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Effect of large- and of small-bodied zooplankton on phytoplankton in a eutrophic oxbow

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Abstract. Macrozooplankton and microzooplankton effects on the phytoplankton were measured *in situ* in a eutrophic lake. Indigenous phytoplankton were incubated for 5 days in 30 l mesocosms with either the macro- and microzooplankton (complete), microzooplankton only (micro) or no zooplankton (none). Changes in phytoplankton biovolume were investigated. Rotifer densities became significantly higher in the 'micro' treatment than in the 'complete' and 'none' treatments. Total algal biovolume changed little in the 'complete' and 'none' treatments, but increased significantly in the 'micro' treatment. The results suggest that macrozooplankton (*Daphnia magna*) suppressed it and microzooplankton (*Keratella cochlearis*) enhanced it. They had opposite net effects on the phytoplankton. Suppression of microzooplankton by *Daphnia* probably had an indirect negative effect on the phytoplankton.

Introduction

Zooplankton affect phytoplankton directly by consuming cells and, indirectly, by recycling nutrients. Direct effects were quantified by Havens (1993). Direct effects also depend on zooplankton composition because the nature of food selection varies among herbivore taxa (Burns, 1968; Bogdan and Gilbert, 1984), as do filtering rates (Bogdan *et al.*, 1980; Havens, 1991). Nutrient recycling by zooplankton can stimulate the growth of both grazed and ungrazed phytoplankton (Lehman, 1980). As with direct effects, rates of nutrient recycling are dependent upon the taxonomic composition of the plankton (Peters and Downing, 1984; Hamilton and Taylor, 1987).

A common approach is to establish a gradient of zooplankton densities in *in situ* enclosures, and determine phytoplankton growth rates during a short days incubation. In different experiments, phytoplankton biomass has been depressed, little affected, or enhanced by increased grazing (Lynch and Shapiro, 1981; Schoenberg, 1990). Non-linear relationships between phytoplankton growth and zooplankton biomass were found (Lehman and Sandgren, 1985; Bergquist and Carpenter, 1986; Elser *et al.*, 1987). Despite extensive research on zooplankton effects, only a few studies (Henry, 1985; Havens, 1993) determined the relative importance of microzooplankton (i.e. rotifers, nauplii, ciliates) and macrozooplankton (cladocerans and copepodids) in regulating the phytoplankton. It is known that both large and small zooplankton are important grazers (Bogdan and Gilbert, 1982; Gulati *et al.*, 1982; Lampert *et al.*, 1986; Gliwicz, 1990b; Havens, 1991) and nutrient remineralizers (Henry, 1985). However, their respective net effects on phytoplankton biomass quality have not been known.

Our main aim was to quantify the net effects of microzooplankton and macrozooplankton on phytoplankton biovolume in a temperate eutrophic oxbow. The

approach was to measure phytoplankton responses to *in situ* incubations with either the complete zooplankton, microzooplankton only, or a zooplankton-free environment.

Method

The investigations were made at Aranyosi-Holt-Körös, Körös area, Békés county, SE Hungary (latitude 46°54′24.75″, longitude 20°36′5.33″), a small (A_o = 10 ha, d_{max} = 4 m) eutrophic oxbow. Filamentous cyanobacteria (especially *Anabaena spiroides*), cryptomonads (*Rhodomonas minuta* var. *nannoplanktonica* and *Cryptomonas erosa*) and colonial chlorophytes (*Oocystis lacustris*) dominate the phytoplankton. The occurrence of >10 Dinophyta species was known from this region of Hungary, Körös area (Grigorszky *et al.*, 1997a,b, 1998), but in this lake no Dinophyta species have been registered for 10 years. Ciliates and other protozoans are usually highly abundant in eutrophic environments (Sherr and Sherr, 1987; Beaver and Crismann, 1989). In spite of this fact, their biomass was <0.05 μg l^{-1} and did not change significantly during the investigation period. The dominant zooplankton were *Daphnia magna* and *Keratella cochlearis*.

The experiment was performed with a duration of 5 days. During the experiment, the treatments were established in triplicates (nine enclosures in total). At 8 h on 22 June 1995, transparent plastic bags were filled by gently pouring 30 l of water column water using a plastic bucket. Replicates were either filled with unfiltered water (hereafter the 'complete' treatment), with water passed through a 180 μm net (the 'micro' treatment) or with water passed through a 45 μm net (the 'none' treatment).

The objective was to establish treatments containing either the complete plankton, the phytoplankton and microzooplankton only, or the phytoplankton only. Preliminary fractionations showed that the 180 μm net removed 100% of cladocerans, copepod adults and copepodids from whole lake water, but allowed nearly all rotifers and nauplii to pass. The 45 μm net retained nearly all zooplankton and did not significantly reduce the biovolume of phytoplankton (*t*-test, $P > 0.05$).

