



Experimental Study of Population Variations on the Morphology and Reproduction of *Daphnia galeata* from Three Chinese Lakes

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Abstract: Environmental heterogeneity affected the genetic differentiation and phenotypic plasticity of *Daphnia* spp. populations in different lakes. However, the effect mechanism of lake population on the morphology and reproduction of *Daphnia* spp. was still unclear. This paper studied the differences of the morphology and reproduction of *D. galeata* populations from three Chinese lakes (CH: Lake Chaohu, NH: Lake Nanhu, EH: Lake Erhai), which the area size, nutrient levels, phytoplankton biomass and dominant fish were obviously various in the three lakes. The results showed that lake population affected significantly the morphology (helmet length and tail spine length) and reproduction (no. offspring at first reproduction per female⁻¹) of *D. galeata*. Both helmet lengths and tail spine lengths of three *D. galeata* populations increased quickly within the first five instars, and afterwards showed various patterns. Multiple comparisons indicated that helmet lengths of NH population were significantly higher than those in EH and CH populations ($P<0.001$) whereas tail spine lengths of NH population were significantly smaller than those in EH ($P=0.001$) and CH ($P=0.003$) populations. The ratio of relative helmet length of CH population was significantly shorter than those of EH population ($P<0.001$) and NH population ($P<0.001$), and the ratio of relative tail spine length at first pregnancy of EH population was significantly longer than those of CH population ($P<0.001$) and NH population ($P<0.001$). Moreover, there is four juvenile instars in EH population whereas there are three juvenile instars in CH and NH populations. With the increase of adult instars, the number of offspring produced by *D. galeata* in all three populations displayed a similar pattern, which increased quickly at first, and then gradually decreased. Average maximum number of offspring at first reproduction (6.3 ± 1.4 ind. per female⁻¹) appeared in CH population, followed by EH (5.2 ± 1.7 ind. per female⁻¹) and NH (4.9 ± 1.4 ind. per female⁻¹) populations. The innate rate of increase of CH population was relatively higher than those of EH and NH populations, but no significant differences among three populations were observed. Our results suggested that environmental heterogeneity could affect the reproduction and morphological plasticity of *Daphnia* spp. in different lakes.

Keywords: *Daphnia galeata*, Morphology, Reproduction, Population, Phenotypic Plasticity

1. Introduction

Daphnia are found to distribute widely in inland freshwater [1], and play an important role in the food chain of aquatic ecosystems. Owing to the characteristics of easy culture, fast reproduction and sensitivity to environmental changes [1, 2], *Daphnia* have been utilized in the research

fields of evolutionary biology, ecology and environmental toxicology [3, 4]. Usually, *Daphnia* become dominant zooplankton in lakes because of the abilities of stronger filtering algae and higher fecundity. In order to avoid fish predation, they can be found to induce morphological or reproductive variability in lakes [5, 6].

Seasonal dynamics of *Daphnia* population in lakes is a

common phenomenon, which is influenced by a variety of environmental factors (e.g. nutrients, predation pressure, food reliability) [7-10]. In lakes, phytoplankton component (such as N, P and C element contents) and structure can be affected by nutrient level [2, 11]. Experimental investigation also showed that nutrient variations in culture medium might cause the change of the nutrient content in phytoplankton [10, 12, 13], and then can lead to the change of *Daphnia* population density [7, 10, 13]. *Daphnia galeata* was observed to distribute widely in eutrophic Chinese lakes [4, 14-16]. However, in some mesotrophic or oligotrophic lakes, *D. galeata* had become dominant species in cladoceras [2, 17]. Our previous investigations indicated that ephippial densities of *D. galeata* were significantly correlated with the nitrogen and phosphorus contents in lake sediments [18- 20]. The predation activity may be other important factor affecting morphological variations and population dynamics of *Daphnia*. Under the pressure of fish predation, the phenotypic plasticity in the life-history traits and morphology (e.g. Body length, helmet and tail spine) of *Daphnia* sp. was observed [6, 21-23], and population dynamic of *Daphnia* sp. were also obviously affected [8]. Moreover, *Chaoborus americanus* predation induced the reproductive difference and the occurrence of neck teeth of *Daphnia pulex* [24]. However, under experimental conditions, few studies of the morphology and reproduction of *Daphnia* populations from different environmental lakes had been reported.

