



Competitor density and food concentration: an empirical approach to elucidate the mechanism of seasonal succession of two coexisting *Bosmina*

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Abstract

To examine the density effect and food concentration in the competitive output of two *Bosmina* species, the population growths of *Bosmina fatalis* were investigated by manipulating the density of *B. longirostris* and the concentration of algae. The *B. fatalis* density did not increase in conditions with abundant *B. longirostris* regardless of the food concentrations. The *B. fatalis* increased only at low densities of *B. longirostris* with high food concentrations. Based on the current results, a possible mechanism underlying the seasonal shift from *B. longirostris* to *B. fatalis* in Japanese eutrophic lakes will be explored below.

Key words: *Bosmina*, Cladocera, competition, priority effect, seasonal succession

INTRODUCTION

Natural communities in freshwater ecosystems show seasonal successions, which are caused by changes in environmental conditions and biological interactions (Connell and Slatyer 1977, Drake 1991, Murdock et al. 2010). Seasonal succession of two small coexisting bosminid cladocerans is commonly observed in Japanese eutrophic lakes, where *Bosmina longirostris* dominate the zooplankton community in spring and *B. fatalis* dominate in summer (Fig. 1).

There are two possible mechanisms explaining this succession pattern. The first is selective predation by *Lepidodora kindtii*, which occurs in early summer (Chang and Hanazato 2003). The direct effect of temperature could not explain the seasonal succession of two *Bosmina* species (Hanazato and Yasuno 1985a), and thus Chang and Hanazato (2003) concluded that selective predation by *L.*

kindtii on *B. longirostris* influenced the competition between two populations of *Bosmina*. The second is food density (Hanazato and Yasuno 1987). When the two species were reared together with the same initial numbers of individuals with a large food supply, *B. fatalis* overcame *B. longirostris*. The opposite occurred with a small food supply. These results indicate that the threshold food concentration (TFC), the ambient concentration of food that allows population losses to be compensated for by the production of offspring (Lampert 1977, Kreutzer and Lampert 1999), for *B. longirostris* is lower than that for *B. fatalis*. Moreover, a high population density of *B. longirostris* inhibits the subsequent increase of *B. fatalis*, indicating a density effect of *B. longirostris* on the population growth of *B. fatalis*. However, the importance of density effects in the seasonal succession of cladocerans has not

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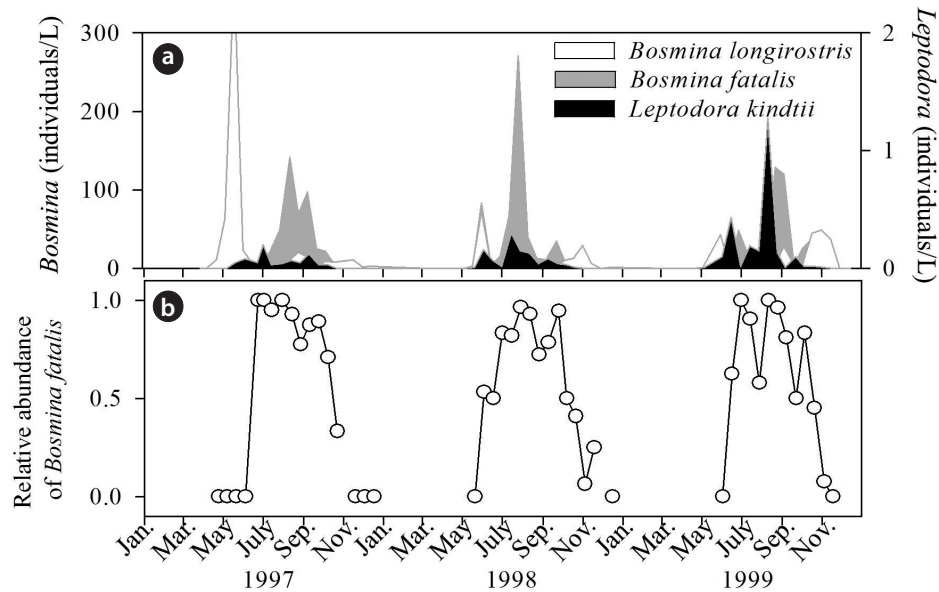


