Role of interference from *Daphnia* and predation by cyclopoid copepods in zooplankton community structure: experimental analysis using mesocosms

JIN-YONG HA* & TAKAYUKI HANAZATO

Institute of Mountain Science, Shinshu University, Suwa, Japan

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**Abstract:** The reduction of planktivorous fish populations in lakes through biomanipulation often results in increased abundance of the large cladoceran *Daphnia* and invertebrate predators, such as cyclopoid copepods, and also in decreased numbers of small zooplankters, such as the cladoceran *Bosmina longirostris* and rotifers. To investigate the factors causing reduced abundance of small zooplankton species in lakes, we performed a mesocosm experiment where the abundance of *Daphnia* and cyclopoid copepods (*Mesocyclops* sp.) were controlled. *Bosmina* populations declined substantially in mesocosms with abundant copepods, implying that predation by cyclopoid copepods is a major factor controlling *Bosmina* populations in lakes. In contrast, rotifer densities were reduced in the mesocosms with *Daphnia*, even though excess food (*Chlorella vulgaris*) was provided. This suggests that rotifer populations are effectively controlled by interference competition with *Daphnia*.

**Key words:** biomanipulation, *Bosmina*, cyclopoid copepods, *Daphnia*, rotifers

**Introduction**

Large-sized zooplankton, such as *Daphnia* and some invertebrate predators (e.g. *Chaoborus*, *Leptodora*), dominate zooplankton communities in lakes where fish are few or absent (Brooks & Dodson 1965, Dodson 1974, Mackay et al. 1990, Benndorf 1995). This is because *Daphnia* out-competes smaller herbivorous zooplankters (Zaret 1980, Burns & Gilbert 1986, Williamson & Butler 1986, Devetter & Seda 2008) and invertebrate predators reduce the abundances of small zooplankters through selective predation. However, large-sized zooplankters are reduced in numbers when the fish population in lakes is high because fish select larger prey items. This results in an increase in small zooplankton due to decreased competitive pressure from *Daphnia* and predation pressure from invertebrate predators.

*Daphnia*’s competitive superiority in the herbivorous zooplankton community is indicative of its effectiveness as a phytoplankton grazer, and lake water transparency can increase if large *Daphnia* populations become established (Shapiro et al. 1982, Carlson & Schoenberg 1983, Lampert et al. 1986, Hosper 1997). These observations have led to the development of a new technique for restoring lake water quality, known as “biomanipulation,” in which the abundance of *Daphnia* is increased by artificially reducing fish abundance (Shapiro et al. 1975, Shapiro & Wright 1984, Hosper 1989, Christoffersen et al. 1993, Drenner & Hambright 1999, Wysujack et al. 2001, Kasprzak et al. 2003).

We performed such a biomanipulation to restore water quality in Lake Shirakaba (Nagano Pref., Japan) by introducing the piscivorous rainbow trout (*Oncorhynchus mykiss* Walbaum) to reduce the abundance of the planktivorous pond smelt (*Hypomesus transpacificus nipponensis* Mcalister) (Ha et al. unpublished). This biomanipulation altered the zooplankton community from one dominated by small zooplankters, such as the cladoceran *Bosmina* Baird and rotifers, to one dominated by the large cladoceran *Daphnia galeata* Sars and invertebrate predators, namely cyclopoid copepods (*Mesocyclops* sp.). These changes in zooplankton community structure appeared before the large decrease in phytoplankton. Therefore, the reduced abundance of small zooplankton species in the lake may be caused by factors other than low food availability due to grazing by *Daphnia*. It has also been shown that *Daphnia* negatively affects rotifer population through interference. This interference was first inferred when *Keratella cochlearis* Gosse populations were cultured with *Daphnia galeata mendotae* Brige and found to have high mortality rates, even though food re-
Materials and Methods

The experiment was conducted in twelve 50-L polyethylene tanks (diameter, 43 cm; height, 45 cm). We tried to establish a zooplankton community from resting stages in lake sediments that would be dominated by the small cladoceran *Bosmina* and rotifers. We used sediment from Lake Suwa, which had a zooplankton community similar to that of Lake Shirakaba until biomanipulation was performed on the latter. The distance between the two lakes was about 15 km.

At the start of the experiment (day 0), we collected sediment from the center of Lake Suwa using an Ekman grab sampler. We added 1 kg of well-mixed sediment to each of the tanks, which were then filled with 46 L of aged (one week) tap water. The tanks were divided into four treatment groups with three replicates each: control, competitor, predator, and predator+competitor.