After filling the bags, initial phytoplankton samples (200 ml) were collected and fixed with 5 ml of Lugol's solution. The bags were tightly closed with line, attached to anchors, and suspended in groups of three at 1.5 m depth (mid-epilimnion) from surface floats. The groups ('complete', 'micro', 'none'—see Table I) contained two replicates from each treatment. After 5 days incubation, the bags were sampled. This experimental duration was chosen for two reasons. First, it has been shown that 3–5 days are sufficient time for phytoplankton responses to zooplankton manipulations to become established (Vanni and Temte, 1990). Second, it was a short enough time period that extensive periphyton growth did not occur on the bag walls.

Phytoplankton were counted by the Utermöhl (1958) technique. At least 400 cells were enumerated. For filaments and colonies, individual cells were counted. Population densities (cells ml^{-1}) were calculated from the counts and converted to biovolume (μm^3 ml^{-1}). This was done by measuring at least 30 cells of each taxon, calculating cell volumes (μm^3 $cell^{-1}$) by approximation of shapes to regular geometric solids, and then multiplying the population densities by average cell volumes.

Zooplankton samples were concentrated to 25 ml using a small plastic cup with a 45-μm-mesh side window. Aliquots of at least 200 animals were counted. Crustacean body lengths were determined by measuring 25 individuals of each taxon. Mean individual biomasses (μg dry weight) were then determined using length–weight relationships given in Culver *et al.* (1985). Population biomasses (μg l^{-1}) were determined for each crustacean taxon as density times mean individual biomass. For *K.cochlearis* and *Asplanchna* sp., dimensions (length, width, depth) of 25 individuals were measured. Biovolumes were calculated by approximating shapes to regular solids, fresh weights were calculated from the biovolumes assuming unit density, and dry weights were calculated as fresh weight × 0.1 (Pace and Orcutt, 1981).

Results

During our experiment, the lake and the complete treatment zooplankton were numerically dominated by *D.magna*, nauplii and *K.cochlearis* (Table I). *Daphnia magna* accounted for >95% of total biomass. In the micro treatment, the abundances of all crustacean zooplankton were significantly lower than in the complete treatment; however, the abundance of *K.cochlearis* was significantly higher. In the none treatment, the abundance of all zooplankton, including *K.cochlearis*, was significantly lower than in the other treatments. Total density and biomass were 10 and 0.3%, respectively, of the complete treatment levels. Mean individual biomass was 0.1 μg.

The phytoplankton biovolumes (Figure 1) were not significantly different in the treatments on day 0, although there was a slight biovolume reduction in the none treatment, where screening removed large *A.spiroides* filaments. This taxon was abundant in the lake, and its filaments averaged 30 μm (younger cells) and 65 μm (adult cells) in length during the experiment. On day 5, biovolume had

Table I
(a) Densities (no. l^{-1}) of the zooplankton in the treatment and lake during the experiment

	DM	KC	NA	AS	Total
Complete	42	64	7	3	116
Micro	2	66	3	1	72
None	0	7	1	0	8
Lake	43	67	7	2	119

(b) Biomass (μg l^{-1}) of the zooplankton in the treatment and lake during the experiment. Values are the means of replicates in each treatment

	DM	KC	NA	AS	Total	Individual biomass
Complete	202	4	2	4	212	1.82
Micro	11	5	1	1	18	0.25
None	0	0.3	0.3	0	0.6	0.075
Lake	206	5	2	1.5	214.5	1.8

DM, *Daphnia magna;* NA, nauplii; KC, *Keratella cochlearis*; AS, *Asplanchna* sp.; Total, all species.

increased in the complete treatment. A significant biovolume increase (187%) did occur in the micro treatment (Figure 1). This was largely due to *A.spiroides*. In the none treatment, total biovolume increased only slightly from day 0 to 5 (Figure 1).

Discussion

The succession among different species and size classis of zoo- and phytoplankton has been suggested to be closely linked (Gliwicz and Siedlar, 1980; Lynch, 1980; Lynch and Shapiro, 1981; Lampert, 1986; Sommer *et al.*, 1986; Elser *et al.*, 1988; Gliwicz and Pijanowska, 1989; Sterner, 1989; Gliwicz, 1990a; Vanni and Temte, 1990; Hansson *et al.*, 1998).

The microzooplankton and macrozooplankton of this eutrophic lake had markedly different net effects on the phytoplankton. This finding is consistent with the results from a previous experiment with a somewhat different design (Bergquist *et al.*, 1985). They exposed phytoplankton of Tuesday Lake (Michigan) to either the indigenous small-bodied zooplankton (small copepods, *Bosmina* and rotifers) or to large-bodied zooplankton (*Daphnia pulex*) taken from nearby Peter Lake. The two zooplankton assemblages had opposite effects on the phytoplankton. Small cells were suppressed by large zooplankton and enhanced by small zooplankton. Conversely, large cells were enhanced by large zooplankton and suppressed by small zooplankton. Although the experimental designs are similar, the present study and that of Bergquist *et al.* (1985) addressed different questions about algal–zooplankton interaction. Bogdan *et al.* (1980) and Bergquist *et al.* (1985) quantified the effects of introduced small grazers, such as rotifers, on phytoplankton normally affected by macrozooplankton.