Daphnia sp. located in different lakes have occurred the microevolution and genetic differentiation in order to adapt to the habitat environment [4, 25-30]. In a Chinese lake, long-term eutrophication process affected the genetic differentiation of *Daphnia similoides sinensis* [31]. Stoks *et al.* [32] found that fish predation could influence the relationship between the plasticity and rapid evolution of *Daphnia magna*. In some lakes located in the middle and lower reaches of the Yangtze River, the genetic diversity and genetic differentiation of *D. galeata* was obvious because of geographic isolation [4]. Previous investigations had showed that the life history parameters of *Daphnia* sp. could be influenced by their genetic diversity and environmental factors [26, 33].

Although many studies on population dynamic and

life-history traits of *D. galeata* from single population have been reported [3, 10, 34-35], the differences on the reproduction and morphology of *D. galeata* from different populations were not well known. In the field, comparative study on morphological variability of *D. galeata* from the lakes of the Todzha Depression (the Bolshi Yenisei River basin) was investigated [5]. In the present study, the experimental study on the morphology and reproduction of *D. galeata* populations from three Chinese lakes, Lake Chaohu (Yangtze River Basin), Lake Nanhu in Huaibei city (Huaihe River Basin) and Lake Erhai (Lancang River Basin), were carried out, in order to reveal the differences and abilities of *D. galeata* adaptation to the heterogeneity of different environments.

2. Material and Methods

2.1. Experimental Materials

Scenedesmus obliquus were purchased from the Freshwater Algae Culture Collection of the Institute of Hydrobiology, the Chinese Academy of Sciences, and cultured in the BG11 medium at (25±1)°C under a illumination intensity of 2500 lx, with a 12 h: 12 h light/dark cycle. *S. obliquus* were collected at the exponential growth period and stored in a refrigerator at 4°C.

Three *D. galeata* populations from Lake Erhai (EH), Lake Nanhu (NH) and Lake Chaohu (CH) were employed. In each population, three clones were collected. Three *D. galeata* clones in EH population were obtained from the different zones of Lake Erhai in Yunnan Province. Three *D. galeata* clones in NH and CH populations were from the hatching of the resting eggs in the sediments of Lake Nanhu and Lake Chaohu, respectively. All *D. galeata* clones were fed on *S. obliquus*, and were cultured at (25±1)°C under a illumination intensity of 2500 lx, with a 12 h: 12 h light/dark cycle. The neonates at third generation of all *D. galeata* clones were used as the experimental animals (Birth time < 6h). Lake Erhai, Lake Chaohu and Lake Nanhu belong to the Lancang River Basin, the Yangtze River Basin and the Huaihe River Basin in China, respectively. The environmental characteristics of the three lakes are shown in Table 1.

Table 1. Environmental factors in the three lakes.

	EH	CH	NH
Total nitrogen (mg L ⁻¹)	0.26-0.93 (0.63)	0.92-6.09 (3.46)	0.13-1.41 (0.56)
Total phosphorus (mg L ⁻¹)	0.016-0.042 (0.03)	0.052-0.215 (0.120)	0.02-0.13 (0.06)
Phytoplankton biomass (mg L ⁻¹)	0.68-3.25	5.05-19.70	0.37-5.04 (1.99)
Dominant fish	(<i>Neosalanx tangkahkeii</i> Taihuensis)	(<i>Coilia ectenes</i>) (<i>N. tangkahkeii taihuensis</i>)	(<i>Aristichthys nobilis</i>) (<i>Hypophthalmichthys molitrix</i>)
Dominant cladoceran species	(<i>Bosmina coregoni</i>) (<i>D. galeata</i>) (<i>Ceriodaphnia quadrangula</i>)	(<i>B. coregoni</i>) (<i>Ceriodaphnia cornuta</i>)	(<i>Bosmina</i> sp.) (<i>Diaphanosoma brachyurum</i>)
References	[17, 36]	[8]	[37]

