Influence of two *Daphnia* species on summer phytoplankton assemblages from eutrophic lakes

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Abstract. We conducted grazing experiments to test whether larger-bodied *Daphnia pulicaria* have a different effect from smaller-bodied *Daphnia galeata mendotae* on the composition of summer algal assemblages in eutrophic lakes. Three separate cubitainer experiments were run for 5 days in a replicated factorial design utilizing two algal community types and the two *Daphnia* species. Inorganic phosphorus and nitrogen were added to prevent nutrient limitation of the algae. Both edible and inedible size fractions of chlorophyll *a* increased in cubitainers without *Daphnia* spp. Grazer addition usually resulted in a reduction in edible chlorophyll; reductions were greater in *D. pulicaria* cubitainers. Grazing by *Daphnia* spp. on presumed inedible chlorophyll was variable. Algal size was not always a good predictor of grazeability. The results of this study indicate that *D. pulicaria*, because of its greater filtration potential and ability to ingest larger particles, provides a stronger control on inedible-sized algae when compared to equal numerical densities of *D. g. mendotae*. However, *Aphanizomenon* increased as a response to heavy grazing pressure by *D. pulicaria* on other algal species. This suggests that biomanipulation efforts that promote large-bodied *Daphnia* may not produce desirable results if nutrient inputs remain high.

Introduction

Inorganic nutrients are of primary importance to the production and biomass of phytoplankton in standing fresh waters (Ohle, 1953; Rodhe, 1958; Vollenweider, 1976; Schindler, 1977). Herbivorous grazing, in contrast, is considered to be one of the major loss processes of phytoplankton (e.g. Uhlnmann, 1954; Nauwerk, 1963; McKauley and Kalff, 1981; Pace, 1984; McQueen *et al.*, 1986; Carpenter and Kitchell, 1988; Cyr and Pace, 1992). However, more recent investigations have shown that the interactions between nutrients, phytoplankton and grazers are largely influenced by food web structure (Benndorf, 1988; Gulati *et al.*, 1990; Carpenter and Kitchell, 1993; Schindler *et al.*, 1993). Moreover, this relationship is modified by levels of nutrient loading and in-lake concentrations (Olsen and Willen, 1980; Benndorf, 1990; Elser and Goldman, 1991; Vanni *et al.*, 1992; Koschel *et al.*, 1993). Depending on the degree of nutrient limitation and the structure of the phytoplankton and herbivore community, grazing may have either an inhibiting or an enhancing effect on the algae (Bergquist and Carpenter, 1986). Nevertheless, zooplankton filtration rates of ≥0.3–0.4 day\(^{-1}\) have been shown to reduce the biomass in many phytoplankton communities (Reynolds, 1984a). *Daphnia* spp. were often found to be the most powerful filter feeders within the community of herbivorous zooplankton (Morgan *et al.*, 1980; Sterner, 1989; Vanni and Temte, 1990).
Food-uptake mechanisms in planktonic animals are diverse, spanning the range from highly selective to non-selective feeders (Joergensen, 1966). *Daphnia* is considered to be non-selective (Kasprzak et al., 1986) but, even in this genus, a number of factors modify the resource-consumer relationship (Knoechel and Holtby, 1986a; Lampert, 1987). Gliwicz (1977) has shown that if particles are beyond the range of availability, a selection is imposed, even on obligate filter feeders like *Daphnia*. Nevertheless, whether a particle can be filtered from the ambient suspension and subsequently ingested is first a function of its size (Burns, 1968). Particles ≤20 μm are usually particularly ingestible, whereas those ≥50–60 μm are not. For the remaining size range of particles (20–50 μm), ingestibility largely depends on the shape of the algae (greatest axial linear dimension; Reynolds, 1984a).

Several authors have shown that filamentous algae, especially blue-green filaments, and large colonies of algae such as *Microcystis*, tend to impair the filtration potential of *Daphnia* (e.g. Webster and Peters, 1978; Gliwicz and Siedlar, 1980; Thompson et al., 1982; Pearl, 1988). Therefore, *Daphnia* is not able to reverse the dominance of an established population of larger *Microcystis* or filamentous blue-green algae (Davidowicz et al., 1988). On the other hand, investigations of *Daphnia* gut contents have sometimes revealed surprisingly large particles, indicating that these animals are also able to graze on the so-called ‘canopy species’ (Horn, 1981; Vyhnalet, 1983; Sommer et al., 1986; Sarnelle, 1992; Epp, 1996). However, differences in grazing potential between small and large *Daphnia* may be significant.