Fig. 1. Seasonal and reciprocal succession of two *Bosmina* species in Lake Suwa from 1997 to 1999 (redrawn from Chang and Hanazato 2003). (a) Seasonal changes in densities of *B. longirostris*, *B. fatalis*, and *L. kindtii*, and (b) relative abundance of *B. fatalis* (density of *B. fatalis* divided by total *Bosmina* density).

been experimentally examined.

Here, the question of whether a high population density of *B. longirostris* inhibits the growth of a *B. fatalis* population will be addressed. In the experiment, the summer decline of *B. longirostris* was simulated by preparing high and low density groups representing their seasonal populations. Food resources were also manipulated to examine whether the effect of *B. longirostris* on the population growth of *B. fatalis* is affected by food concentrations.

MATERIALS AND METHODS

The stock culture of each species (single clone) was established from an individual collected in Lake Suwa (36°2' N, 138°5' E) a year before the experiment. The animals were maintained in a 20-L cylindrical polyethylene tank (30 cm diameter, 31 cm height) with 20 L of dechlorinated tap water for two weeks before the experiment. The tanks (one tank for each *Bosmina* species) were kept at a constant temperature of 22 ± 1 °C and a regime of 16 h light and 8 h darkness. The green alga, *Chlorella vulgaris* (Chlorella Industry Co. Ltd., Fukuoka, Japan; 2 × 10⁹ cells), was introduced into tanks as food for *Bosmina* every second day. The culture medium in each tank was exchanged 24 h before the experiment, in which aggregated individuals near the light source (*Bosmina* shows positive phototaxis) were transferred to a new tank by pipetting. After the ex-

change of medium, no food was added into the tank until the start of the experiment.

The experiments were carried out in sixteen 2-L polymethylpentene beakers (Sanplatec Co. Ltd., Osaka, Japan) as experimental aquariums. To create conditions of high and low *B. longirostris* densities, 40 ml of the *B. longirostris* stock culture was added to 8 experimental beakers and 200 mL to the other beakers before the inoculation of *B. fatalis*, respectively. The numbers of individuals in three samples of the 40-mL and 200-mL stock culture media were counted, and the initial densities (mean ± SE) of *B. longirostris* (N_{Bi-0}) were 22.0 ± 1.0 individuals/L and 126.0 ± 8.4 individuals/L in low- and high-density conditions, respectively. The balance of each beaker was filled with dechlorinated tap water so that each contained 2 L. Experimental aquariums were assigned to low and high food concentrations of 0.5 × 10⁵ and 5 × 10⁵ cells/mL, respectively, every second day. All combinations of *B. longirostris* initial density and food concentration were run in four replicates. Experimental aquariums were maintained for eight days to increase populations of *B. longirostris*.

Eight days after the start of the experiments, the contents of the beakers were gently mixed, and 500 mL of water from each was sampled to estimate the density of *B. longirostris* (N_{Bi-8}). Each of the collected media was filtered through a 40 µm mesh net and preserved in a 4% sugar-formalin solution. After the sampling, *B. fatalis* was introduced into each beaker by adding 40 mL of gently mixed