2.2. Experimental Design

In the present study, three *D. galeata* clones in each population were respectively incubated. Fifteen individuals

from third generation neonates (birth time <6 h) in each clone were employed. A total of forty-five individuals were used as experimental animals in each population, and each of them was respectively placed in a 50ml beaker, with 40ml culture medium which was from filtered tap water (aerated over 48

h). *S. obliquus* with a concentration of 2×10^5 cells ml^{-1} was used as the food of *D. galeata*. The experiment was conducted in a constant temperature illumination incubator at $(25 \pm 1)^\circ\text{C}$, with a 12h:12h light/dark cycle and a light intensity of 2500 lx. During the experiment, the culture medium was changed each day and the experiment lasted until all experimental animals died out. Number of offspring at each adult instar (including number of offspring at first reproduction) and innate rate of increase of *D. galeata* were recorded or calculated. All larvae produced by experimental animals were timely removed from the beaker during the experiment. Body length, helmet length and tail spine length of *D. galeata* were measured in a microscope (Olympus, CX21). Ratio of relative helmet length (helmet length/body length) and relative tail spine length (tail spine length/body length) were calculated.

The formula of innate rate of increase (r_m) is:

$$\sum_{i=1}^n l_x m_x e^{-rx} = 1$$

in which x is the experimental day, l_x is the survival rate at the specific day, and m_x is the fecundity at the specific day.

2.3. Data Analysis

SPSS 20.0 software was used to analyze the experimental

data. One-way ANOVA was used to analyze the effects of population on the morphological and reproductive parameters of *D. galeata*, and multiple comparisons (Tukey HSD) were employed to detect their differences among different populations. Statistical data are transformed through $\ln(x+1)$.

3. Results

Body lengths of three *D. galeata* (Sars) populations increased all gradually with the increase of instar number (Figure 1). Body lengths of EH population were shorter than those of CH and NH populations, but there were no significant differences among three populations.

Helmet lengths of all three *D. galeata* populations showed a quickly increasing trend within the first five instars, and then displayed different patterns after the sixth instar (Figure 1). The effect of population on helmet length of *D. galeata* was significant ($F=62.944$, $P<0.001$) as well as helmet length at first pregnancy. Multiple comparisons Tukey HSD showed that Helmet length of NH population was significantly longer than those of EH and CH populations ($P<0.001$) as well as helmet length at first pregnancy (Table 2), and helmet length of EH population was significantly longer than that of CH population ($P<0.001$).