Most of the experimental work on phytoplankton–grazing interactions was carried out in oligotrophic or mesotrophic systems (e.g. Lehman and Sandgren, 1985; Bergquist and Carpenter, 1986; Elser and Goldman, 1991). This paper, however, concentrates on the grazing influence of *Daphnia pulicaria* and *Daphnia galeata mendotae* on summer phytoplankton assemblages of eutrophic lakes. Both *Daphnia* species are found in many northern eutrophic US lakes. Their relative dominance during the spring clear-water phase and into the early summer months appears to be controlled by the degree of planktivory (Luecke et al., 1992; Rudstam et al., 1993; Lathrop et al., 1996). While both species have similar carapace length, *D. pulicaria*, with a much greater body mass, only dominates when planktivory is low. Promoting the dominance of *D. pulicaria* (and the similar *Daphnia pulex*) is often the desired outcome of biomanipulation to reduce the summer algal problems in lakes (Shapiro et al., 1975; Benndorf, 1988; Gulati et al., 1990; Kitchell, 1992). Our interest was in evaluating the differential grazing impacts of *D.pulicaria* and *D.g.mendotae* on phytoplankton as they develop from the clear-water phase into the summer bloom. Special emphasis was placed on those groups or genera of algae that are considered resistant to grazing. The majority of these algae may not be avoided except on the basis of size. If they are small enough relative to the size of grazers, they are liable to be consumed.

**Method**

The experimental design followed an idea developed by Lehman and Sandgren (1985). Three separate grazing experiments (*C₁*, *C₂*, *C₃*) were carried out in 20 l
Influence of two *Daphnia* on phytoplankton assemblages

translucent plastic bags (cubitainers) suspended in the littoral zone of Lake Mendota at a depth of approximately one-half of incident solar radiation and water temperatures of ~25°C. Each experiment ran for 5 days in the summer of 1996 (Table I). Six eutrophic lakes in southeastern Wisconsin, USA, served as sources for natural phytoplankton assemblages, *D.pulicaria* (*Dpul*) and *D.g.mendotae* (*Dgm*). In all three experiments, Pike Lake was selected as a source of filamentous algae dominated by *Aphanizomenon*. Lake Marie, Lake Wingra and Silver Lake were chosen because their phytoplankton was characterized by non-filamentous forms. *Daphnia* spp. was taken from Pike Lake, Lake Mendota and Lake Ripley.

This phytoplankton was exposed to *Daphnia* grazing at three different stages in the summer algal development: (i) middle of the clear-water phase; (ii) transition stage between the clear-water phase and summer bloom; (iii) and summer bloom, respectively. In order to remove most of the crustacean zooplankton, the test water was filtered through a 350 μm screen. Microscopic analysis confirmed that the composition of phytoplankton was not changed by screening.

To prevent nutrient limitation of the phytoplankton and to exclude the influence of their various mechanisms of nutrient recycling due to grazing, the cubitainers were supplemented with dissolved inorganic phosphorus (DIP, KH₂PO₄) and nitrogen (DIN, NH₄NO₃). The nitrogen addition amounted to 300 μg N l⁻¹. The phosphorus addition was 100 μg P l⁻¹ in experiment C₁, and 200 mg

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**Table I. Schematic representation of the treatments**

<table>
<thead>
<tr>
<th>Exp. no.</th>
<th>Date</th>
<th>Phytoplankton source lake</th>
<th>Daphnia source lake</th>
<th>Treatments</th>
</tr>
</thead>
<tbody>
<tr>
<td>C₁</td>
<td>15-20.06.96</td>
<td>Pike Lake</td>
<td><em>D.pulicaria</em></td>
<td>C₁/Pike/N</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lake Mendota</td>
<td>C₁/Pike/N/Dgm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>D.g.mendotae</em></td>
<td>C₁/Pike/N/Dpul</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Pike Lake</em></td>
<td>C₁/Marie/N</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lake Marie</td>
<td><em>D.pulicaria</em></td>
<td>C₁/Marie/N/Dgm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lake Mendota</td>
<td>C₁/Marie/N/Dpul</td>
</tr>
<tr>
<td>C₂</td>
<td>30.06-0.5.07.96</td>
<td>Pike Lake</td>
<td><em>D.pulicaria</em></td>
<td>C₂/Pike/N</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lake Mendota</td>
<td>C₂/Pike/N/Dgm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>D.g.mendotae</em></td>
<td>C₂/Pike/N/Dpul</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Pike Lake</em></td>
<td>C₂/Wingra/N</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lake Wingra</td>
<td><em>D.pulicaria</em></td>
<td>C₂/Wingra/N/Dgm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lake Mendota</td>
<td>C₂/Wingra/N/Dpul</td>
</tr>
<tr>
<td>C₃</td>
<td>21-26.08.96</td>
<td>Pike Lake</td>
<td><em>D.pulicaria</em></td>
<td>C₃/Pike/N</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lake Mendota</td>
<td>C₃/Pike/N/Dgm</td>
</tr>
<tr>
<td></td>
<td>27.08-01.09.96</td>
<td></td>
<td><em>D.g.mendotae</em></td>
<td>C₃/Pike/N/Dpul</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Pike Lake</em></td>
<td>C₃/Silver/N</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Silver Lake</em></td>
<td>C₃/Silver/N/Dgm</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>D.g.mendotae</em></td>
<td>C₃/Silver/N/Dpul</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Pike Lake</em></td>
<td></td>
</tr>
</tbody>
</table>

N, nutrients added; *Dgm, D.g.mendotae* added; *Dpul, D.pulicaria* added. All experiments were run in triplicates.
P l⁻¹ in C₁ and C₃. DIP and DIN analyses were performed at the State Laboratory of Hygiene in Madison using widely accepted procedures.

