

Effectiveness of phytoplankton control by large-bodied and small-bodied zooplankton

Piotr Dawidowicz

Department of Hydrobiology, Institute of Zoology, University of Warsaw, Nowy Swiat 67, 00-046
Warsaw, Poland

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Abstract

Employing *in situ* enclosures containing inocula of the lake zooplankton (mainly *Daphnia galeata*, *Daphnia cucullata* and *Bosmina* spp.) from a moderately eutrophic Lake Ros (Northern Poland) or large-bodied *Daphnia magna*, the following observations on succession of phytoplankton were made: 1) whereas *D. magna* could control the density of all the phytoplankton size classes, the lake zooplankton could not suppress the large-sized phytoplankters or net phytoplankton; 2) the lake zooplankton was able to control the density of small algae (< 50 µm), but its effect on large algae may be opposite: a promotion of net phytoplankton growth by removing small-sized algae which can out-compete net phytoplankton for limited PO₄-P resources (< 5 µg P l⁻¹).

Since efficiency of phytoplankton density control by *D. magna* decreased with an increase in net phytoplankton abundance, biomanipulation could not be successful without introducing or maintaining a high population of large-bodied cladoceran species before high densities of large algae would make the control of phytoplankton inefficient.

Introduction

The biomanipulation in the open-water planktonic communities should promote the domination of large filter-feeding cladocerans, mainly *Daphnia*, which are able to control algal biomass (Shapiro *et al.*, 1975; Shapiro, 1980; Shapiro & Wright, 1984; Benndorf *et al.*, 1984; Carpenter *et al.*, 1985). According to Lampert (1988) the biomass level of herbivorous zooplankton required to control phytoplankton density is not unreasonably high, and is occasionally observed even in eutrophic lakes e.g. during 'clear water phase'.

However, filter-feeding zooplankton cannot

graze upon all algal cells or colonies, since upper size of particles ingested by largest cladoceran species only slightly exceeds 50 µm; the size limit decreasing linearly with decreasing animal body size (Geller & Müller, 1981). Heavy grazing pressure exerted by small- and medium-sized cladocerans, which remove nanoplankton that compete with net phytoplankton for limiting resources, may even promote the growth of net algae. Moreover, the zooplankton excretion may pass available nutrients from edible nanophytoplankton to inedible net phytoplankton, as suggested by Dawidowicz & Gliwicz (1987) and Haney (1987). Therefore, the increase in small and medium-sized herbivorous zooplankton den-

sity may cause a shift in phytoplankton size spectrum rather than a desired decline in total phytoplankton biomass.

The aim of this study was to compare the pattern of changes in biomass of phytoplankton in 2 types of *in situ*, fish-less enclosures: 1) containing lake zooplankton with dominant medium-sized *Daphnia galeata*, and 2) lake zooplankton enriched with inoculum of large-bodied *Daphnia magna*.

The lake and its plankton

Lake Ros (surface area 1888 ha; mean depth 8.1 m; maximum depth 31.8 m) is a dimictic, mesotrophic lake in Mazurian Lake land in north-eastern Poland.

At the start time of the experiment, the lake phytoplankton was dominated by diatoms (mainly *Asterionella*, *Melosira*, *Fragillaria*, *Nitzschia*, *Synedra*, *Navicula* and *Cyclotella*) which comprised >70% of algal cell number; green algae and blue-green algae (Cyanobacteria) were much less abundant, each group forming up to 10% of the total phytoplankton density. Chlorophyll *a* concentrations did not exceed $10 \mu\text{g l}^{-1}$ (Dawidowicz, 1989). Zooplankton was numerically dominated by rotifers. Among cladocerans, four species of *Daphnia* (*D. galeata*, *D. hyalina*, *D. cucullata* and *D. cristata*) and three species of *Bosmina* (*B. coregoni*, *B. longirostris* and *B. berolinensis*) were important (Dawidowicz, 1989). The water temperature during the experiment ranged from 19.5 °C to 22.0 °C.

Materials and methods

The experimental enclosures consisted of two sets of 3 polyethylene bags of 3 m³ capacity each. The three enclosures of the first set were filled with lake water with natural zooplankton (DG set, with *D. galeata* dominating), while the three enclosures of the second set were, besides natural lake zooplankton, additionally inoculated with *D. magna* (DM set, with 3000 ind. per bag).

These daphnids come from the laboratory clone maintained in the Department of Hydrobiology, University of Warsaw (Poland).

Zooplankton samples were collected every 1 to 4 days during three weeks with 1-l Patalas sampler from 5 random places at 1-m depth in each enclosure; they were filtered through 50 μm plankton net and preserved with 4% formalin, and then analyzed under dissecting microscope. The animals were determined to species, length of 20 individuals in sample was measured and the entire sample was counted, but a subsample was enumerated if there were >100 ind. The total zooplankton biomass was estimated from the numbers and length-weight regression relationships (Downing & Rigler, 1984). Similarly, the total community clearance rate was assessed, using the density data and individual clearance rate (Reynold, 1984).