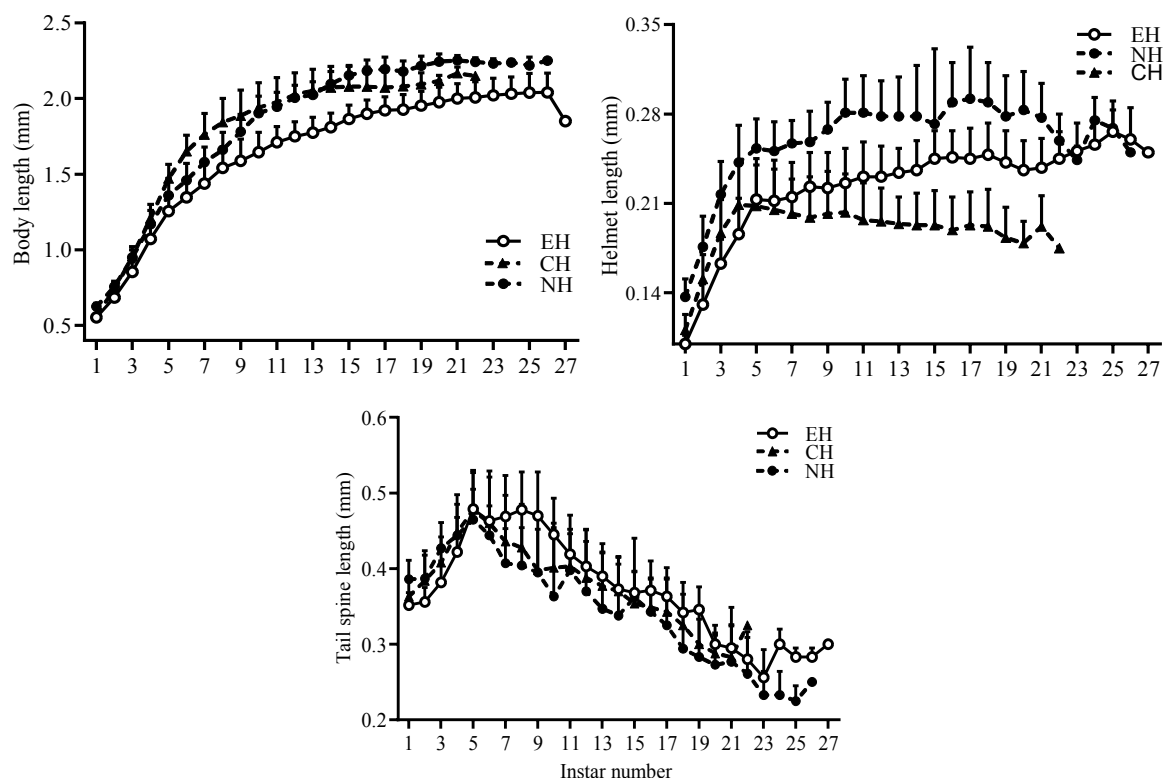


Figure 1. Changes of body length, helmet length and tail spine length in three *D. galeata* populations.

Tail spine lengths of all three *D. galeata* populations showed a quickly increasing trend within the first five instars, and then dropped gradually (Figure 1). The effects of population ($F=8.410$, $P<0.001$) on the tail spine length of *D.*

galeata were significant. Tail spine length of NH population was significantly shorter than those of CH ($P=0.003$) and EH ($P=0.001$) populations. There were no significant differences in tail spine lengths at first pregnancy of *D. galeata* among

three populations (Table 2).

Table 2. Morphological and reproductive parameters of three *D. galeata* populations.

Parameters	EH	CH	NH
Body length at first pregnancy (mm)	1.26±0.05	1.42±0.11	1.34±0.04
Helmet length at first pregnancy (mm)	0.21±0.02	0.21±0.01	0.25±0.01
Tail spine length at first pregnancy (mm)	0.48±0.03	0.47±0.03	0.46±0.03
No. offspring at first reproduction (ind. · per female ⁻¹)	5.2±1.7	6.3±1.4	4.9±1.4

With the increase of adult instars, the number of offspring produced by *D. galeata* in all three populations displayed a similar pattern, which increased quickly at first, and then gradually decreased (Figure 2). The mean maximum (16.4 ind. · per female⁻¹) appeared in the 16th instar in NH population. The influence of population on number of offspring at first reproduction of *D. galeata* was significant ($F=3.111$, $P=0.048$), but it was no significant effect on number of offspring of *D. galeata* ($F=2.769$, $P=0.066$). Average maximum number of offspring at first reproduction (6.3±1.4 ind. · per female⁻¹) appeared in CH population, followed by EH (5.2±1.7 ind. per female⁻¹) and NH (4.9±1.4 ind. · per female⁻¹) populations (Table 2). Moreover, there is four juvenile instars in EH population whereas three are three juvenile instars in CH and NH populations.

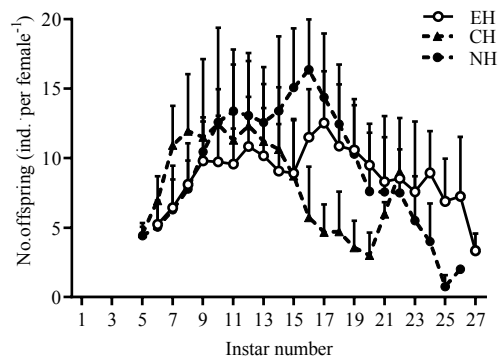


Figure 2. Changes of number of offspring produced by per female in three *D. galeata* populations.

The innate rate of increase of *D. galeata* in CH population was relatively higher than those in EH and NH populations (Figure 3). Multiple comparisons (Tukey HSD) indicated that no significant differences in the innate rate of increase of *D. galeata* among three populations were observed ($P>0.05$).

