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

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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 Mcallister) (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-

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sources were abundant. Interference occurs when the ro-
tifers are swept into the branchial chamber of a feeding
Daphnia (Gilbert 1988a).

To clarify the interference competition by daphnids and
predation of cyclopoid copepods on small zooplankton, we
conducted a laboratory experiment using mesocosm tanks
where *D. galeata*, *Mesocyclops* sp., or both were introduced
into a zooplankton community dominated by *Bosmina* and
rotifers under excess food conditions.

Materials and Methods

The experiment was conducted in twelve 50-L polyethyl-
ene tanks (diameter, 43 cm; height, 45 cm). We tried to es-
tablish a zooplankton community from resting stages in
lake sediments that would be dominated by the small clado-
ceran *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 sedi-
ment 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 zoo-
plankton. Adult female *Daphnia galeata* (1.5 mm<body
size<2.0 mm) were added to the competitor tanks to a den-
sity of 6 indiv. L^{-1}. These *Daphnia* were from a laboratory
culture cloned from an individual collected from Lake Shi-
rakaba. 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 (ro-
tifers and small cladocerans) for a week until 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 cy-
clopoid copepods reached a maximum of only 0.72 indiv.
L^{-1} in the control tanks and 2.46 indiv. L^{-1} in the competi-
tor 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 de-
scribed above. The green alga *Chlorella vulgaris* Beijerinck
(Chlorella Industry, Fukuoka, Japan) was added to all the
tanks (including controls) to a final density of 5×10^5 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 bot-
tom flap that collected 4.6 L of water from the surface to
near the bottom. Because the zooplankters were often ag-
gregated near the tank wall, the water was gently mixed be-
fore 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
$100\times$ magnification.

We collected water quality data along with zooplankton
samples. Water temperature and dissolved oxygen concen-
tration (DO) were measured at the surface with a ther-
mometer 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 spectrophoto-
metrically 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 sig-
nificant 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 re-
mained 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 differ-
ences 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 den-
sities were markedly higher in the tanks where they had
been added (the *Mesocyclops* and *Mesocyclops*+*Daphnia*
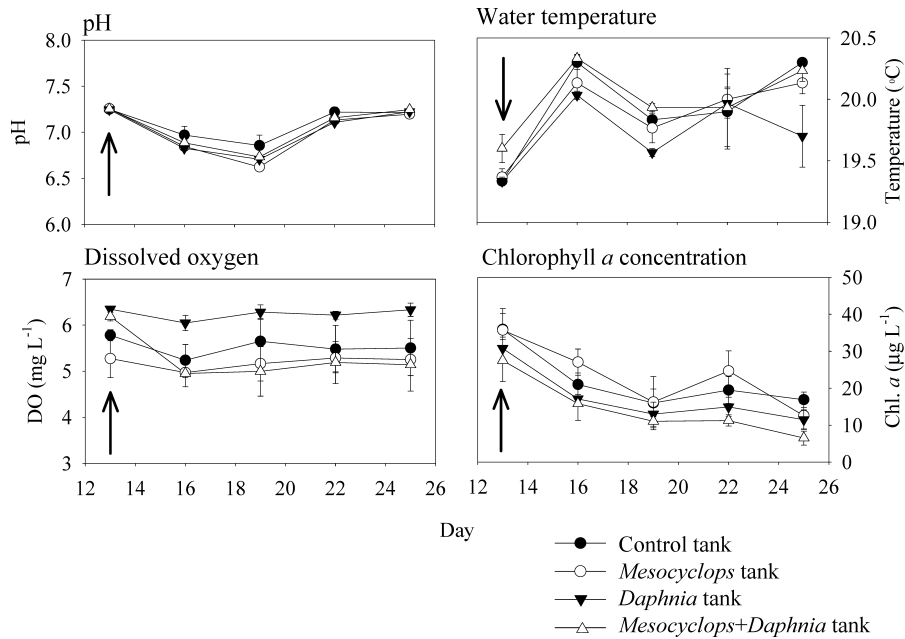tanks) compared to the other tanks.

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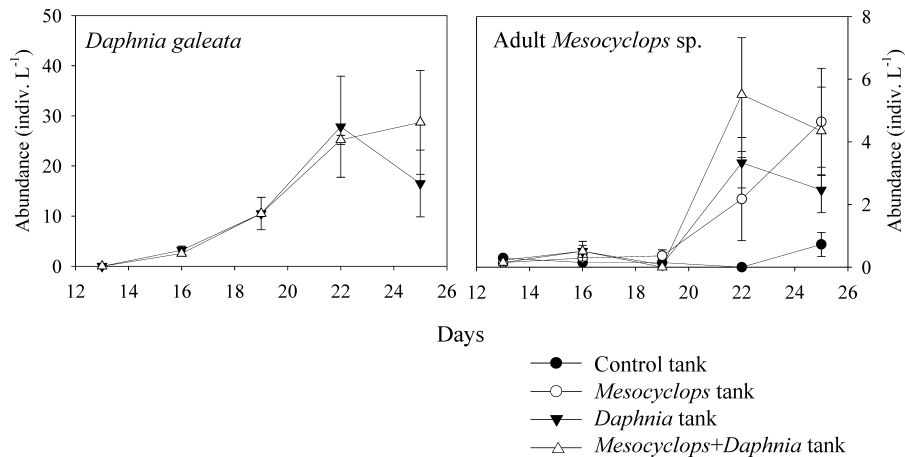

Fig. 2. Temporal changes in abundances of *Daphnia galeata* and *Mesocyclops* sp. in the tanks (mean±SE).