In order to obtain a sufficiently high grazing rate, a Daphnia concentration of ~40–50 ind. l⁻¹ was intended. For that reason, the density of the particular population in each of the Daphnia source lakes was estimated 1 day prior to the experiment using a 30 cm diameter Wisconsin plankton net of 350 μm mesh size. The next day, an appropriate number of animals was sampled by vertical net hauls, put into a bucket, gently stirred and then added to the cubitainers. Microscopic inspection showed that there were only a few copepods and other cladocerans in the Daphnia inocula.

After the termination of the three experiments, all cubitainers were individually processed. Daphnia were separated from the water using the same 350 μm net, fixed with a buffered formalin–sugar mixture, and stored for later counting. A phytoplankton sample fixed with glutaraldehyde was also taken.

To measure the chlorophyll (Chl) a concentration of the samples, an appropriate volume of water was filtered through glass fiber filters (Gelman Scientific) and cold-extracted in methanol for at least 2 weeks. The measurement was made using a Turner Model 450 fluorometer. Calibration was performed using Anacystis nidulans Chl a extracts (Sigma Chemical Co.). Pheopigments were estimated following acidification of the samples. Using a screen, edible Chl a was estimated in the particle fraction ≤35 μm, whereas total Chl a was determined in the untreated sample. Supposedly inedible Chl a was calculated by subtracting edible from total Chl a.

For the Daphnia treatments, the volume containing ~100 individuals was counted and their size measured. In the nutrient-only treatments, triplicate 25 ml samples were counted to confirm the low crustacean densities. Daphnia body mass was calculated according to published length–dry weight relationships (Lynch et al., 1986).

**D.g.mendotae:**

\[
\text{DW (μg)} = 5.48 \, L \text{ (mm)}^{2.200}
\]

**D.pulicaria:**

\[
\text{DW (μg)} = 10.67 \, L \text{ (mm)}^{2.093}
\]

The Daphnia filtration potential in each cubitainer was calculated using a model developed by Peters and Downing (1984). The mean maximum size of particles that can be ingested by either D.pulicaria (MPP) or D.g.mendotae (MPG) was calculated according to Burns (1968).

The abundance and size structure (greatest axial linear dimension, GALD; Lehman and Sandgren, 1985) of the phytoplankton were determined using an inverted microscope following the technique of Utermöhl (1958). To get a good estimate of the number and size distribution of the phytoplankton community assemblage, the GALD of individual cells, colonies, and filaments was usually determined until the standard error was ≤10% of the mean GALD. The size distribution of algae was estimated in a sample taken from the source lake at the beginning of the experiment and in the cubitainers at the end of each of the experiments. Algal identification followed Prescott (1970).
Results

Nutrients

Excess concentrations of DIP and DIN after the termination of experiment C1 indicated that nutrient limitation did not occur (Table II). Concentration differences between nutrient-alone and nutrient-grazer treatments were relatively small, indicating that recycling due to grazing and/or uptake by different phytoplankton biomass were negligible in comparison to the amount of nutrients added. In experiment C2, about two-thirds of the added DIP and again one-third of the DIN were taken up by the Pike Lake seston. DIP and DIN were undetectable in C2/Wingra nutrient-alone treatments, indicating that nutrient limitation may have occurred by the end of the experiment. In both C2/Pike and C2/Wingra cubitainers with Daphnia, measurable amounts of DIP and DIN remained, most likely as a result of recycling due to grazing or less uptake as a consequence of lower phytoplankton biomass. In experiment C3, the same amount of DIP and DIN as in treatment C1 was added, but no nutrient measurements were made at the end of the experiment.

Daphnia

The number of Daphnia found in the cubitainers of experiments C1, C2 and C3/Pike was similar within the triplicates as well as between the experimental sets (Figure 1, Table III). However, the abundance of Daphnia spp. in C3/Silver was ~25 ind. l⁻¹, which was much lower than intended.

While the numerical densities of the two Daphnia species added to the cubitainers were relatively similar, D.pulicaria biomasses were always much larger because of that species’ greater weight per unit length. Because individual

Table II. Nutrient addition and concentration in the cubitainer experiments (μg l⁻¹)