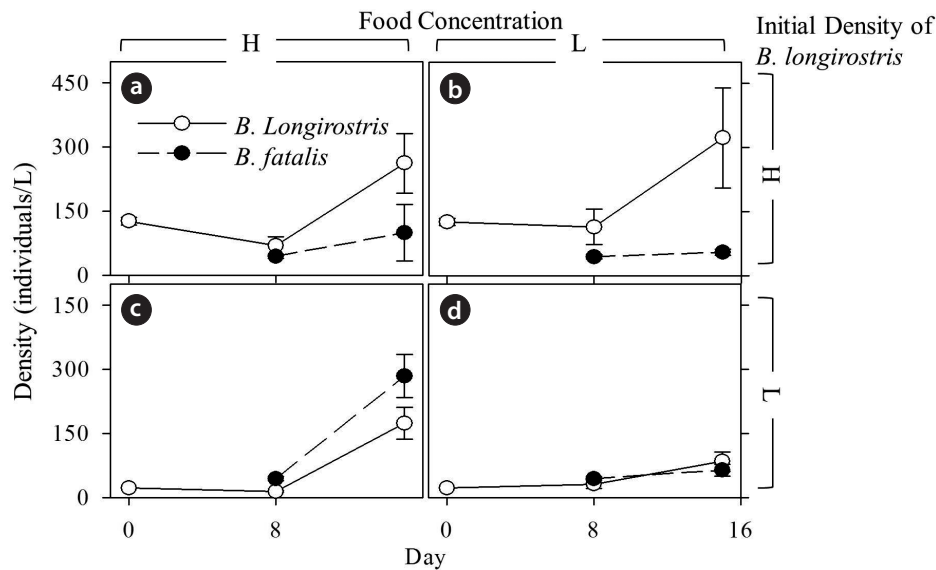


Fig. 2. Changes in density (mean \pm SE) of *Bosmina longirostris* and *B. fatalis* cultured with high (a, c) or low (b, d) food concentrations, which is 5×10^5 or 0.5×10^5 cells/mL, respectively. Upper (a, b) and lower (c, d) figures show results of high and low *B. longirostris* initial density treatments, respectively. High- and low initial density of *B. longirostris*, are 22.0 ± 1.0 individuals/L and 126.0 ± 8.4 individuals/L, respectively. Open and filled circles indicate *B. longirostris* and *B. fatalis*, respectively.

stock culture medium. The density of *B. fatalis* (N_{BF-8}) was estimated by counting the individual numbers in 40 mL of medium obtained from the other three samplings. Fifteen days after the start of experiments, the water remaining in each beaker (1.54 L) was filtered, and the samples were preserved in a 4% sugar-formalin solution. To estimate the densities of *B. fatalis* and *B. longirostris* at 15 days (N_{BF-15} and N_{BL-15}), the number of each species in each sample was counted under a dissecting microscope and the total was recalculated into number per liter. The experiment was conducted under the same laboratory conditions as used for the stock cultures.

Population densities of *B. longirostris* and *B. fatalis* were analyzed to test the hypothesis. To confirm the *B. longirostris* density treatment and to examine the temporal change in its density for each condition, the population densities of *B. longirostris* at 8 and 15 days (N_{BL-8} and N_{BL-15}) were analyzed with three-way repeated-measures ANOVA with time, initial density, and food concentration. The effects of *B. longirostris* population density and food concentration on the population density of *B. fatalis* (N_{BF-15}) were tested with two-way ANOVA. To test increases in the population density of *B. fatalis* for each condition, a multiple comparison between the density of *B. fatalis* (N_{BF-8}) and the *B. fatalis* density of each condition at 15 days (N_{BF-15}) was performed using Dunnett's test. Before statistical analyses, the densities of *B. longirostris* and *B. fatalis* were log-transformed to achieve variance homo-

geneity. Statistical analyses were conducted with R ver. 2.11.1 (R Development Core Team 2010).

RESULTS AND DISCUSSION

Temporal changes in densities of *B. longirostris* and *B. fatalis* cultured with high and low food concentrations were shown in Fig. 2. Although density treatment and time significantly affected the density of *B. longirostris*, there were no effects of food concentration or interaction terms (Table 1). These results confirmed that the density of *B. longirostris* increased with time irrespective of food concentrations.

The N_{BF-8} value was 43.3 ± 4.6 individuals/L (Fig. 2). The values of N_{BF-15} were influenced by *B. longirostris* density, food concentration, and the interaction term between them (Table 2). Only the N_{BF-15} in the condition with low initial density of *B. longirostris* and high food concentration was significantly higher than all N_{BF-8} (Dunnett's test, $t = 3.718$, $P = 0.007$). These results support the prediction that the growth of *B. fatalis* population was inhibited by the abundant *B. longirostris*. That *B. fatalis* increased only with a low *B. longirostris* density at a high food concentration suggests the presence of a density-dependent effect.