As a measure of phytoplankton biomass, chlorophyll *a* concentration was determined spectrophotometrically, after acetone extraction (Golterman & Clymo, 1969), separately in the two seston fractions: below and above 50 μm . Concentration of phosphorus (SRP) was determined spectrophotometrically (Molybdenate Method); however, SRP was not detectable except for the day 11th when a concentration of about $5 \mu\text{g l}^{-1}$ was found in five of the six bags.

Results

The zooplankton biomass remained stable in both sets of enclosures for the first week of incubation; thereafter it increased rapidly, exceeding 0.7 mg DW l^{-1} of *D. magna* in the DG set, and 1.0 mg DW l^{-1} of *D. magna* in the DM set at the end of the experiment (Fig. 1). These increases in biomass were accompanied by a shift in zooplankton composition. After three weeks of incubation (Fig. 2) the share of rotifers in the density which had exceeded 90% of total zooplankton before the experiment declined dramatically to 18% and 10% in DG and DM enclosures, respectively. Simultaneously, the relative abundance of cladocerans increased from <1%

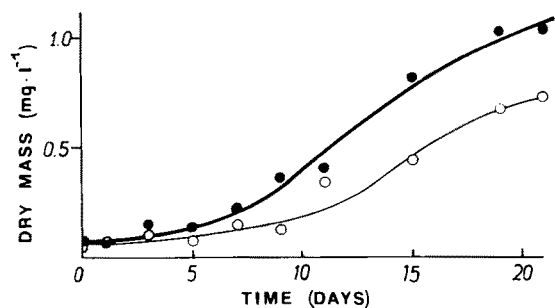


Fig. 1. A comparison of zooplankton biomass in the two types of enclosures: DG, containing lake zooplankton (open circles, thin line); and DM, with *Daphnia magna* (shaded circles, thick line).

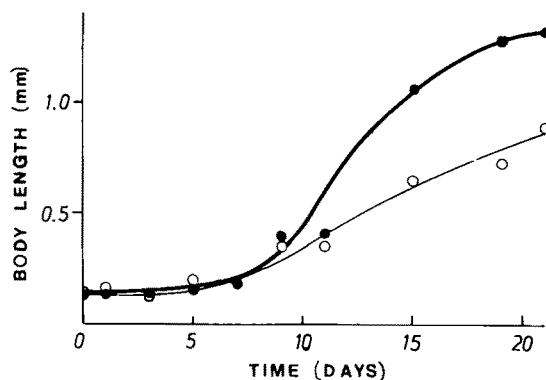


Fig. 3. Average individual body size in zooplankton in the enclosures DG and DM; for Fig. codes see Fig. 1.

to > 50% in DG and to almost 70% in DM set. Distinct domination, among the cladocerans, of *D. galeata* in DG set and of *D. magna* in DM set was observed after first week of incubation (Fig. 2).

A shift from small-sized zooplankton (rotifers) to large cladocerans resulted in the increase of the mean individual size of animals in the enclosures:

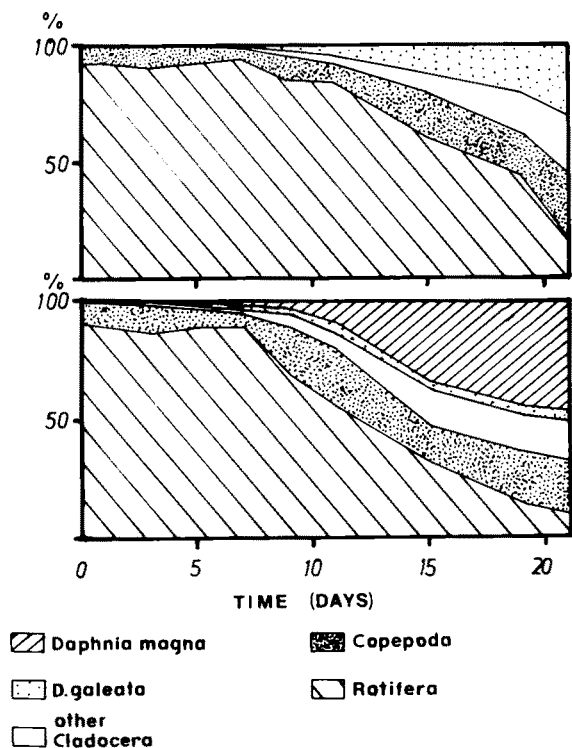


Fig. 2. The composition of zooplankton in the two types of enclosures: DG, top; and DM, bottom.