The control tanks did not receive any additional zooplankton. Adult female *Daphnia galeata* (1.5 mm < body size < 2.0 mm) were added to the competitor tanks to a density of 6 indiv. L⁻¹. These *Daphnia* were from a laboratory culture cloned from an individual collected from Lake Shirakaba. Each predator tank received 156 individuals of adult *Mesocyclops* sp. (final density, 3.4 indiv. L⁻¹; 1.0 mm < body size < 1.5 mm), which were collected from Lake Suwa and reared in the laboratory with prey animals (rotifers and small cladocerans) for a week before the start of the experiment. The predator+competitor tanks received both predator and competitor at final densities of 3.4 indiv. L⁻¹ of *Mesocyclops* sp. and 6 indiv. L⁻¹ of *D. galeata* adults. All tanks were kept in a temperature-controlled room at 20°C with a light: dark photoperiod of 16: 8 h.

It was not possible to completely exclude *Mesocyclops* sp. from all the tanks because some cyclopoid copepods emerged from resting stages in the sediment (Thorp & Covich 1991). However, the average densities of these cyclopoid copepods reached a maximum of only 0.72 indiv. L⁻¹ in the control tanks and 2.46 indiv. L⁻¹ in the competitor tanks, which was lower than in the predator and predator+competitor tanks (See Results).

The experiment ran for 25 days from 7 May (day 0) to 2 June 2007 (day 25). *Mesocyclops* sp., *Daphnia*, or both were introduced into treatment tanks on day 13, as described above. The green alga *Chlorella vulgaris* Beijerinck (Chlorella Industry, Fukuoka, Japan) was added to all the tanks (including controls) to a final density of 5×10⁵ cells mL⁻¹ beginning on day 10 and every three days thereafter to maintain the zooplankton under excess food conditions (Nandini & Sarma 2003).

Quantitative sampling of zooplankton from each tank began on day 13 and was repeated every three days. The sampling was conducted with a column sampler (65 cm in length, 5 cm in diameter) with a hydraulically opened bottom flap that collected 4.6 L of water from the surface to near the bottom. Because the zooplankters were often aggregated near the tank wall, the water was gently mixed before sampling. Zooplankton were collected by filtering the sampled water through a 40-μm-mesh net and were fixed with sugar-formalin at a final concentration of 4% (Haney & Hall 1973). Fixed zooplankton were identified to the genus or species level and counted under a microscope at 100× magnification.

We collected water quality data along with zooplankton samples. Water temperature and dissolved oxygen concentration (DO) were measured at the surface with a thermometer and a dissolved oxygen meter (model YSI-55; YSI Inc, Yellow Springs, Ohio, USA), respectively. The pH was measured with a pH meter (model HM-20P; DKK-TOA Corp, Tokyo, Japan). Chlorophyll *a* concentrations, an indicator of food abundance, were analyzed spectrophotometrically using the methanol extraction method (Marker et al. 1980). Aged tap water was added to the tanks after each sampling to replace the water removed.

We used repeated-measures ANOVA (StatView version 5; SAS Institute, Cary, North Carolina, USA) to test for significant differences in zooplankton densities in the different treatment tanks.

Results

Water quality parameters

From day 13 to day 25 the pH in the experimental tanks ranged from 6.62 to 7.25 (Fig. 1). Water temperature remained between 19.3 and 20.3°C. The DO concentration was slightly higher in the *Daphnia* (competitor) treatment than in the other ones. Chlorophyll *a* concentrations ranged from 35.9 to 6.4 μg L⁻¹. There were no significant differences between the tanks for any of the water parameters measured (Table 1).

Zooplankton community structure

The densities of *D. galeata* increased steadily in both the competitor (*Daphnia*) tanks and the predator+competitor (*Mesocyclops + Daphnia*) tanks soon after the introduction of *Daphnia* (Fig. 2). The density of adult *Mesocyclops* sp. started increasing on day 19 in all tanks but by day 25 densities were markedly higher in the tanks where they had been added (the *Mesocyclops* and *Mesocyclops + Daphnia* tanks) compared to the other tanks.
The Daphnia and Mesocyclops additions affected the rotifer and cladoceran populations. The populations of small rotifer species increased significantly only in the Mesocyclops tanks, while densities remained low in the control, Daphnia, and Mesocyclops + Daphnia tanks (Fig. 3, Table 1). The dominant rotifer species during the entire experimental period was Filinia longiseta Ehrenberg except in the control tanks on day 22 when a relatively large population of Asplanchna sieboldi Leydig, a predacious species, appeared. Two other species (<210 indiv. L⁻¹) were found in fewer numbers than F. longirostris (<2,300 indiv. L⁻¹).