Results suggest that food competition can be a possible mechanism underlying the observed density-dependent effect of *B. longirostris*. In previously conducted compe-

Table 1. The result of three-way repeated-measures ANOVA with time, initial density, and food concentration for population densities of *B. longirostris* at 8 and 15 days

Source of variation	Df	MS**	F***	P****
Between beakers				
Initial density	1	9.562	24.902	<0.001
Food concentration	1	0.058	0.152	0.703
Initial density × food concentration	1	0.257	0.669	0.429
Error*****	12	0.384		
Within beakers				
Time	1	17.305	40.419	<0.001
Time × initial density	1	0.537	1.254	0.285
Time × food concentration	1	1.482	3.461	0.087
Time × initial density × food concentration	1	0.652	1.523	0.241
Error*****	12	0.428		

*Degrees of freedom, ** Mean of squares, *** F value, **** Probability, ***** Error term for between- beakers variables, ***** Error term for within-beakers variable Time and interactions of the between-beakers variables and the within-beaker variable.

Table 2. The result of two-way ANOVA with initial density of *B. longirostris*, and food concentration for the density of *B. fatalis* at 15 days (N_{Bf-15})

Source of variation	df	MS**	F***	P****
Initial density of <i>B. longirostris</i>	1	2.833	6.028	0.030
Food concentration	1	2.325	4.946	0.046
Initial density × food concentration	1	2.218	4.728	0.049
Error	12	0.467		

*Degrees of freedom, ** Mean of squares, *** F value, **** Probability.

tition experiments, *B. fatalis* was depressed by *B. longirostris* at low food concentrations (Hanazato and Yasuno 1987, Chang and Hanazato 2004). Therefore, *B. fatalis* may have a higher TFC than does *B. longirostris*. In the present experiment, the algal concentration in the low-food conditions might be comparable with the TFC value for *B. fatalis* and higher than that for *B. longirostris*. In the condition with a high food concentration and a high density of *B. longirostris*, consumption by abundant *B. longirostris* individuals might decrease the algal concentration down to the TFC of *B. fatalis*. On the other hand, in the condition with a high food concentration and a low density of *B. longirostris*, *B. fatalis* was able to feed enough to reproduce. Previous studies showed that when they had the same initial density, the larger of two species was a better competitor than the smaller species under high food conditions because it could feed more (Romanovsky and Feniova 1985). As *B. fatalis* is larger than *B. longirostris* (Hanazato and Yasuno 1987), the feeding rate of *B. fatalis* may be higher than that of *B. longirostris* and thus be dominant under conditions with a high food concentration and a low density of *B. longirostris*.

CONCLUSION

The population shift from *B. longirostris* to *B. fatalis* is commonly observed during the early summer season in Japanese eutrophic lakes, as shown in Fig. 1 (Hanazato and Yasuno 1985b, Chang and Hanazato 2003). The present results demonstrate that the seasonal succession unconditionally requires very low population densities of *B. longirostris*. *L. kindtii* is an effective predator, which can reverse the dominance relationship between the two species through selective predation of *B. longirostris* (Chang and Hanazato 2003, 2004). In this study, laboratory experiments were conducted by using *B. longirostris* and *B. fatalis* collected from one site, Lake Suwa. Because *B. longirostris* is a cosmopolitan species and *B. fatalis* inhabits in East and Southeast Asia, they can present intraspecific variations in traits related to food competition. To test the effect of the intraspecific variations on the density effect of *B. longirostris* on the population growth of *B. fatalis*, further experiments by using the two species from other lakes are required. Investigating the density effect of species that are already present in a community on other species that appear in the community at some later time may help us to explain seasonal successions in zooplankton communities in natural lakes and ponds.

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