7-fold in DG set and 10-fold in DM set (Fig. 3). The increase in both the total zooplankton biomass and the mean size of planktonic herbivores led to an increase in community clearance rates in the enclosures, from the initial 10% to 60% d⁻¹ (DG) and over 100% d⁻¹ (DM) at the end of the experiment (Fig. 4). The increased community clearance rate should cause decrease in phytoplankton abundance. However, only in DM set of enclosures did the phytoplankton decrease. On the other hand total chlorophyll *a* concentration in DG set started increasing after the rapid decline in the first week of exposure (Fig. 5). This initial decline in both sets could not be attributed to zooplankton grazing, since neither did the herbivore zooplankton increase, nor did its composition change or its clearance rate increase in the first 7 days. Sedimentation of the algae inside the bags, due to decreased water

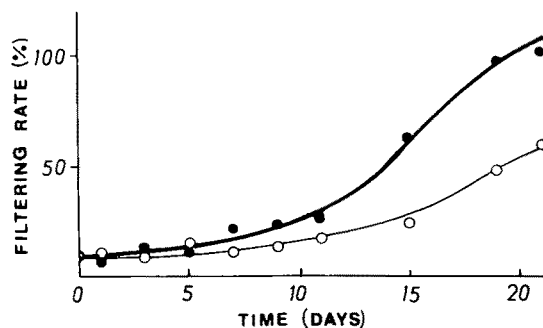


Fig. 4. Zooplankton filtering rates in the enclosures DG and DM; for Fig. codes see Fig. 1.

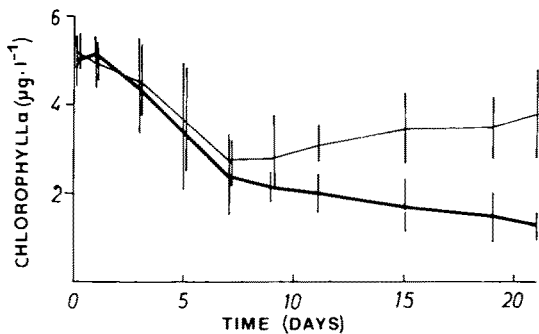


Fig. 5. Total chlorophyll-*a* concentration in the enclosures DG and DM; for Fig. codes see Fig. 1.

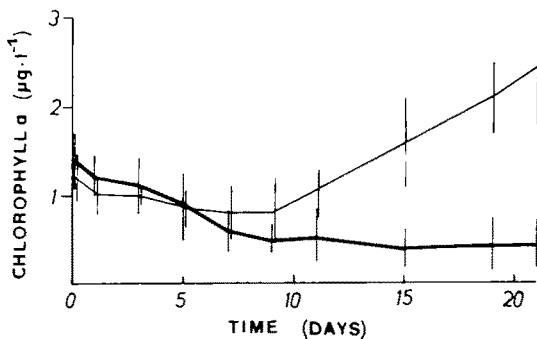


Fig. 6. Chlorophyll *a* concentration in algal fraction > 50 µm in the enclosures DG and DM; for Fig. codes see Fig. 1.

turbulence, most probably caused the observed decrease in phytoplankton biomass.

The growth of algal biomass in DG enclosures, after 9th day of incubation was related to the increase in net phytoplankton (Fig. 6). The biomass of net algae in DM enclosures remained low, < 0.5 µg Chl-*a* l⁻¹.

Discussion

Changes in the density and biomass of zooplankton, relieved of predation by fish in isolated enclosures, were in accordance with the theoretical assumptions of biomanipulation approach. The rapid increase in zooplankton biomass, as reflected in the increase of mean individual body size of herbivores, should intensify herbivore grazing pressure on phytoplankton. An increased

rate of algal biomass elimination, however, was restricted to bags containing large *D. magna*. On the contrary, the enclosures with natural lake zooplankton, total phytoplankton biomass increased, the algal populations being under relatively weak grazing pressure of herbivores. Despite the weak pressure of herbivores, however, the severe P limitation did not allow for the observed growth in phytoplankton biomass. Moreover, biomass of nano-phytoplankton was decreasing which suggests that at least the nano-phytoplankton was controlled by herbivores. Only the inedible net phytoplankton biomass increased. Apparently, the net phytoplankton in the absence of large filter-feeders, thus relieved of their grazing pressure, benefits from pool of nutrients (P, N) regenerated from nanoplanktonic algae on which small-sized zooplankton feed. This mechanism is probably of paramount importance especially under the severe P limitation, when virtually all the P available for primary production comes from zooplankton regeneration (Hargrave & Geen, 1968; Lehman, 1980a, 1980b).

Unlike small herbivore grazers, *D. magna* feeding is not restricted to the smallest particles within the phytoplankton size range, but it can ingest algal filaments up to about 240 µm long (Dawidowicz *et al.*, 1988). Even a low elimination rate of net algae is enough to prevent their increase in numbers and biomass, in view of their low reproduction and growth rates compared with nanophytoplankton (Reynolds, 1984).

In this experiment, *D. magna* appeared to be able to keep in check the net phytoplankton. However, the initial density of net algae was low, and the share of filamentous blue-greens in phytoplankton negligible. Obviously, *D. magna* will be much less efficient if densities of blue-greens are high because these densities will interfere with filtering processes and thus inhibit the filtering rate of large cladocerans which in turn will adversely affect the reproduction as well as population growth rates (Gliwicz, 1977; Webster & Peters, 1978; Gliwicz & Siedlar, 1980; Dawidowicz *et al.*, 1988). Concluding: first, the effectiveness of biomanipulation measures may

be questionable in highly eutrophic water bodies, since large cladocerans will be inhibited by filamentous blue-green algae; second, small cladocerans which can neither utilize net plankton, nor are they very sensitive to interference by blue-greens, will stimulate the growth of net algal populations, if grazing can significantly compensate for the nutrients in limiting supply.

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