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 densi-

ties 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 compare 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.
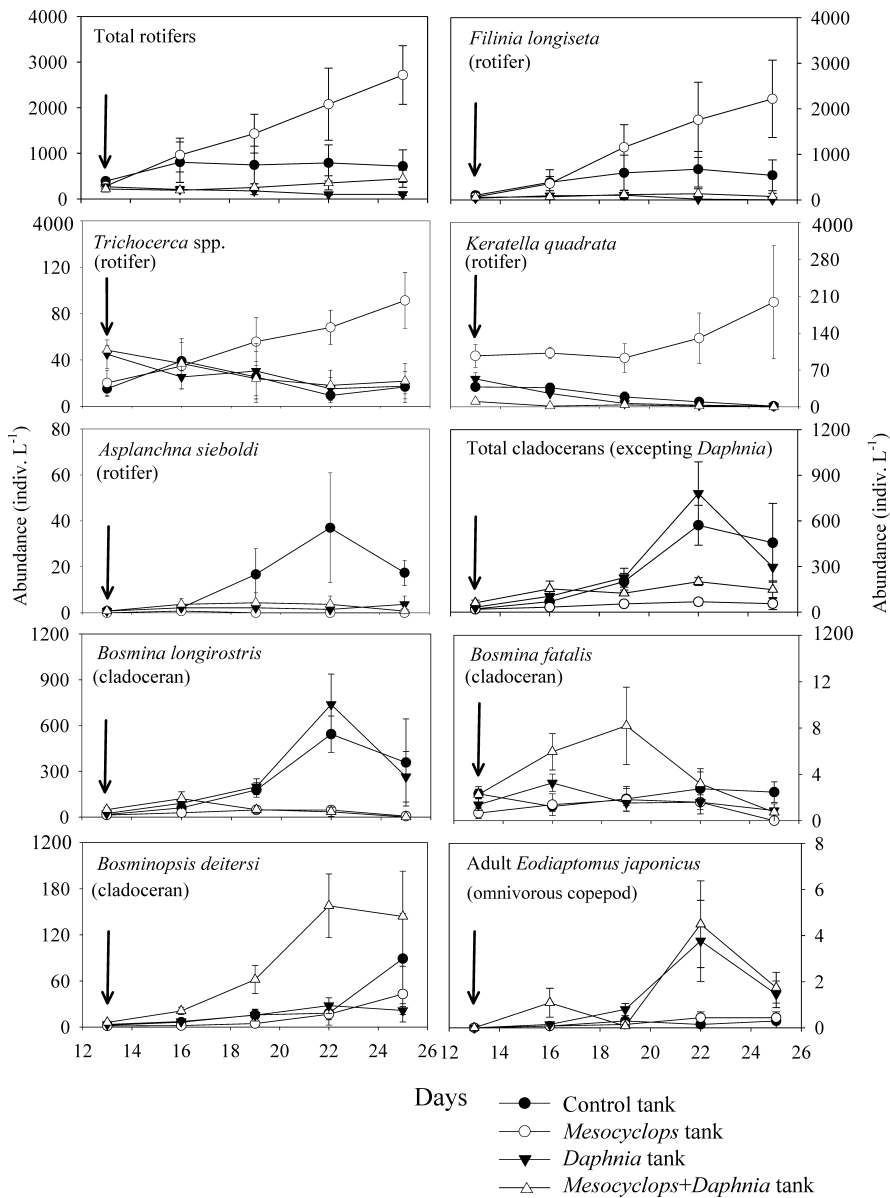
Fig. 3. Temporal changes in the densities of zooplankters (mean±SE) in the tanks. Arrow in each panel shows the time when *Daphnia galeata* and/or *Mesocyclops* sp. were introduced.

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 results 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*

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 day was 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			
Mesocyclops sp.	12	3.159	0.0046**
Calanoid copepoda			
Eodiaptomus japonicus	12	2.434	0.0222*

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 5×10^5 cells mL^{-1}, 2.5 times the concentration in the previous study (2×10^5 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 (6×10^5 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 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 (*Filinia longiseta*)	Iyer & Rao (1996) Sarma (1993) Williamson (1983)
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* (MacIsaac & 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.

Acknowledgements

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