The common cladoceran species observed were Bosmina longirostris Müller, Bosmina fatalis Burckhardt, and Bosminopsis deitersi Richard (Fig. 3). The most dominant species was B. longirostris, with significantly higher densities in the control and Daphnia tanks than in the Mesocyclops and Mesocyclops + Daphnia tanks (Table 1). Both B. fatalis (<9 indiv. L⁻¹) and B. deitersi (<160 indiv. L⁻¹) were present in quite small numbers compared to B. longirostris (<750 indiv. L⁻¹).

Eodiaptomus japonicus Burckhardt was the only omnivorous copepod species that appeared during the experimental period. Its numbers increased in the Daphnia and Mesocyclops + Daphnia tanks, reaching densities significantly higher than in the other tanks (Fig. 3, Table 1), through the densities were extremely low, <8 indiv. L⁻¹ throughout the study period.

Fig. 1. Temporal changes in the water parameters (mean±SE) of each tank during the experiment. Arrows in each panel show the time when Daphnia galeata and/or Mesocyclops sp. were introduced.

Fig. 2. Temporal changes in abundances of Daphnia galeata and Mesocyclops sp. in the tanks (mean±SE).
**Discussion**

*Bosmina longirostris* dominated the cladoceran community in all mesocosm tanks. However, its densities were higher in the control and *Daphnia* tanks than in the *Mesocyclops* and the *Mesocyclops + Daphnia* tanks. This suggests that the presence of *Mesocyclops* sp. is the major factor controlling the *Bosmina* populations (population growth rate \( r = \ln N_t - \ln N_0 \)/\( t \), where \( N_0 \) = initial population density and \( N_t \) = population density after time \( t \)) in the *Mesocyclops* and the *Mesocyclops + Daphnia* tanks, \( r = -0.07 \) and \( -0.49 \) (Nandini & Rao 1998); predation rate \( (K = Bo(No - Ns)/t \cdot Bp \), where \( Bo \) = initial mean biomass of one prey item, \( No \) = initial number of prey items per predator, \( Ns \) = the number of surviving prey items per predator after time \( t \) and \( Bp \) = the mean biomass of one predator) of *Mesocyclops* sp. on *B. longirostris*, \( K = 0.26 - 0.39 \) (Brandl & Fernando 1975)). Species in the genus *Mesocyclops* are well known as predators of *Bosmina* (Kerfoot 1978), and the impact of copepod predation on *B. longirostris* populations has been demonstrated in previous mesocosm studies (Chang & Hanazato 2005, Nagata & Hanazato 2006) (Table 2). The density of *Mesocyclops* sp. increased in the *Daphnia* tanks and *B. longirostris* was also present at a high density on day 22. This was an unexpected result and the reason why this phenomenon occurred could not be elucidated clearly. However, it might be due to the existence of a time lag for the *Mesocyclops* sp. to reduce the *B. longirostris*...
population by predation, because the density of *B. longirostris* decreased within three days, when the experiment ended (day 25). *Daphnia* can suppress the abundance of *Mesocyclops* sp. through competition for food sources (Vanni 1986) when *Mesocyclops* sp. is at the naupliar stage. However, under excess food conditions as occurred during our experiment, nauplii did not seem to face a food shortage due to competition with *Daphnia* and were able to develop to the adult stages.

Previous mesocosm experiments have shown that predation by *Mesocyclops* sp. is strong enough to suppress rotifer populations (Nagata & Hanazato 2006). However, in our study, rotifer populations increased in the *Mesocyclops* tanks (population growth rate, \(r = 0.189\); predation rate of *Mesocyclops* sp., \(K = 0.06–0.12\) (Brandl & Fernando 1975)). These contrasting results could be due to the difference in food abundance between the two experiments. In the present study, *C. vulgaris* was added to tanks to a density of \(5 \times 10^5\) cells mL\(^{-1}\), 2.5 times the concentration in the previous study (2 \(\times 10^5\) cells mL\(^{-1}\); Nagata & Hanazato 2006). Thus, our experiment had the potential to support larger rotifer populations, which might have compensated for losses to copepod predation. Chang & Hanazato (2005) also observed an increase in the total rotifer density and a decrease in cladoceran density following the introduction of *Mesocyclops* in mesocosm tanks with abundant food (6 \(\times 10^5\) cells mL\(^{-1}\)).