<table>
<thead>
<tr>
<th>No. of experiment/nutrient</th>
<th>Add</th>
<th>Nut</th>
<th>Nut/Dp</th>
<th>Nut/Dg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1/Pike</td>
<td>200</td>
<td>104</td>
<td>104</td>
<td>127</td>
</tr>
<tr>
<td>C1/Marie</td>
<td>200</td>
<td>136</td>
<td>128</td>
<td>154</td>
</tr>
<tr>
<td>C2/Pike</td>
<td>100</td>
<td>17</td>
<td>37</td>
<td>34</td>
</tr>
<tr>
<td>C2/Wingra</td>
<td>100</td>
<td>&lt;2</td>
<td>28</td>
<td>5</td>
</tr>
<tr>
<td>C3/Pike</td>
<td>200</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C3/Silver</td>
<td>200</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Nitrogen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1/Pike</td>
<td>300</td>
<td>162</td>
<td>137</td>
<td>204</td>
</tr>
<tr>
<td>C1/Marie</td>
<td>300</td>
<td>160</td>
<td>144</td>
<td>191</td>
</tr>
<tr>
<td>C2/Pike</td>
<td>300</td>
<td>160</td>
<td>227</td>
<td>228</td>
</tr>
<tr>
<td>C2/Wingra</td>
<td>300</td>
<td>&lt;2</td>
<td>103</td>
<td>62</td>
</tr>
<tr>
<td>C3/Pike</td>
<td>300</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C3/Silver</td>
<td>300</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

add, amount of added nutrients; Nut, concentration in the nutrient treatment; Nut/Dp, concentration in the D.pulicaria treatment; Nut/Dg, concentration in the D.g.mendoitae treatment. Phosphorus was added as KH₂PO₄, nitrogen was added as NH₄NO₃.
Biomass is one of the major factors in the filtration rate model used, the filtration potential in *Dgm* cubitainers was lower than in *Dpul* treatments.

**Chlorophyll a**

In the nutrient-only treatments, nutrient addition was followed by a strong increase in Chl *a* relative to concentrations found in each lake at the beginning of the experiments (Figure 2). This response was especially pronounced for edible Chl *a*, but the inedible fraction also increased to varying degrees. Other than these general patterns, the increase in inedible Chl *a* in *C*2/Wingra/N was especially pronounced. In addition, the relatively low concentration of edible Chl *a* in this experiment was most likely due to contamination of these cubitainers with *Dgm*. With the exception of *C*2/Wingra/N (*Daphnia* contamination), there was a clear increase in the edible/inedible Chl *a* ratio in *C*1 and *C*2, whereas little change was found in *C*3 (Figure 3).
Table III. Characterization of Daphnia in the cubitainer experiments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Daphnia (ind. l⁻¹)</th>
<th>Mean size (mm)</th>
<th>MPP/MPG (μm)</th>
<th>Biomass (μg DW ind.⁻¹)</th>
<th>Biomass (μg DW l⁻¹)</th>
<th>Filtr. pot. (ml l⁻¹ day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C₃/Pike/Dₚ</td>
<td>49 (6)</td>
<td>1.33 (0.15)</td>
<td>34</td>
<td>19.4 (4.6)</td>
<td>952 (111)</td>
<td>859 (97)</td>
</tr>
<tr>
<td>C₃/Pike/D₃g</td>
<td>40 (13)</td>
<td>1.14 (0.26)</td>
<td>34</td>
<td>7.5 (3.5)</td>
<td>287 (70)</td>
<td>246 (36)</td>
</tr>
<tr>
<td>C₃/Marie/Dₚ</td>
<td>55 (4)</td>
<td>1.29 (0.15)</td>
<td>33</td>
<td>18.3 (4.3)</td>
<td>1010 (308)</td>
<td>1351 (515)</td>
</tr>
<tr>
<td>C₃/Marie/D₃g</td>
<td>41 (23)</td>
<td>1.08 (0.02)</td>
<td>29</td>
<td>6.5 (0.2)</td>
<td>266 (153)</td>
<td>331 (206)</td>
</tr>
<tr>
<td>C₃/Wingra/Dₚ</td>
<td>67 (6)</td>
<td>1.62 (0.15)</td>
<td>41</td>
<td>29.4 (5.7)</td>
<td>1996 (558)</td>
<td>1298 (117)</td>
</tr>
<tr>
<td>C₃/Wingra/D₃g</td>
<td>52 (5)</td>
<td>1.14 (0.04)</td>
<td>30</td>
<td>7.3 (0.6)</td>
<td>381 (17)</td>
<td>336 (29)</td>
</tr>
<tr>
<td>C₃/Silver/Dₚ</td>
<td>63 (2)</td>
<td>1.50 (0.15)</td>
<td>38</td>
<td>25.0 (5.6)</td>
<td>1572 (365)</td>
<td>788 (294)</td>
</tr>
<tr>
<td>C₃/Silver/D₃g</td>
<td>76 (10)</td>
<td>1.11 (0.06)</td>
<td>29</td>
<td>6.9 (0.8)</td>
<td>521 (64)</td>
<td>294 (43)</td>
</tr>
<tr>
<td>C₄/Pike/Dₚ</td>
<td>55 (13)</td>
<td>1.31 (0.08)</td>
<td>34</td>
<td>18.8 (2.3)</td>
<td>1044 (298)</td>
<td>564 (240)</td>
</tr>
<tr>
<td>C₄/Pike/D₃g</td>
<td>51 (10)</td>
<td>1.34 (0.00)</td>
<td>34</td>
<td>10.4 (0.0)</td>
<td>526 (104)</td>
<td>353 (83)</td>
</tr>
<tr>
<td>C₄/Silver/Dₚ</td>
<td>26 (2)</td>
<td>1.55 (0.07)</td>
<td>39</td>
<td>26.8 (2.7)</td>
<td>701 (29)</td>
<td>480 (190)</td>
</tr>
<tr>
<td>C₄/Silver/D₃g</td>
<td>24 (5)</td>
<td>1.20 (0.00)</td>
<td>31</td>
<td>8.1 (0.0)</td>
<td>191 (40)</td>
<td>185 (67)</td>
</tr>
</tbody>
</table>