We wanted to quantify phytoplankton regulation by two components of its natural grazer assemblage. In the micro bags, where macrozooplankton were

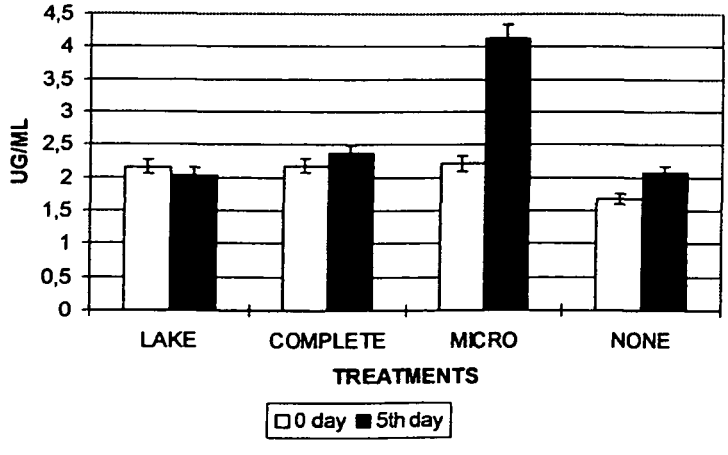

Fig. 1. The phytoplankton biovolumes at day 0 and the fifth day in the treatment and lake during the experiments. Vertical bars are ± SE.

removed by screening, *K.cochlearis* densities increased, suggesting net negative impacts of macrozooplankton on this taxon. This suggests that the microzooplankton increases in the micro treatment were due to *D.magna* removal. For *K.cochlearis*, such a response is consistent with the findings of Gilbert and Stemberger (1985), who concluded that 'interference competition' was responsible for the negative impact of *Daphnia* on *K.cochlearis*. They observed that rotifers carried into *Daphnia*'s branchial chamber were rejected by the postabdominal claw and were often mortally wounded. These findings lend support to the view that the increases in *K.cochlearis* observed in the micro treatment were a direct result of *D.magna* removal.

Suppression of plankton by *D.magna* is also consistent with previous results. Alteration in individuals of *D.magna* and *K.cochlearis* feed on bacteria and picoalgae (Stenson, 1984; Beaver and Crismann, 1989) showed that even the smallest metazoan herbivores can out-compete ciliates. Hamilton and Taylor (1987) found that ciliates increased upon removal of crustaceans, and Pace and Funke (1991) found that ciliates declined when *Daphnia* was introduced. In the present experiment, *D.magna* was of a similar size, but occurred at a much greater biomass (>320 $\mu g\ l^{-1}$).

Most interesting were the differential impacts of the two zooplankton groups on the phytoplankton. Previous studies have shown that the zooplankton have both grazing and nutrient-recycling effects on the phytoplankton (Lehman, 1980; Elser *et al.*, 1988; Gliwicz and Lampert, 1990).

The net effects at any given time depend upon the relative magnitude of the positive and negative impacts, which are a function of both the phytoplankton and zooplankton composition. During this study, the dominant phytoplankter, *A.spiroides*, existed as short (30–65 μm) filaments. While such filaments can be grazed by *Daphnia* (Lynch, 1980), they are too large for consumption by *Keratella*. *Keratella* consumes cryptomonads, chrysomonads, bacteria and a wide range of detritus (Bogdan *et al.*, 1980; Bogdan and Gilbert, 1984; Hansson *et al.*, 1998), and it has high efficiencies on small cells, *Synechococcus* sp., *Chlamydomonas reinhardtii*, *Ankistrodesmus* sp., *Stephanodiscus* sp. (Bogdan and Gilbert, 1987).

Our results suggest the following scenario during the experiments. *Keratella*, being unable to graze the dominant filamentous cyanobacteria, had a net positive impact on their growth. They may have served as 'nutrient pumps', consuming small unicellular phytoplankton species and bacteria, and returning a portion of previously unavailable nutrients to the water. Thereby, the microzooplankton may have stimulated growth of the ungrazed cyanobacteria. Previous studies have shown that microzooplankton rapidly recycle nutrients (Henry, 1985), and protozoans have been shown to play the major role in summer planktonic phosphorus cycling (Hamilton and Taylor, 1987).

In contrast to the microzooplankton, *Daphnia* likely grazed phytoplankton, recycled nutrients, and inhibited the microzooplankton. Overall, *Daphnia* had a detrimental impact on the cyanobacteria-dominated phytoplankton and *Daphnia* may negatively affect phytoplankton by suppressing microzooplankton. Although numerous cases of rotifer inhibition by *Daphnia* have been documented (Gilbert and Stemberger, 1985; Gilbert, 1988; Schneider, 1990), the

present study demonstrates the impacts of that inhibition on the phytoplankton community. Further research is needed to determine the changes with season and trophic state.

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