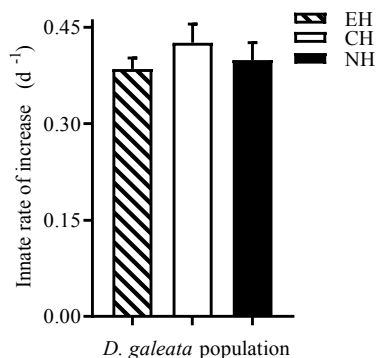


Figure 3. Changes of the innate rate of increase (r_m) in three *D. galeata* populations.

Ratio of relative helmet lengths of all three *D. galeata* populations declined gradually except within the first two instars (Figure 4). The effect of population on the ratio of relative helmet lengths of *D. galeata* was significant ($F=18.502$, $P<0.001$) as well as the ratio of relative helmet lengths at first pregnancy ($F=41.689$, $P<0.001$). Multiple comparisons (Tukey HSD) indicated that there were all significant differences in the ratio of relative helmet lengths of *D. galeata* among three populations ($P<0.001$), and the ratio of relative helmet lengths of CH population was significantly shorter than those of EH population ($P<0.001$) and NH population ($P<0.001$).

Ratio of relative tail spine lengths of all three *D. galeata* populations declined gradually (Figure 4). There was a significant effect of population on the ratio of relative tail spine lengths at first pregnancy of *D. galeata* ($F=15.231$, $P<0.001$). Multiple comparisons (Tukey HSD) indicated that the ratio of relative tail spine lengths at first pregnancy of EH population was significantly longer than those of CH population ($P<0.001$) and NH population ($P<0.001$).

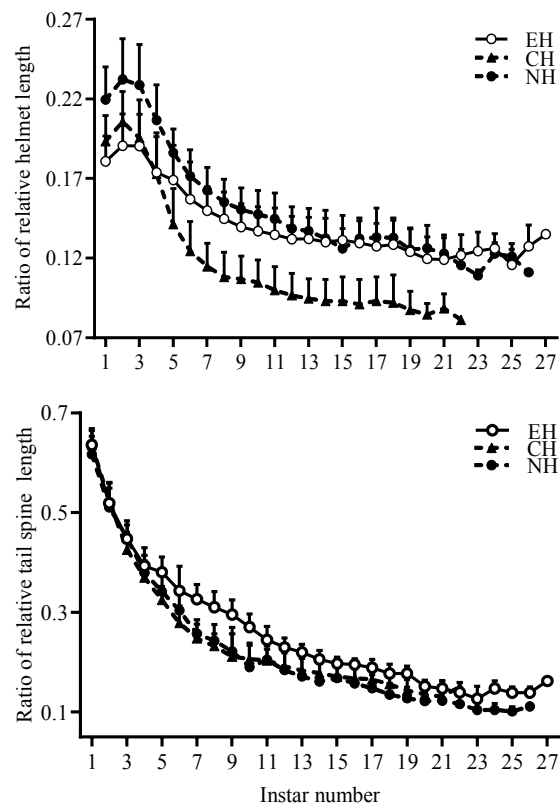


Figure 4. Changes of the relative helmet length and tail spine length in three *D. galeata* populations.

4. Discussion

In general, the phenotypic plasticity of aquatic organisms can be induced in order to adapt to rapid changes of biotic and abiotic factors [38]. Previous studies have shown that cladocera can transfer the information of the mothers obtaining from local environment to their offspring through maternal effects [39-41], so that their offspring showed more adaptation to similar environment [42]. Usually, *Daphnia* sp. has undergone the alternation of generations in a lake. Therefore, the morphological and reproductive parameters of *Daphnia* sp. from different lakes obtained in the experiment could reveal their response to environmental pressures in their habitats to some extent.