MPP/MPG, mean maximum particle size ingestible by D.pulicaria and D.mendotae calculated according to Burns (1968); filtr. pot., filtration potential calculated according to Peters and Downing (1984). Individual biomass was calculated according to Lynch et al. (1986), numbers in parentheses are 95% CL.

Addition of both nutrients and Daphnia to the cubitainers led to three general results (Figure 2). By comparison with the nutrient-only treatment, both Daphnia species in experiment C, compensated for almost all the growth of edible algae. The inedible Chl a concentration was lower in the Dpul than in the Dgm treatments, which were similar to the nutrient-only concentrations. This suggests that D.pulicaria was grazing inedible-sized algae. In C₂, the pattern was different. Both species of Daphnia were able to keep the edible fraction of Chl a under control. Inedible Chl a remained unchanged in the C₂/Pike experiment, but D.pulicaria suppressed inedible Chl a in C₂/Wingra. In C₃ another pattern was observed. Both Daphnia species were not able to control the growth of either chlorophyll fraction in C₃/Pike, whereas only edible Chl a was reduced in C₃/Silver. In general, herbivore addition usually resulted in an increased ratio of edible/inedible Chl a with no consistent difference between Dpul and Dgm treatments (Figure 3).

The pooled data from all D.pulicaria experiments indicated a tendency toward a decreasing concentration of inedible Chl a with increasing Daphnia filtration potential (Figure 4). The probability of having high concentrations of inedible Chl a is rather low at a filtration potential >800 ml l⁻¹ day⁻¹. Nevertheless, the slope was found to be not significant. Filtration potential and edible Chl a showed a clear and significant inverse relationship (r² = 0.668, P < 0.001). The same was true for the ratio edible/inedible Chl a (r² = 0.338, P < 0.002), i.e. the share of the edible fraction decreased with higher filtration intensity.

There was no significant relationship between the filtration potential of D.mendotae and inedible Chl a (Figure 4). The concentration of edible Chl a, however, was significantly reduced by grazing (P < 0.001). Less of the Chl a variability was explained by grazing in the Dgm treatments (r² = 0.484) than in the Dpul treatments. If the results of the nutrient-only treatments were excluded.
Fig. 2. Concentrations of edible and inedible Chl a in experiments C₁, C₂ and C₃. Sources of the algal assemblages were Pike Lake, Lake Marie, Lake Wingra and Silver Lake. N, nutrient-only treatments; Dp, Dg, nutrient addition and D.pulicaria or D.g.mendotae addition, respectively. Vertical bars are 95% confidence limits.

from the regression analysis of Dgm treatments, no significant relationship due to increased filtration potential was found. Grazing by D.g.mendotae significantly changed the ratio of edible/inedible Chl a ($r^2 = 0.3856$, $P < 0.001$).

Algal groups

Some examples of the response of different groups and genera of phytoplankton to nutrient addition and grazing are summarized in Figures 5 and 6. The size distributions of Microcystis colonies in the source lake sample at the beginning of the experiment and in the nutrient-only treatment of C₂/Wingra at the end of the experiment were completely different from the mean maximum particle sizes.
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Fig. 3. Percentage of edible and inedible Chl *a* in experiments C₁ and C₃. The x-axis indicates the source lakes of the phytoplankton assemblages and the treatments. N, nutrients; Dp, nutrients plus *D.pulicaria*; Dg, nutrient plus *D.g.mendotae*.

(Burns, 1968) ingestible by *D.pulicaria* (MPP) or *D.g.mendotae* (MPG; Figure 5). On the other hand, there was a clear overlap between the size of the colonies and MPP and MPG, respectively, in the *Daphnia* treatments, indicating that parts of the algal population should have been grazeable. Compared to the lake sample, *Microcystis* concentrations in experiment C₂ increased as a response to nutrient addition when no grazers were added. It seems that by grazing, *D.pulicaria* was able to compensate for part of this growth, although the differences between the two treatments were not significant. However, algal densities were greater in the Dgm treatments than in the nutrient-alone treatments. The difference in algal densities between the Dgm and the Dpul treatments was even more striking. While *D.pulicaria* suppressed the growth of *Microcystis*, *D.g.mendotae* enhanced its growth.

In experiment C₃/Silver, the situation differed (Figure 5). The mean size of *Microcystis* colonies in the lake sample and in the nutrient-only treatments was smaller than in both *Daphnia* treatments. Moreover, there were remarkable differences in colony size distribution. Only *Microcystis* in the Dgm treatments and MPG were found to overlap. Although variability was high, nutrient addition
again enhanced the growth of the alga, but this time grazing by both *D. pulicaria* and *D. g. mendotae* totally compensated for the increase.

