 ind./L and 29.7 ind./L in April and May, respectively) in 2002–2003 (Deng et al., 2008) and remained at a higher level (the maximum value of 172.9 ind./L at a sampling site in April) in 2013 (Li et al., 2015). In this study, the density of *Daphnia* species reached also 116.5 ind./L at a sampling site in June. In addition, *Daphnia* dominated in spring, had higher density in early summer, and then disappeared in mid-summer in Lake Chaohu (Deng et al., 2008; Li et al., 2015). Therefore, environmental changes (including water temperature, phytoplankton biomass and structure and fish predation) determined *Daphnia* population size, and then might accelerate *Daphnia* gene exchange and affect *Daphnia* population genetic structure. Hairston et al. (1999, 2001) also confirmed that *Daphnia* could evolve to tolerate toxic cyanobacteria in the diet in response to nutrient enrichment in freshwater lakes. Therefore, understanding the drivers and consequences of *Daphnia* traits, such as co-evolutionary dynamics with cyanobacteria, was very important for future studies of eutrophic lakes (Ger et al., 2016).

During the seasonal sampling period, our results showed that DTP concentration was negatively correlated with Nei's gene diversity (h) and effective number of alleles (N_e), and had significant effects on Fis index in May and June groups. Water temperature had negative correlations with Nei's gene diversity (h) and observed number of alleles (N_a) whereas it was positively related to haplotype diversity (H_d). Therefore, water temperature and P level played important roles in the short-term microevolution of *D. sinensis* population in Lake Chaohu. DeMott et al. (2004) found that the differences of P-content in natural lakes affected the seasonal distribution of *Daphnia* species. Frisch et al. (2017) also observed that the increasing phosphorus contents of the sediments strongly affected the population genetic structure of *Daphnia pulex* under the anthropogenic environmental change in South Center Lake of North America, and thought that ancient clones with limited phosphorus supplied more adaptive to low phosphorus diet whereas the phenotype plasticity of modern clones to phosphorus change enhanced (such as higher growth efficiency under high phosphorus condition and lower growth efficiency under low phosphorus condition). Through conducting an in-lake mesocosm experiment, Chislock et al. (2019) also confirmed that *D. pulex* could rapidly evolve to adapt to eutrophication and grazing-resistant cyanobacteria stresses. In a European lake, Lake Constance, the changes in P-levels seemed to

facilitate the coexistence of *Daphnia* species and interspecific hybridization, causing lasting changes in the genotype architecture of *Daphnia* (Brede et al., 2009).

However, both N and P nutrients were related to the short-term and long-term changes of genetic diversity and microevolution of *D. sinensis* in Lake Chaohu. This phenomenon might result from the unique cause of eutrophication and the geological structure of the lake. Phosphate rocks were abundant in the north shore of Lake Chaohu, and the exploitation of phosphate rock had led to a long-term phosphorus-rich state in the lake since the 1960s (Xie, 2009). In this study, the fluctuation of TP contents in the sediments of Lake Chaohu was relatively small (0.26–0.41 g/kg), but the TN contents have gradually increased since the 1970s (0.28–1.18 g/kg). The genetic diversity indexes (h , N_a , N_e , P and I) of the five historic *D. sinensis* groups in the sediments had significantly correlated with TN contents but not with TP contents. Therefore, phosphorus played an important role in the short-term (seasonal) genetic differentiation of *D. sinensis* population in Lake Chaohu, whereas nitrogen could promote the long-term microevolution of *D. sinensis* population in the stable high-phosphorus environment (about 50 years), which was inconsistent with the results in other lakes that phosphorus concentration increased rapidly during the lake eutrophication (Brede et al., 2009; Frisch et al., 2014). Rellstab et al. (2011) also verified that the change of *Daphnia* population structure in the pre-alpine lakes of Central Europe was the result of anthropogenic eutrophication, it depended not only on the general nutritional level of the lake but also the range of nutritional increase. Usually, higher nitrogen level could promote the growth and development of small-sized edible phytoplankton (such as *Tetrademus*) and larger-sized phytoplankton (especially cyanobacteria such as *Microcystis*), and then favor the growth and reproduction of crustacean zooplankton (Sommer et al., 1986; Deng et al., 2008). *Daphnia* which were phosphorus-limited could rapidly increase population size in higher phosphorus environment and then accelerate their microevolution. Therefore, the changing pattern of *D. sinensis* population genetic structure in Lake Chaohu was one of the environmental selections probably combined with co-evolutionary, where the rapid-increasing nitrogen levels had a large impact on *D. sinensis* genetic structure in a lasting high phosphorus environment. Previous investigation indicated also that environmental selection directly impacted genetic variation at loci of *Daphnia magna* from nineteen shallow ponds in Belgium (Orsini et al., 2013b).

Conclusion

The genetic diversity of the *D. sinensis* population in Lake Chaohu varied over time. During seasonal environmental variations and lake eutrophication, the population genetic structure of *D. sinensis* was experienced adaptive microevolution. The genetic structure of the six modern *D. sinensis* groups had two dominant clusters (the WG cluster and SG cluster) during the seasonal dynamics. Moreover, the five historic *D. sinensis* groups

had two different evolutionary centers of haplotypes in the sediments of Lake Chaohu, which seemed to be related to a rapid increase of total nitrogen contents. Based on the microsatellite markers, the genetic structure network showed that *D. sinensis* population had evolved the four dominant clusters, and the population differentiation experienced a time-dependent genetic isolation in the sediments of Lake Chaohu.

The phylogenetics of *D. sinensis* population was related to the accumulation of N and P nutrients in Lake Chaohu, but lake eutrophication exhibited a hysteresis effect on the genetic differentiation of *D. sinensis* population. Water temperature and dissolved total phosphorus were associated with the short-term genetic differentiation of *D. sinensis* population in Lake Chaohu, whereas total nitrogen content was significantly related to the microevolution of *D. sinensis* population in the long-term high phosphorus environment. Therefore, the changing pattern of *D. sinensis* population genetic structure in Lake Chaohu was one of the environmental selections probably combined with co-evolutionary, where the rapid-increasing nitrogen level had a large impact on *D. sinensis* population genetic structure in a lasting high phosphorus environment.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

KZ and JW: formal analysis, investigation, data curation, and writing original draft. DD: resources, methodology, software, writing review and editing, project administration, supervision, and funding. HZ, QL, and SP: data collection. YZ: software and validation. ZZ: review and editing. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

The 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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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.913738/full#supplementary-material>

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