Many studies have shown that the predation pressure can lead to the occurrence of phenotypic plasticity of prey [43-45], including the change in morphology of *Daphnia* sp. [22-24, 46]. Weber and Vesela [46] found that the pheromone of perch affected significantly the helmet lengths of different *D. galeata* clones [22]. Tilapia-mediated water enhanced tail spine lengths in *Daphnia laevis* and *Daphnia similis* clones. Tams et al. [23] observed intraspecific phenotypic differences in body length and life-history traits of four *D. galeata* populations under fish kairomones. Moreover, in the presence of invertebrate predator, the predation of *C. americanus* induced the occurrence of neck teeth of *D. pulex* [24]. In the field, Zuykova and Bochkarev [5] found that highly morphological variability (such as helmet and spine length) of *D. galeata* in the lakes of the Todzha Depression varied markedly among populations, depending on the environmental conditions. In the present study, the helmet lengths of *D. galeata* in NH population were significantly longer than those in EH and CH populations as well as helmet lengths at first pregnancy, whereas the tail spine lengths of NH population were significantly shorter than those of EH and CH populations. Moreover, the effects of population on the ratios of relative helmet lengths and relative tail spine lengths at first pregnancy of *D. galeata* were all significant. The dominant species of fish in the three lakes were different to some extent (Table 1), and this may be one of the reasons to cause the differences on the helmet length and tail spine length of three *D. galeata* populations in the present study. In some Chinese lakes, the individuals of *D. similodites sinensis* from lakes in the presence of fish showed significantly shorter body lengths and prominent recurvate helmets compared with the individuals from fishless lakes [6]. Therefore, the presence of predator could induce the intraspecific variation of *Daphnia*, and then lead to phenotypic plasticity and improve their adaptability to the environment.

Usually, the innate rates of increase of *Daphnia* sp. are affected by nutrient level, food reliability and fish predation [12, 47-48]. In eutrophic lake, Lake Dongdu, the innate rate of increase of *D. galeata* was 0.46 ind. d⁻¹ [47]. Weers and Gulati [12] found that *D. galeata* fed P-limited alga deceased obviously their growth and reproduction (e.g. the innate rate of increase). In the present study, the innate rates of increase

of *D. galeata* were respectively 0.40 ind. d⁻¹ in Lake Nanhu (mesotrophic), 0.39 ind. d⁻¹ in Lake Erhai (mesotrophic), and 0.43 ind. d⁻¹ in Lake Chaohu (eutrophic). Repka [48] also reported that the innate rates of increase of *Daphnia* sp. from different nutrient lakes had greater differences. In general, higher nutrient level favored the increase of edible phytoplankton biomass, and then improved population densities of *Daphnia* sp. [8]. Moreover, Tolardo et al. [22] found that fish-mediated water enhanced intrinsic rates of population increase (*r*) in *D. laevis* and *D. similis* clones. Therefore, the heterogeneity of the three lakes in nutrient level, phytoplankton biomass and fish predation might affect the reproductive ability of *D. galeata* together in the present study.

5. Conclusions

Environmental heterogeneity affected the genetic differentiation and phenotypic plasticity of *Daphnia* spp. populations in different lakes. In the present study, the differences of the morphology and reproduction of *D. galeata* populations from three Chinese lakes (CH: Lake Chaohu, NH: Lake Nanhu, EH: Lake Erhai) were studied. The area size, nutritive levels, phytoplankton biomass and dominant fish of the three lakes were obviously various. Our results showed that lake population affected significantly the morphology (helmet length and tail spine length) and reproduction (no. offspring at first reproduction per female⁻¹) of *D. galeata*. Both helmet lengths and tail spine lengths of three *D. galeata* populations increased quickly within the first five instars, and afterwards showed various patterns. Multiple comparisons showed that helmet lengths of *D. galeata* NH population were significantly higher than those in EH and CH populations whereas tail spine lengths of *D. galeata* NH population were significantly smaller than those in EH and CH populations. Moreover, the significant effects of population on the ratios of relative helmet and relative tail spine length at first pregnancy of *D. galeata* were also all observed. With the increase of adult instars, the number of offspring produced by *D. galeata* in all three populations displayed a similar pattern, which increased quickly at first, and then gradually decreased. Average maximum number of offspring at first reproduction appeared in CH population, followed by EH and NH populations. In addition, the innate rate of increase of CH population was relatively higher than those of EH and NH populations, but no significant differences among three populations were observed. Our results suggested that environmental heterogeneity could affect the reproduction and morphological plasticity of *Daphnia* spp. in different lakes.

Acknowledgements

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