*Aphanizomenon* in C1/Pike had shorter filaments in both *Daphnia* treatments than in the lake sample (Figure 5). MPP and MPG overlapped very little with the size of the algae in the grazer-containing cubitainers. Nutrient addition had no significant effect on the growth of *Aphanizomenon*. *Daphnia pulicaria* was able to decrease the abundance of the *Aphanizomenon* by~50% of that of the nutrient-only treatments. *Daphnia g. mendotae* did not influence *Aphanizomenon* densities.

In C2/Wingra, a similar pattern in size distribution of *Aphanizomenon*, MPP and MPG was found. Nevertheless, the results in abundance were completely different (Figure 5). Nutrient addition alone had a negative effect on *Aphanizomenon*; the species virtually disappeared in the cubitainers. In combination with *D. pulicaria*, however, *Aphanizomenon* clearly increased in density. The influence of *D. g. mendotae* was again insignificant.

The size distributions of *Ankyra*, MPP and MPG in C1/Pike obviously overlapped (Figure 6). Moreover, the algae in the grazer cubitainers were much smaller compared to those in the nutrient-only treatments. Nutrient addition caused no effect on the abundance of *Ankyra*, whereas *Daphnia* grazing clearly stimulated the alga. *Daphnia pulicaria* had the strongest enhancing effect.
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The size distribution of gelatinous green algae, MPP and MPG overlapped completely, as shown by the example of C2/Wingra (Figure 6). Nutrient addition showed an insignificant increase in algal concentration. Both *D.pulicaria* as well as *D.g.mendotae* decreased algal densities.

The size distributions of *Melosira*, MPP and MPG are completely different (Figure 6). Nutrient addition caused remarkable growth. Only *D.pulicaria* decreased algal densities. The same pattern was true for *Fragilaria* in C2/Wingra, except that the reduction by *D.g.mendotae* was also significant (Figure 6).

**Discussion**

The addition of nutrients was always followed by an increase in the concentration of edible Chl a, which is in good agreement with many other field and laboratory investigations (Figure 2; e.g. Schindler and Fee, 1974; Lund and Reynolds, 1982; Koschel and Scheffler, 1985; Bergquist and Carpenter, 1986; Harris, 1986; Schindler, 1990). However, this may not apply to all populations of all species at all times. Species not limited by nutrients will not react to an increased supply (Olsen and Willen, 1980; Vyhnalek, 1983; Lehman and Sandgren, 1985). Nutrients also stimulated growth of inedible Chl a, though the enhancement was usually less pronounced. Larger phytoplankton tend to grow at a lower rate, perhaps because of a lower surface to volume ratio (Banse, 1976; McCauley and Briand, 1979; Reynolds, 1984b). This factor may explain why some investigators found inedible phytoplankton not to benefit greatly from increasing nutrient concentrations (Watson and McCauley, 1988; Watson et al., 1992). The short duration of the experiments and the restriction of water movement to within the cubitainers may have enhanced this tendency by providing better growing conditions to small algae and by selective sedimentation in disfavor of large phytoplankton (Bloesch and Buergi, 1989).

The increase in inedible Chl a showed remarkable differences between the three single experiments (Figures 2 and 3). One reason may have been the size and the composition of the inoculum. The results indicated a tendency towards higher concentrations of inedible Chl a when the percentage in the lake sample (source of the inoculum) was high as well.

Another aspect is the seasonal development of natural phytoplankton communities in eutrophic lakes. According to the ‘PEG-model’ of phytoplankton succession, the period immediately after the clear-water phase is commonly characterized by colonial green algae followed in many cases by filamentous cyanobacteria (Sommer et al., 1986). Both of these algal groups are known to be relatively non-digestible, non-ingestible, or both (Porter, 1976; Gliwicz and Siedlar, 1980). The inoculum of C2/Wingra (Figure 6), for instance, had the highest abundance of gelatinous green algae found in all experiments. They responded to nutrient addition but were also able to withstand high grazing pressure. *Aphanizomenon* was below detection level in the nutrient treatment, but grew well in the presence of grazers (Figure 5).

For edible Chl a, nutrient addition in the presence of grazers led to the expected results in experiments C1 and C2 (Figures 2 and 3). *Daphnia pulicaria* and
Figs 5 and 6. Size distribution (greatest axial linear dimension, GALD) and abundance development of groups and genera in the cubitainer experiments. Lake, size distribution in the source lake sample at the beginning of the experiment; N, size distribution in the nutrient-only treatments at the end of the experiment; Dp, size distribution in the nutrients plus *D.pulicaria* treatments at the end of the experiment; Dg, size distribution in the nutrients plus *D.g.mendotae* treatments at the end of the experiment. Vertical bars indicate 1.5 times the standard deviation of the mean. MPP and MPG, mean maximum ingestible particle size by *D.pulicaria* and *D.g.mendotae*, respectively, calculated according to Burns (1968). Vertical bars indicate 95% confidence limits.