The growth of rotifer populations was severely suppressed in the tanks with *Daphnia* added (population growth rate: \(r = -0.08\) (the *Daphnia* tanks) and 0.059 (the *Mesocyclops+Daphnia* tanks)). Gilbert (1985, 1988b) and Schneider (1990) demonstrated that two mechanisms are at work in these interactions: exploitative competition and interference competition. However, it is unlikely that exploitative competition was a factor in our experiment be-

### Table 1.
Results of repeated-measures ANOVA of the zooplankton species densities after the introduction of *D. galeata* and *Mesocyclops* sp. (days 13–25). The three treatments were the *D. galeata*, *Mesocyclops* sp. and *Mesocyclops* sp.+*D. galeata*, and the repeated measure. *p*<0.05; **p*<0.01; ***p*<0.001.

| Source | Treatment×Day | df | F   | p    |
|--------|---------------|----|-----|------|
| Water parameters |               |    |     |      |
| pH     |               | 12 | 2.060 | 0.0510 |
| Temperature |         | 12 | 1.287 | 0.2730 |
| Dissolved oxygen |   | 12 | 1.904 | 0.7230 |
| Chlorophyll a |       | 12 | 0.416 | 0.9450 |
| Zooplankton |               |    |     |      |
| Rotifers |               |    |     |      |
| Total rotifers |       | 12 | 6.600 | <0.0001*** |
| Keratella quadrata | | 12 | 1.219 | 0.3130 |
| Filinia longiseta |     | 12 | 4.465 | 0.0003*** |
| Asplanchna sieboldi |   | 12 | 1.519 | 0.1683 |
| Trichocerca sp. |       | 12 | 4.035 | 0.0008*** |
| Cladocerans |               |    |     |      |
| *Daphnia galeata* |           | 12 | 0.789 | 0.5492 |
| Total cladocerans (excepting *Daphnia*) | | 12 | 3.056 | 0.0057** |
| *Bosmina fatalis* |     | 12 | 3.533 | 0.0020** |
| *B. longirostris* |     | 12 | 3.091 | 0.0053** |
| *Bosminopsis detersi* | | 12 | 2.187 | 0.0385* |
| Cyclopoid copepoda |   | 12 | 3.159 | 0.0046** |
| *Mesocyclops* sp. |       | 12 | 3.159 | 0.0046** |
| Calanoid copepoda |     | 12 | 3.159 | 0.0046** |

### Table 2.
The feeding habits of major zooplankters in the experiment.

| Taxon | Feeding habits | Reference |
|-------|----------------|-----------|
| Rotifers (excepting *Asplanchna* sp.) | Herbivorous and detritivorous | Arndt & Nixdorf (1991), Schlüter et al. (1987) |
| *Asplanchna sieboldi* | Carnivorous: small rotifers (*Filibnia longiseta*) | Iyer & Rao (1996), Sarma (1993), Williamson (1983), Böing et al. (1998), Kamjunke et al. (1999), Urabe & Watanabe (1991), Bogdan & Gilbert (1982), DeMott (1982) |
| *Daphnia galeata* | Herbivorous and detritivorous | Böing et al. (1998), Kamjunke et al. (1999), Urabe & Watanabe (1991) |
| Small cladoceran | Herbivorous and detritivorous | Bogdan & Gilbert (1982), DeMott (1982) |
| *Mesocyclops* sp. | Carnivorous: small cladoceran (*Bosmina longirostris*), *Asplanchna* sp. | Gilbert & Williamson (1978), Williamson (1980), Chang & Hanazato (2005), Nagata & Hanazato (2006) |
| *Eodiaptomus japonicus* | Omnivorous | Kawabata (1987), Nagata & Okamoto (1988), Yoshida et al. (2001) |
cause an abundance of *C. vulgaris* was supplied in the tanks. Therefore, it seems likely that rotifers were out-competed by *Daphnia* primarily through interference competition (that is, through damage incurred by being swept into the branchial chambers of *Daphnia*), which apparently is more important than exploitative competition in the interaction between *Daphnia* and rotifers (Williamson 1987, Gilbert 1988a, Ronneberger et al. 1993). The relative importance of interference competition compared to exploitative competition has been demonstrated experimentally for interactions between cladocerans and the rotifer *K. cochlearis* (Maclsaac & Gilbert 1991).

In the control tanks, small rotifer densities also maintained at a low level. *Asplanchna*, which is well-documented as a predacious large rotifer, was observed at high abundances in the control tanks. According to Gilbert & Williamson (1978), small rotifers are critical prey items for *Asplanchna*, and therefore the predation pressure by *Asplanchna* on the small rotifer community was severe. Therefore, the small rotifers in the control tanks might be suppressed by *Asplanchna* species (Table 2).

In Lake Shirakaba, the abundance of *Bosmina* and rotifers in the zooplankton community decreased while that of *D. galeata* and *Mesocyclops* sp. increased after biomanipulation by the introduction of the piscivorous rainbow trout. The results of our mesocosm experiment help to explain these changes in the lake zooplankton community. Specifically, the reduced rotifer density resulted from interference competition with *Daphnia* and the decline in the *Bosmina* population was caused primarily by *Mesocyclops* sp. predation.

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