*D.g.mendotae* grazed heavily on this fraction. However, this was not true for *C3/Pike* or, to some extent, for *C3/Silver*. Here again, seasonal differences in the composition of edible phytoplankton may explain the differences. *Daphnia* grazing may cause rapid shifts within the phytoplankton community, resulting in the dominance of ingestible but non-digestible algae (Kerfoot et al., 1988).

The influence of *Daphnia* grazing on inedible Chl *a* showed almost all combinations of possible results. Nevertheless, there seems to be a seasonal trend in the
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results (Figures 2 and 3). Experiment C₁ occurred during the clear-water phase. At that time, inedible algae did not grow very much. Consequently, there was not much available to *Daphnia*, although some difference was found between the *Dpul* and *Dgm* treatment. Later, during experiment C₂, which was run near the end of the clear-water phase, inedible algae played a much bigger role, but at least *D.pulicaria* was able to offset some of the algal growth. Finally, in experiment C₃, which was carried out in the middle of the summer bloom, both daphnids stimulated the development of inedible Chl a, possibly through the elimination of competition from smaller, faster growing algae. This time-dependent development is also in agreement with the existing literature (Pace, 1984; Buergi et al., 1985; Lehman and Sandgren, 1985; Bergquist and Carpenter, 1986; Sommer et al., 1986; Elser and McKay, 1989; Vanni and Temte, 1990).
As a general result of this investigation, *D. pulicaria* was found to have a stronger negative influence on the concentration of edible Chl a and on the edible/inedible ratio. A smaller effect was found for *D. g. mendotae*, although the concentration of animals and their length were similar to the *D. pulicaria* treatments. Therefore, it remains uncertain whether this difference was a property of the species or simply a consequence of biomass and allometry (Figures 2–4).

As shown by the length–dry weight relationships, *D. g. mendotae* at a given size has a much smaller individual biomass than *D. pulicaria* (Lynch et al., 1986). Because biomass is a major factor in the filtration rate model used, higher filtration potential was calculated for the *D. pulicaria* treatments (Peters and Downing, 1984). Although filtration of planktonic animals was found to be notoriously variable, size-dependent rate models may provide a basis for comparison (Peters, 1983; Knoechel and Holtby, 1986a). However, Lampert (1988) has shown remarkable differences between model calculations and *in situ* measurements of community filtration rates (see also Cyr and Pace, 1993).

Burns (1969a), using a suspension of different sized plastic beads, found a very similar distribution of particle sizes ingested by both species. Morgan et al. (1980) indicated a maximum ingestible particle size of 35 and 40 μm for *D. g. mendotae* and *D. pulicaria*, respectively. Kasprzak et al. (1986) found no size-selective grazing of *D. pulicaria* in a mixture of big and small *Chlamydomonas geitleri*. Burns (1969b), however, refers to higher specific filtration rates in *D. g. mendotae*. Because she found almost no differences in size-specific body weight between the two species, the same is true for the absolute clearance rate. In eutrophic Lake Mendota, substantially lower phytoplankton biomass and clearer water occurred in years when *D. pulicaria* and not *D. g. mendotae* dominated the crustacean plankton (Lathrop and Carpenter, 1992; Lathrop et al., 1996).

Body size is generally considered to be a good predictor of the maximum particle size ingested as well as the filtration rate of cladocerans (Geller, 1975; Hopp and Horn, 1984; Pace, 1984; Schoenberg and Carlson, 1984; Knoechel and Holtby, 1986b; Sterner, 1989). The upper limits of ingestible particle size for either species, calculated according to Burns (1968), indicate maximum differences of 5 μm in experiment C₁, 10 μm in C₂ and 8 μm in C₃. Especially in C₂, *D. pulicaria* could take particles larger than 35 μm, the supposed threshold of inedibility, whereas the maximum size ingestible by *D. g. mendotae* was always lower than this. Therefore, different abilities to ingest larger particles may explain at least some of the differences found.

Another factor is the metabolic rate, as influenced by the above-mentioned size-dependent biomass difference in both species. Given a body size of 1 mm, *D. g. mendotae* has a dry weight of 5.5 μg compared to 10.7 μg in *D. pulicaria*. According to Konoplev et al. (1978; quoted in Peters, 1983), this is equivalent to a difference in metabolic rate of ~1.71. Because metabolism is in close correlation with food uptake (Lampert, 1977), the higher metabolic demands in *D. pulicaria* may be another reason for its greater influence on phytoplankton.

Nevertheless, Reynolds (1984a) indicated community filtration rates >0.3 day⁻¹ to be critical for grazeable phytoplankton. *Daphnia g. mendotae* clearly exceeds this level; therefore, the missing relationship between filtration potential and Chl
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A concentration within the group of grazing treatments (~100–480 ml l⁻¹ day⁻¹) is still somewhat surprising. One reason might be that some small grazeable algae can grow much faster than 0.3 day⁻¹.

The different results of *Daphnia* grazing concerning the fractions of edible and inedible Chl a are not necessarily reflected at the level of genera and groups (Figures 5 and 6). Compared to copepods, *Daphnia* is considered to be a non-selective grazer (Joergensen, 1966; DeMott and Moxter, 1991). Therefore, one of the major prerequisites making an alga grazeable and ingestible to this group of animals is size (Sterner, 1989). Other factors are also important (reviewed by Lampert, 1987).

The experiments in *C₂/Wingra* indicate that *D.pulicaria* had little effect on *Microcystis* growth, whereas *D.g.mendotae* enhanced the development. On the contrary, the results of *C₃/Silver* show a strong inhibition (Figure 5). *Microcystis* is considered to be difficult to ingest because the colonies are usually too big and toxic strains sometimes inhibit filtration (Thompson et al., 1982; Fulton and Pearl, 1987; Jungmann and Benndorf, 1994). However, Ferguson et al. (1982) occasionally found colonies up to a size of 60 μm in the gut of *D.hyalina*. As shown in Figure 5, an overlap occurred between the maximum particle size ingested by *D.pulicaria* (MPP) as well as *D.g.mendotae* (MPG); therefore, grazing may have suppressed algal growth. The differences between the outcome of both experiments may be explained in terms of nutrient competition (Tilman, 1981). *Microcystis* from Lake Wingra faced a lack of nutrients, as indicated by both the intensive uptake and high Chl a concentrations. The opposite was true for *Microcystis* in Silver Lake (Table II). Consequently, grazing at different levels of nutrient limitation may have quite different results.

A similar pattern was found for *Aphanizomenon* (Figure 5). In *C₁/Pike*, *D.pulicaria* was able to decrease the concentration significantly (see Epp, 1996). However, nutrient-only addition in *C₂/Wingra* resulted in a decreased abundance of *Aphanizomenon*, whereas in the presence of *D.pulicaria* an increased concentration was found.

For *Ankyra*, nutrient addition was not sufficient for net growth (Figure 6). Both *Daphnia* species stimulated *Ankyra*, although the cell size indicated the species to be ingestible. Reynolds et al. (1982), however, found no grazing resistance in this genus.

Colonial green algae are considered to be ingestible, but non-digestible due to their gelatinous capsule (Porter, 1976). However, it is unclear whether there is a functional relationship between the thickness of the mucilage layer and the degree of protection. The results of our experiments indicate the group to be susceptible to grazing, but it is also able to sustain rather high numbers (Figure 6).

*Melosira* and *Fragilaria* were surprisingly inhibited in both *Daphnia* treatments, although there was almost no overlap between the size distribution of the algae and MPP and MPG, respectively (Figure 6). Nevertheless, Horn (1981) and Vyhnałęk (1983) found both diatoms in the gut of *Daphnia*. Dawidowicz et al. (1988) observed *Daphnia* breaking filaments of blue-green algae in order to ingest them, so a similar breaking of the diatoms may have occurred in our experiments.
In summary, nutrient addition always had an enhancing effect on the concentrations of Chl \( a \), although the edible and inedible fractions reacted differently. The influence of \( D.\) pulicaria and \( D.g.\) mendotae was not uniform, but indicated a seasonal change in the interaction between phytoplankton and grazers. \( Daphnia\) pulicaria had a bigger influence on both fractions of Chl \( a \) than did \( D.g.\) mendotae. The results concerning the interaction of both \( Daphnia\) species and different groups and genera of phytoplankton reflect a variable picture. They indicate that at least under the conditions of these experiments, remarkably large algae can be handled by \( Daphnia\). On the other hand, species which are considered to be grazeable increased in abundance at rather high filtration potentials.

With respect to biomanipulation as a tool in water quality management, our results indicate that large-bodied \( Daphnia\) are desirable because of their greater influence on the edible fraction of phytoplankton. Moreover, because the maximum size of particles that can be handled by these larger \( Daphnia\) is a function of its body size, the amount of inedible algae being grazed may also increase. Therefore, the duration of the spring clear-water period may be extended because large-bodied \( D.\) pulicaria effectively graze those algae typical of the transition stage between the clear-water phase and the beginning of the summer bloom. Our results further indicate that the direct influence of \( Daphnia\) grazing on the community structure of summer phytoplankton is rather small. However, the indirect influence of large-bodied grazers such as \( D.\) pulicaria may be large. Because large-bodied grazers have much greater filtration rates than equal numerical densities of small-bodied grazers, small, fast-growing algae are eliminated. Then large slow-growing algae such as \( Aphanizomenon\) can develop especially when nutrient supply rates are high. This association between \( D.\) pulicaria (or \( D.\) pulex) and \( Aphanizomenon\) has been reported in many eutrophic lakes (Hrbacek, 1964; Lynch, 1980; Ganf, 1983; Andersson and Cronberg, 1984; Pechar and Fott, 1991). Consequently, biomanipulation may not produce substantial improvements in water clarity in lakes unless nutrient control is also implemented (Reynolds, 1994; Benndorf, 1995; Lathrop et al., 1996).

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